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Classifying federal public land grazing permittees

BRADLEY J. GENTNER AND JOHN A. TANAKA

Authors are Economist, National Marine Fisheries Service F/ST 1, 1315 East West Highway, Silver Spring, Maryland 20910, formerly graduate Research Assistant, Agricultural and Resource Economics, Oregon State University, and Associate Professor, Agricultural and Resource Economics, Oregon State University, Corvallis, Ore..

Abstract

This study identifies the characteristics and attitudes of public land ranchers. Data from a random survey of 2,000 U.S. Forest Service and Bureau of Land Management grazing permittees (53.5% response rate) were cluster analyzed and 8 distinct groups of ranchers were identified. Each cluster differed with respect to why they were in ranching and how they would respond to public land policy changes related to grazing fees, grazing reductions, and changes in grazing season. Profit motivation for being in ranching was found to be a relatively low objective for all 8 types of ranchers.

Key Words: grazing fee, grazing reductions, grazing season, public land policy

Resumen

El objetivo fue estudiar las características productivas y las expresiones de pensamiento de los productores que explotan terrenos comunales federales. Los datos fueron obtenidos por encuestas aleatorias de 2000 permisionarios del Servicio Forestal y de la Fauna, y de la Oficina de Manejo de los Suelos. El análisis de las encuestas permitió la formación de ocho diferentes grupos de productores con características comunes. La diferencia entre los grupos se basó en las motivos particulares por los cuales ellos estan produciendo en los terrenos comunales federales y el impacto que tienen los cambios en las políticas del manejo de terrenos comunales federales relacionados con las cuotas de pastoreo, la reduccón de las areas de apacentamiento y los cambios en las estaciones de pastoreo sobre la rentabilidad financiera global de la explotaciones. Los resultados indicaron que la ganancia monetaria no es el objetivo principal de los productores que explotan terrenos comunales federales.

Traditional uses of public land were established by a national policy of expansion in an effort to settle the west. Communities have since evolved dependent on traditional consumptive uses. These communities have strong ties to this traditional way of life and their culture reflects this tie. Despite efforts to settle the west, the federal government is the largest single landowner in the 11 western states. The Bureau of Land Management (BLM) and the United States Forest Service (USFS) administer the bulk of this public land that totals some 42% of the total land area in the region. Federal ownership by state varies from 22% in Washington to 77% in Nevada. The BLM and the USFS manage these lands to provide timber, grazing, recreation and mineral production, among other goods and services.

Approximately 85% of federal land is grazed by domestic livestock (CAST 1996). The 2 management agencies administer 29,925 grazing permits across the west. These permits cover approximately 21.6 million federal animal unit months (AUMs) of grazing (CAST 1996). Grazing permit holders account for over half of the commercial beef cattle in these 11 western states (CAST 1996). Levels of yearlong dependence on public forage vary across the West: some ranches utilize federal lands for a large part of their seasonal grazing capacity and some ranches, in areas where yearlong grazing is possible, depend on federal lands for most, if not all, AUMs of grazing capacity.

In recent times, the use of public lands for non-consumptive uses, such as recreation and preservation, has increased dramatically. In the 1980s, visitor days on USFS lands increased by approximately 50% (CAST 1996). Also, some individuals that don't actively use public land have become advocates of preservation of these lands for environmental reasons. These 2 new and growing groups are typically from urban areas and are much more active and vocal than urbanites from the past regarding rural land use matters. Generally, these new activists feel non-consumptive resource uses, such as recreation and preservation, should be given higher weight than consumptive uses such as grazing, timber production and mining when decisions are made concerning public land management. Specifically, these new activists feel that the grazing of public lands is a destructive use governed by obsolete policies serving narrow economic interests (Power 1996). These activists feel that the ranching way of life is subsidized through low grazing fees and government supplied range and water improvement practices. Activists also feel that the shift to non-consumptive uses will not cause the collapse of communities built on traditional uses, as recreation and other service industries will make up for the losses from elimination of traditional uses (Power 1996). As a result, public land management decisions today are usually hotly contested by new activists. Additionally, these new activists have become strong advocates for changes in our existing public land policies.

Conceptual Framework

Changing land management paradigms means changing the allocation of economic resources on regional and local levels. In addition, changing public land grazing policies will impact the social and cultural importance of public lands to local communities. When policies are considered with such broad ranging impacts, these decisions should be made with due care.

To assist policy makers in making these difficult policy choices, ranch, community, and local/regional level impacts of policy changes need to be analyzed in a scientific manner. Assessing impacts involves many layers of information and many procedures. Individuals affected by policy changes must be identified and defined in a way that is relevant to the situation. This becomes difficult when dealing with western public land ranchers because it has been suggested that ranchers are very heterogeneous. Both Workman (1986) and Fowler and Gray (1988) speak of the heterogeneity of ranchers. Fowler and Gray (1988) call it the "double infinity" of ranching. The first infinity arises from the wide array of physical variation existing across western grazing lands. The second infinity stems from the different institutional and social aspects of ranchers. Rancher characteristics, such as managerial ability, skill, and knowledge vary widely across the West. Because of this heterogeneity, the typical production function approach has been difficult to apply to the ranching industry. Fowler and Gray (1988) concluded that efforts should be made to categorize the diverse population of ranchers so that progress can be made in this direction.

In the 1970s, Arizona ranches had return rates that ranged from negative to 1–2%, while prices for ranches seemed well above a "rational value" based on the capitalized value of ranch earning potential (Smith and Martin 1972). Arizona ranch prices remained constant between 1961 and 1971, maintaining an unexplained, almost constant opportunity cost above a ranch's value in use (Smith and Martin 1972). These results are supported for small, medium, and large ranches across the west (Harper and Eastman 1980, Young and Shumway 1991, Fowler and Gray 1988, Workman 1986). This suggests that profit maximization is not the primary goal of public land ranchers. Instead, Smith and Martin (1972) suggested that the theory of economic satisficing is more applicable in the case of the western ranchers. This framework allows for a whole range of desired returns, or levels of profit preference, across the popula-

tion of all public land ranchers, further supporting a high degree of heterogeneity in the population of ranchers west-wide.

The objective of this paper is to define subgroups of public land ranchers based on a continuum of management goals from economic satisficing to strict profit maximization. Past research has led to the conclusion that the goals and objectives of these ranchers vary across these subgroups. Because all public land ranchers cannot be broadly categorized under the classical profit maximizing assumption, policies crafted and decisions made based on economic analyses using this assumption will not provide the desired outcomes. Specifically, a household production function approach would be more appropriate for ranchers on the consumptive side of this continuum while a more typical production function approach would be more appropriate for ranchers on the profit oriented end of the continuum. By defining the subgroups of this population and modeling their behavior based on their place on the continuum, informed choices can be made based on the attributes of the sub-group the policy is targeted towards, providing more effective solutions to today's complex and controversial public land management decisions.

Cluster Analysis

Cluster analysis identifies natural groupings within a mixture of observations that are believed to represent several distinguishable populations (Lorr 1983). Rosenburg and Turvey (1991) go on to add that cluster analysis includes a set of methods that apply "exploratory techniques to an initially unclassified data set

to discover the underlying categorical structure and to establish a categorization scheme that allows a mathematical-statistical interpretation or results." The cluster analysis process is comprised of a series of steps (Aldenderfer and Blashfield 1984, Romesburg 1984) detailed below.

Selection of Observational Units

The observational units, public land permittees, to be categorized must be selected. In this case, public land permittees are the observational units. Because basic socioeconomic and demographic data for federal land grazing permittees were not available from a published data source, a survey of the population federal land grazing permittees was conducted. A comprehensive list of all permittees was obtained from both the USFS and the BLM. According to these lists, 29,925 grazing permits were issued in 1998. Address duplicates, cross agency duplicates, and institutional permits were culled from the population leaving 21,018 individual ranch operators.

A random sample of 2,000 operators was drawn from the population and mailed surveys based on Salant and Dillman's (1994) Revised Total Design Method (RTDM). We used a series of 4 mailings spread over the course of 8 weeks. If the respondent left less than 3 items blank, those respondents were kept and missing values were imputed from the rest of the data. The useable response rate for the survey is 53.5%. Figure 1 shows the proportion of the total population and the survey respondents from each state. The "other" category includes respondents from 37 different states. A follow-up telephone sur-
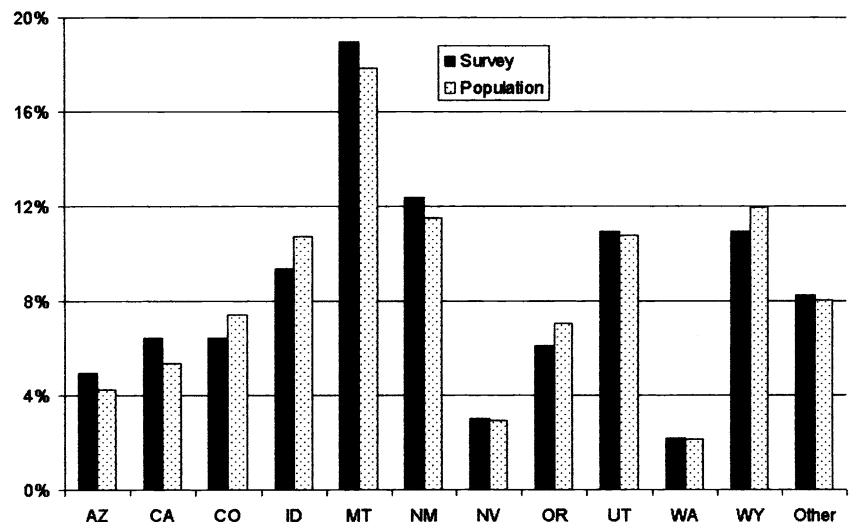

Fig. 1. Percent of the population and survey respondents from each state.

vey of 100 randomly selected non-respondents revealed that the means of several key demographic characteristics were not significantly different between respondents and non-respondents. Therefore, the data presented can be interpreted to accurately represent the population of all public land permittees.

Selection of Rancher Attributes

The variables, or attributes, within each observational unit to be clustered must be selected based on explicitly stated theory that supports classification (Aldenderfer and Blashfield 1984). Drawing from previous literature, ranchers appear to maximize a utility function composed of profit and many other attributes. Perceived goals and objectives are strongly tied to whether or not profit maximization is the primary goal for continuing in ranching. Both Bartlett et al. (1989) and Smith and Martin (1972) used a survey method to elicit the reasons public land ranchers continued ranching in the West. Ranchers were asked to rank the importance of many goals and objectives that ranged from profit motivated objectives to lifestyle objectives. The same methodology was used for this analysis. The list of goals and objectives used in this analysis grew out of Bartlett et al.'s (1989) and Smith and Martin's (1972) work. In addition, focus group interviews in Oregon and New Mexico were used to hone the list into 7 goals and objectives for continuing ranching. These goals are listed below with attribute names in parentheses:

1. Owning land and a ranch is consistent with my family's tradition, culture, and values (TRAD).
2. A ranch is a good place to raise a family (FAMILY).
3. Living on a ranch allows me to live closer to my friends and family (FRIEND).
4. I want to obtain a good return on my investment (PROFIT).
5. With my skills it would be difficult to obtain a job outside of the ranch (SKILLS).
6. I own a ranch primarily for environmental purposes (ENVIRO).
7. I continue ranching so I will have a business to pass on to my children (PASS).

The respondents were asked to rank the importance of each objective on a scale of 1 to 5, with 1 being the most important.

Much past work has shown that as dependence on agricultural income increases, the likelihood that the farmer or rancher is a profit maximizer increases (Young and Shumway 1991, Smith and Martin 1972, Biswas et al. 1984, Harper and Eastman 1980, and Birkenfeld 1994). Conversely, the lower the dependence on agricultural income, the more likely an agricultural producer will be in the industry for consumptive reasons (Smith and Martin 1972, Biswas et al. 1984, Harper and Eastman 1980, and Birkenfeld 1994). For these reasons, income from different sources will be used as a clustering attribute. Ranchers were asked the percentage of their total income coming from the following sources (variable names in parentheses): ranching (RANCH), production of other agricultural commodities (AGRI), forestry (FOREST), off-farm job (OFFRNCH), retirement income (RETIRE), investment income (INVST), providing on-ranch recreation services (REC), and other sources (OTHERC). It is thought that there may be an additional difference in operators that ranch for consumptive purposes. Some may be retired hobbyists and others may be hobbyists that are still working a full time job outside of the ranch (Birkenfeld 1994). Because categorical variables cannot be mixed with quantitative variables for cluster analysis (Everitt 1993), these percent income variables were converted to categorical responses using 6 categories (<5%, 6%–25%, 26%–50%, 51%–75%, 76%–95%, >96%)

Labor and education have been used to describe differences in management objectives (Young and Shumway 1991, Smith and Martin 1972, Biswas et al. 1984, Harper and Eastman 1980, and Birkenfeld 1994). Ranchers were asked how many months of full time and part time labor were supplied by themselves, their spouse, their children and hired employees. These variables were transformed into full time months and combined into 2 variables FAM and HIRED representing the number of months of family supplied labor and the number of months of hired labor required to run their operation. It is thought that small ranchers on the consumptive end of the scale will have the smallest labor requirements, hiring few laborers and supplying small amounts of family labor. Medium sized ranchers that depend on most of their income from ranching will have the most family supplied labor, but will not hire many employees. Also, large ranchers that have little income from off ranch sources will depend heavily on hired labor while the family supplied component will be small relative to the hired portion.

The effect of education is slightly less transparent. Typically, as the level of education increases, the likelihood that the individual is operating as a profit maximizer also increases. However, it is hypothesized that some hobbyists part-time ranchers may be highly educated business professionals who own a ranch for consumptive purposes, and do not function as strict profit maximizers. In this case, education may play a slightly different role in developing clusters.

Operation scale has also been shown to explain choice of management goals. The larger the operation, the more likely the goal of profit maximization supercedes all other goals (Young and Shumway 1991, Smith and Martin 1972, Biswas et al. 1984, Harper and Eastman 1980, and Birkenfeld 1994). The survey provides 2 possible scale variables, deeded acres and herd size across three animal types. Herd size across 3 animal types will be used as the scale variable over deeded acreage because land productivity varies greatly over the West and herd size describes scale in more absolute terms by controlling for land quality. The respondents were asked to circle a category indicating the number of cows, ewes, and horses they own. The categories included 0, 1–49, 50–99, 100–249, 250–499, 500–999, and greater than 999 animals. These categories represent accepted size classes in ranch management (Workman 1986).

Finally, respondents were asked to characterize the business organization of their ranch. Choices included sole proprietorship, limited partnership, general partnership, sub-chapter S-corporation, sub-chapter C-corporation, and Limited Liability Company. Each type of organizational structure offers protection from financial risk of varying degrees. One would expect that profit maximizing firms would choose to organize their ranch in a fashion that provided the most protection and that ranchers most interested in consumptive values would have little reason to pursue organizational structures more complicated than sole proprietorship. For these reasons, level of business organization was included. Two other variables that help explain risk preparedness and degree of profit maximization include debt load and financial stress. For debt load, one would expect those with high debt loads to be more concerned about the returns from ranching and vice versa. Respondents were asked to give the percentage of ranch sale price retained, if they were to sell their ranch, and were presented with 4 responses that include: <5%, 5%–29%, 30%–59%, 60%–100%, as taken from the USDA's Farm Cost and Return Surveys

(USDA 1993). Finally, financial stress was used as an indicator of a respondent's ability to obtain loans. The response was limited to a Likert scale with 1 representing severe financial stress and 5 representing no stress. It is thought that those involved in ranching for consumptive use will express a low degree of stress while those involved in ranching for profit will exhibit higher degrees of stress related to their debt load and other financial factors.

Selection of the Clustering Algorithm

The clustering algorithm computes similarities among observational units and differentiates observational units into subgroups. We used a K-means algorithm, a non-parametric method, that uses a Euclidean distance similarity measure and iterative partitioning to differentiate observational units into sub-groups or clusters. K-means clustering requires that the number of clusters be established a priori (Bernhardt et al. 1996). Procedures used to find a local partition optimum, based on the a priori selection of the optimum number of partitions, are heuristic and can be described mathematically as follows:

Minimize:

$$e[P(M,K)] = \sum_{i=1}^{m} D[i,L_{ki}]^2 \quad (1)$$

Subject to:

$$D(i,L) = \left[\sum_{j=1}^{j} [A(ij)-B(Lj)]^2 \right.\text{ for all K} \quad (2)$$

where D(i, L) is the Euclidean distance between the ith observation and the cluster mean of the Lth cluster, and e[P(M,K)] is the error of partition. The letter i indexes observations from 1 to M, j indexes the attributes from 1 to J, and L_{Ki} is cluster K containing the ith observation. Additionally, A(i, j) equals the value of the ith observation of the jth attribute and B(L, j) is the mean of the jth attribute of observations in the Lth cluster. P(M, K) is the partition composed of K clusters where each of the M observations lie in 1 of the K clusters..

Attributes are first sorted according to their distance from the overall attribute mean. Initial centroids are then chosen based on [1+(L_K-1)•M/K] observations. Given the above, the algorithm searches for the partition with the smallest e[P(M,K)]. Iterations stop when e[P(M,K)] cannot be reduced further. Beginning with the initial partition, each observation, i, is transferred from its current cluster L_{Ki} into every other cluster L_K, where K≠i. If at least 1 cluster has a Euclidean distance less than D(i, L_K), the

observation i is transferred to that cluster. Transferring all M observations continues until e[P(M,K)] is minimized across all partitions. This procedure was conducted using the FASTCLUS procedure in SAS (SAS 1989). Local optimums are found by iteratively running the K-means algorithm, each time with a different number of clusters. This analysis followed the SAS Institute's recommendation, running the algorithm beginning at 2 clusters and continuing through 10% of the total number of observations in the data set (SAS 1989).

Solution Validation

The final step in cluster analysis involves testing the validity of the analysis. First, the number of clusters must be determined. This can pose problems, as analytical determination of the number of clusters for a given data set is not definitive. However, several indices can serve as guides (Jain and Dubes 1988). The ratio of the within sum of squares for the cluster grouping being analyzed to the within sum of squares for 1 group is 1 appropriate index (Bernhardt et al. 1996). In other words, this index is the percent of total variation in all variables not accounted for by clustering (Bernhardt et al. 1996). Another, more rigorous index is the Cubic Clustering Criterion (CCC) (SAS 1983). This index is based on minimizing the within cluster sum of squares. This index can also be a good diagnostic tool. Peaks greater than 2 or 3 indicate good clusters (SAS 1983). Very negative values of the CCC indicate outliers in the data (SAS 1983). Very distinct non-hierarchical spherical clusters usually show a sharp rise to the peak number of clusters with a

gradual decline thereafter (SAS 1983). Graphing these indices on the number of cluster groups can identify the appropriate number of clusters. The appropriate number of clusters can be identified by graphing the index on the number of cluster groups. The point where the slope of this these graphs begins to drop dramatically indicates the appropriate number of groups. This occurs where the within sum of squares for the cluster grouping is reduced very little by the addition of another cluster group (Jain and Dubes, 1988) (SAS 1983).

Looking at Figure 2, these indices show that we have good, non-hierarchical, spherical clusters, with no outliers, and local optimums at both 5 and 8 clusters. Unfortunately, within FASTCLUS there is no method within FASTCLUS to test whether the 5-cluster solution is better than the 8-cluster solution. The 8-cluster solution appears better because 8 clusters describe 15.7% more variation. Because this method is not definitive, qualitative judgments also count. Rosenburg and Turvey (1991) suggested that the appropriate number is simply the number that fulfills the objectives of the study. After looking at the means of the attributes across clusters, 8 clusters provide a better, more explicit set of rancher subgroups than 5 clusters.

Because choice of clustering method, attributes, and number of clusters is inexact, the validation process is very important. Aldenderfer and Blashfield (1984) provide descriptions of the various tests while Jain and Dubes (1988) provided in depth technical coverage. Two tests will be used in this analysis: a significance test on attributes used to create clusters and a sig-
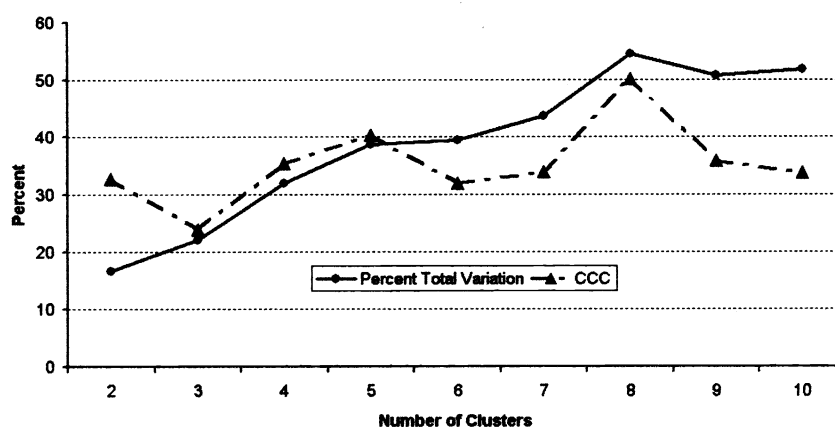

Fig. 2. Optimum Cluster cluster Comparison comparison using the percent of total variation in all variables not accounted for by clustering and the Cubic Clustering Criterion (CCC) methods.

Table 1. Clustering attribute means by cluster groups.

	Hobbyists				Professionals				
Clustering attribute	Small Hobbyist (n = 117)	Retired Hobbyist (n = 189)	Working Hobbyist (n = 162)	Trophy Rancher (n = 63)	Diversified Family Rancher (n = 142)	Dependent Family Rancher (n = 196)	Corporate Rancher (n = 138)	Sheep Rancher (n = 45)	p-value[7]
				(Means)					
Objectives[2]									
TRAD	3.7	4.6	4.5	3.4	4.1	4.9	4.5	4.4	
FAMILY	3.7	4.6	4.6	3.3	4.2	4.9	4.5	4.5	0.0001
FRIEND	2.8	3.9	3.5	2.1	2.9	4.4	3.5	3.2	0.001
PROFIT	2.6	3.7	3.6	2.6	3.7	4.2	3.6	3.5	0.0001
SKILLS	1.5	2.3	1.8	1.3	2	3.3	2.3	2.3	0.001
ENVIRO	2.4	2.2	2.3	2.1	1.9	2.3	2	2	0.001
PASS	1.5	4.3	4	2.4	2.3	4.8	4.1	3.8	(NS)
Education[3]									
Did no finish HS	5.1	11.1	3.1	0	4.2	16.8	3.6	6.7	0.001
Graduated HS	16.2	23.3	25.3	6.3	25.4	44.9	14.5	11.1	
Some college	28.2	36.5	40.7	22.2	45.1	30.6	40.6	35.6	
4 year degree	22.2	15.9	21.6	44.5	21.1	6.1	38.4	44.4	
Graduate degree	28.2	13.2	9.3	27	4.2	1.5	2.9	2.2	
Business Organization[3]									
Sole proprietor	70.1	66.7	69.1	22.2	80.3	65.3	9.4	378	0.001
General partner.	18.8	17.9	15.4	9.5	9.2	20.4	8.7	20	
Limited partner.	4.3	15.3	11.7	6.3	4.2	19.4	11.6	11.1	
S. corp.	4.3	10.6	1.9	33.4	4.2	9.7	36.2	15.6	
C. corp.	0.9	0	1.2	12.7	1.4	3.6	20.3	4.4	
LLC	1.7	1.6	0.6	15.9	0.7	1	13.8	11.1	
# of Animals[4]									
Cows	79.5	122	143	466.7	276.2	295.7	615.2	385.8	0.001
Ewes	27.5	4.4	10.1	0.8	7.8	10.6	3.1	796	0.001
Horses	17	21.5	20.3	28.6	20.9	20.6	26.1	24.4	0.001
Labor									
FAM	10.5	17.2	14.9	13.5	20.7	24.6	26.7	27.5	0.001
HIRED	4.5	4.8	2.3	28.2	4.3	3.6	32	45.3	0.001
Income									
RANCH	13	21.5	18.2	21.1	74.9	84.7	71.9	80.8	0.001
AGRI	2.3	15.3	1.9	6.9	7.4	5	7.1	1.4	0.001
FOREST	2.2	6.1	0.4	0.8	3	1	2.1	0.7	0.001
OFFRNCH	57.2	5.1	77.4	15.7	7.6	4.8	9.2	6.2	0.001
RETIRE	12.9	36.5	0.5	9.1	1.4	2.5	2.6	0.7	0.001
INVST	11.7	8.8	1.2	40.7	3.2	1.4	3.3	7.1	0.001
REC	1.5	2.8	0.3	3.7	1.2	0.2	2.3	1	(NS)
OTHER	0.3	3.1	0.1	1.4	1	0.3	1.4	2	0.009
Debt Load[5]	3.7	3.5	3.3	3.8	3.4	3.3	3.4	3.4	0.001
Financial Stress[6]	3.5	2.9	2.5	3.2	2.4	4.5	2.3	2.3	0.001

[1] 23 percent of total variation in variables is accounted for by the cluster groups.
[2] Average Likert scale score, 1 = least important, 5 = most important reason for continuing to ranch.
[3] Represents percentage selecting each category.
[4] Means based on midpoints of response categories.
[5] 1 = high debt load, 4 = low debt load. Based on USDA debt load categories.
[6] 1 = severe financial stress, 5 = low financial stress.
[7] Probability of obtaining Pearson's chi-square statistic for testing independence between cluster grouping and response to the question from the survey. P-values reported as not significant (NS) if greater than 0.05.

nificance test on the external indicator attributes. The first type of significance test is Pearson's chi-squared test of independence between each variable cluster analyzed and the cluster groups revealed. This procedure tests which variables are significant in explaining the variation across all cluster groups. The null hypothesis is independence between cluster attributes and cluster groups.

The external variable test, on the other hand, directly tests the generality of the cluster solution against the relative criteria. Aldenderfer and Blashfield (1984) suggested that cluster solutions passing this test are better than those that don't. Indicator attributes are those attributes that "represent characteristics of other hierarchical levels especially the socio-economic subsystem" (Bernhardt et al. 1996). Within this survey, those attributes include age, number of social organizations respondent is involved in, animal production system, income, family tenure (HIS-

TORY), deeded acres, environmental attitude score (ENVSCOR), conservation participation score (PARTSCOR), and seasonal dependence on public forage. The null hypothesis is independence between cluster attributes and cluster groups. A strong cluster solution should strongly reject this hypothesis. Finally, multivariate analysis of variance (MANOVA) can be used to test whether the vector of indicator means is different across groups (Bernhardt et al. 1996). The null hypothe-

Table 2. Means of external indicator attributes by cluster.

External Indicator Attribute	Hobbyists Small Hobbyist	Retired Hobbyist	Working Hobbyist	Trophy Rancher	Professionals Diversified Family Rancher	Dependent Family Rancher	Corporate Rancher	Sheep Rancher	p-value[7]
					(Means)				
Age (years)	57.46	64	51.27	59.02	53.85	61.05	55.61	57.8	0.001
Social Organizations[1]	2.53	2.78	2.77	3	2.77	2.44	3.15	3.13	(NS)
Production System[2]									
Cow-calf	67	71.6	70.6	71	73.9	68.8	529	43.2	0.001
Cow-calf-yearling	10.4	14.8	21.3	21	20.4	28.6	42.8	13.6	
Stocker	3.5	3.8	1.9	4.8	2.1	1	4.3	2.3	
Sheep	6.1	1.1	1.9	0	0	1	0	38.6	
Horse	7	4.4	2.5	0	2.8	0.5	0	0	
Other	6.1	4.4	1.9	3.2	2.8	0	0	2.3	
Income ($)1	65,857	44,602	53,491	94,245	42,970	46,926	50,116	53,000	0.001
History (years)[3]	22.39	29.23	36.86	13.25	35.33	29.49	32.99	32.02	0.001
Deeded Acres	1,398	2,620	1,563	11,134	4,765	4,058	12,554	14,849	0.001
Envscore[4]	3.22	3.06	3.13	3.05	2.96	3	3.02	3.03	(NS)
Partscore[5]	2.97	2.78	2.99	2.99	2.85	2.6	2.84	3	0.206
Spring Dependency(%)[6]	17.22	19.74	28.23	17.93	23.44	25.29	21.4	29	0.001
Summer Dependency (%)[6]	42.28	43.69	51.03	36.5	50.15	51.14	45.84	51.18	0.01
Fall Dependency (%)[6]	31.38	26.84	37.2	24.35	32.1	34.34	30.94	35.64	0.002
Winter Dependency (%)[6]	14.19	13.76	20.44	25.03	10.27	14.01	13.43	32.84	0.002

[1] Means based on midpoints of response categories.
[2] Represents percentage selecting each category.
[3] History = respondent's family tenure - personal tenure in years.
[4] Average Likert scale importance of 8 environmental 1 = high debt load, 4 = low debt load. Based on USDA debt load categories.issues, 1=not important, 5=very important.
[5] Average Likert scale participation score. 1=not willing to participate, 5=willing to participate in 6 riparian conservation practices.
[6] Percent dependency on public forage sources by season.
[7] Probability of obtaining Pearson's chi-square statistic for testing independence between cluster grouping and response to the question from the survey. P-values reported as not significant (NS) if greater than 0.05.

sis is no difference between cluster groups and rejection of this null would strengthen the validity of the cluster solution.

Of the 24 attributes used to form the clusters, only 2, the PASS objective and the percentage of income from the provision of recreation services, proved insignificant. Table 1 presents the means of the attributes by cluster and the significance test on each variable. Of the 12 external indicator attributes (Table 2), only 2, number of social organizations and ENVS-COR, proved insignificant, meaning that these 2 external indicator variables were not significant in explaining the variation across cluster groups

Results of the MANOVA analysis are presented in Table 3. From this analysis, one can see that the means of 4 external indicator attributes of the number of memberships in social organizations, ENVS-COR, summer dependency, and fall dependency were not significantly different across cluster groups. However, the overall test rejects that the vector of all external indicator attribute means are the same across cluster groups.

Results

Looking at Figure 1, two knees occur in the percent of total variation in all attributes accounted for by the clustering solution graph: 1 at 5 clusters and 1 at 8 clusters. Unfortunately, within FASTCLUS there is no method to test whether the 5 cluster solution is better than the 8 cluster solution. The 8 cluster solution appears better because 15.7% more variation is described by 8 clusters than 5. Because this method is not definitive, qualitative judgements also count. Rosenburg and Turvey (1991) suggested that the appropriate number is simply the number that fulfills the objectives of the study. After looking at the means of the attributes across clusters, 8 clusters provide a better, more explicit set of rancher subgroups than 5 clusters.

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In summary, all groups rank consumptive objectives above profit maximizing objectives suggesting that all ranchers are economic satisficers with varying degrees of importance placed on earning potential from the ranch. In fact, all groups ranked the TRAD and FAMILY objectives as the first or second most important objectives (Table 1) and the PROFIT objective was ranked in the middle of the pack across all groups. From comments written in the margins of the returned surveys and subsequent follow-up telephone calls, many do not believe that earning an adequate return is possible given current market condi-

Table 3. MANOVA results.

External Indicator Attributes	Univariate Probability[1]	Multivariate Probability[2]
Age	0.0001	
Social Organizations	(NS) 0.2460	
Production System	0.0001	
Income	0.0001	
History	0.0001	
Deeded Acres	0.0001	
Envscore	(NS) 0.7272	
Partscore	0.0108	
Spring Dependency	0.0189	
Summer Dependency	(NS) 0.1995	
Fall Dependency	(NS) 0.1306	
Winter Dependency	0.008	
Percent Reduction		
25%	0.025	
50%	0.0006	
100%	0.0007	
Fee Increase		
$2–$5/AUM	(NS) 0.2259	
$5–$8/AUM	0.0242	
>$8/AUM	0.0079	
Eliminate Season		
Winter	0.0008	
Spring	0.0032	
Summer	0.0423	
Fall	0.0156	
Overall Test		0.0001

[1]Probability value for chi-square test. $\alpha<0.05$ reject the hypothesis that the mean value is the same across cluster groups.
[2]Probability value for Wilks' Lambda likelihood ratio test. $\alpha=0.05$ reject the hypothesis that the vector of means are is the same across all cluster groups.

tions. Therefore, instead of ranking the importance of this objective, some may have ranked the ability to earn a profit, thus offering some explanation as to why investment performance was ranked low by most groups. Naming cluster groups has been widely used within cluster analysis to aid in broadly identifying cluster groups (Bernhardt et al. 1996, Bartlett et al. 1989). To identify cluster groups in this analysis, these groups are given names that describe their central characteristics. These groups include small (diversified) family ranchers, working hobbyists, sheep herderranchers, medium (dependent) family ranchers, small hobbyist, retired hobbyist, trophy rancher, and corporate rancher. Their general characteristics are described below.

Small Hobbyist

Small hobbyists, 11.1% of respondents, have the lowest dependence on ranching and other on-ranch sources of income of any group. Most of their income comes from off-ranch jobs, but they are slightly more diversified into retirement income and investment income than the working hobbyists. This group is also highly educated with a large percentage of its members having graduate degrees. They also have the smallest herd size and smallest deeded acreage. They rank PROFIT the lowest of any group. This group has a low overall dependence on federal forage although they are not the lowest.

Retired Hobbyist

Retired hobbyists, 18% of respondents, are the most dependent on ranching and agriculture for income compared to the other 2 groups of hobbyists. In fact, their dependence on-ranch sources of income is 49.5%, making the dependence line harder to draw. It may be more appropriate to classify this group as retired ranchers rather than retired hobbyists because it is possible they were once family ranchers who have scaled back their ranching operation in recent years substituting retirement income, investment income, and off-ranch jobs for the lost ranch income. Unfortunately, there are no data from this survey to support this claim. They also have the highest average age.

Working Hobbyist

This group is characterized by a low dependence on ranching income and other on-ranch income sources and has the highest degree of dependence on off-ranch job income. They have a relatively small herd size, although they are the largest of the hobbyists, and own an average of 1,563 deeded acres. While they have ranked the profit maximization objective high relative to the other groups, they still value consumptive uses above profit maximization. It appears that tradition motivates many in this group because the family tenure variable, HISTORY, is largest for this group (Table 2). This suggests that individuals in this group ranches to continue a business started by their family because they appreciate the consumptive value of ranching, not because they are supporting their family with the income. Overall, this is the youngest group and represents 15.4% of the ranchers responding.

Trophy Rancher

This group ranks the PROFIT objective very low yet they have very large herds, large deeded acreages, and high overall labor requirements. In fact, they hire twice as much labor as their family supplies. They also have the highest income of all the groups, but most of this income comes from off-ranch sources, particularly investment income. They are very willing to use business organization to reduce risk as evidenced by the fact that they are second to the last in terms of using the least risk reducing organization, sole proprietorship and most involved in LLC's limited liability corporations. Trophy ranchers are also the best educated with the largest percentage of 4 year college graduates and the second highest percentage of graduate school graduates. This group is also the least dependent on public forage sources. This group constitutes 6% of the ranchers responding. Although individuals in this group ranked the consumptive objectives low relative to the other groups, it appears that they are using ranching as a consumptive good. It appears that this group is independently wealthy and owns very large ranches for purposes other than generating income. It could be argued that these ranchers are practicing conspicuous consumption (Smith and Martin 1972). In other words, the value of owning just any ranch is less to them than the value of owning a very large, extensive, publicly visible ranch. Unfortunately, this objective was not represented in the choice set presented in the survey.

Dependent Family Rancher

This group has the highest dependence on ranching income and is the least diversified into other income sources. This group has very interesting objective rankings. They give the highest rank to all objectives, with the exception of the ENVIRO objective, across all clusters, yet

they still rank PROFIT fifth. This suggests that this group feels very strongly about ranching as a way of life. In addition, this group feels the most trapped in ranching given its ranching skill set and is also the least educated. This group is organized into partnerships, both limited and general, more than any other group, however, most of the ranches in this category are organized as sole proprietorships. This group exhibits the highest debt load, but feels a low degree of financial stress. This group is also the least willing to participate in riparian conservation practices. This group contains 18.6% of the ranchers responding, making it the largest group.

Diversified Family Rancher

This group, 13.5% of respondents, has the smallest herd size of any group dependent on ranching income (Table 1). However, they are only slightly smaller than the dependent family ranch. The family label is given because of their relative dependence on family labor. This group also has the lowest income of any other group. The most striking difference between dependent and diversified family rancher groups is their degree of diversification. Diversified family ranchers are less dependent on ranch income and are more diversified into production of other agricultural commodities, forestry, and off-ranch jobs. Also, this group ranked the profit maximizing objective the second highest of all groups, suggesting a high degree of profit maximizing behavior. On the other hand, this group still ranks consumptive objectives higher than the profit-maximizing objective. Overall, this group uses business organization the least to reduce risk. On average, this group owns 4,765 deeded acres.

Corporate Rancher

This cluster, 13.1% of respondents, is highly dependent on ranching for income, has the largest herds, in terms of animal units, and large deeded acreages (second only to sheep herderranchers). This group also hires the second largest labor force. Interestingly, however, this group still holds consumptive objectives in high regard, and the INVEST objective is ranked again in the middle of the pack. The corporate label stems from the use of the sub-chapter S and sub-chapter C corporate status more than any other group. In addition, this group comes in second in the use of LLCslimited liability corporations. Interestingly, this group and the sheep herders are the most financially stressed of any other group. This is intuitively appeal-
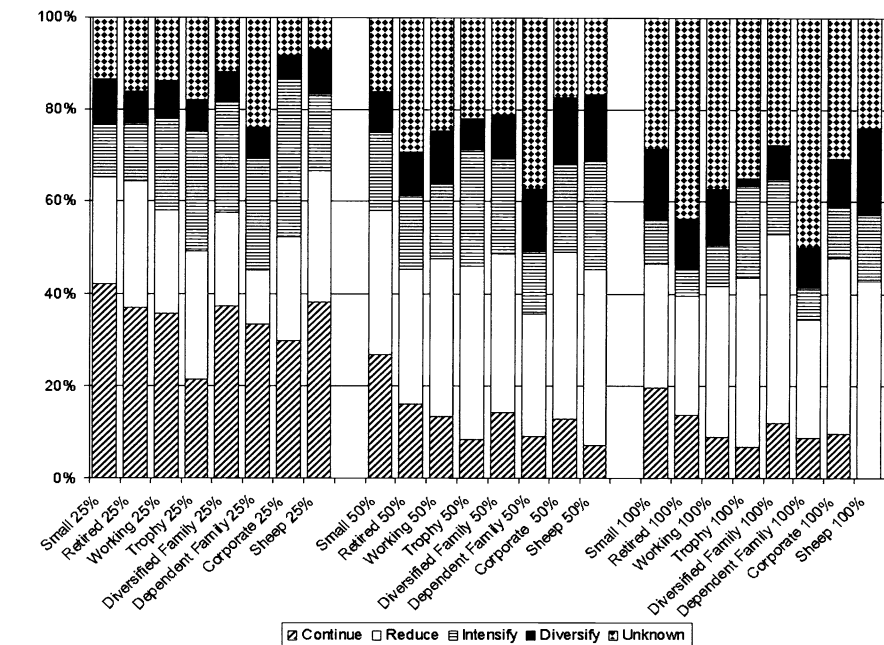
Fig. 3. Responses Response by group to percent reductions in AUM's.

ing as both may require large seasonal loans to pay their hired labor. While most of the other groups indicate that cow-calf operations are their mainstays, with the exception of sheep herder ranchers of course, this group contains a large number of cow-calf-yearling operations.

Sheep HerderRanchers

This group, 4.3% of respondents, is characterized by its dependence on sheep as its primary animal production system. This group has large herds and the largest deeded acreage holding. This group has the highest overall labor requirement, as would be expected given the nature of sheep herding, and hires the most labor. They have a very large percentage of 4 year college graduates. This group is highly dependent on ranching income. Also, this group indicated the highest willingness to participate in riparian conservation activities (Table 2). Finally, this group has the highest dependence on public grazing across all seasons.

Policy Implications

From the above results it appears that public land ranchers are very heterogeneous. Their motivations represent a continuum that varies from consumption of ranching as a good to profit. As a result, one-size-fits-all policies may prove disastrous for those ranchers dependent on ranching for their livelihood. To explore this idea further, respondents were presented a series of questions that asked how

they would respond to 3 different percent reductions in permitted AUMs, 3 different increases in the grazing fee, and the elimination of each of 4 seasons of use. They were presented with 5 discrete response strategies. These strategies are:

1. Continue = you think your current operation will work in the future or do not have the resources to change.
2. Reduce = you will cut back on livestock production, pass operation down to the next generation, reduce your herd, or sell your ranch.
3. Intensify = you will intensify your use of private grazing land. Examples include purchasing or leasing more private land, increasing irrigated acres, improving forage, instituting a new grazing system, etc.
4. Diversify = you will diversify your operation either on-ranch or off-ranch. Examples include pursuing more or better off-ranch employment, growing different crops for cash sale, offering ranch based recreation, or adding a new class of livestock.
5. Unknown = you are not sure what you would do in the face of change.

These categories were developed using advice from peers and rancher focus groups. Although intensification includes characteristics more generally considered under extensification, or increasing the scale of an operation, the focus group participants felt that intensification more

Fig. 4. Responses Response by group to changes in the grazing fee.
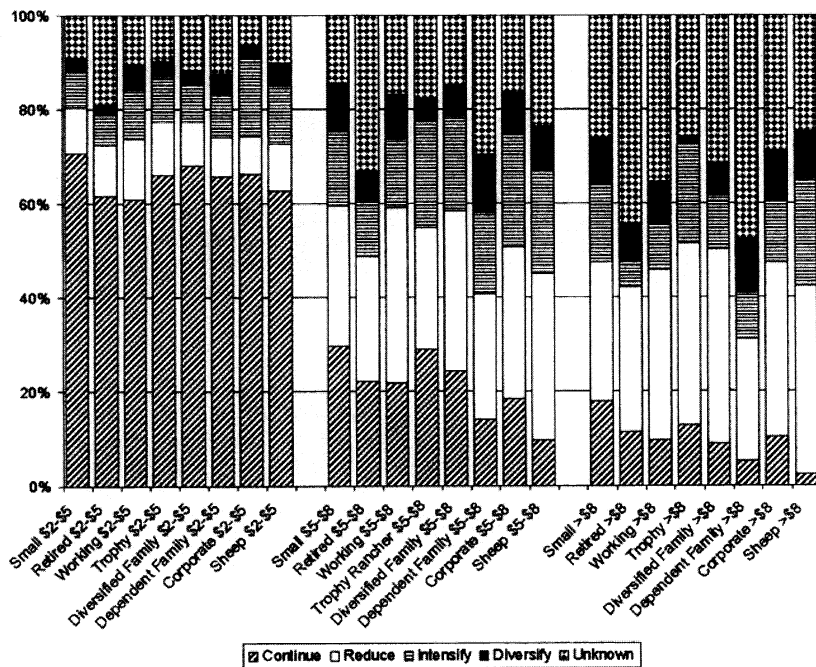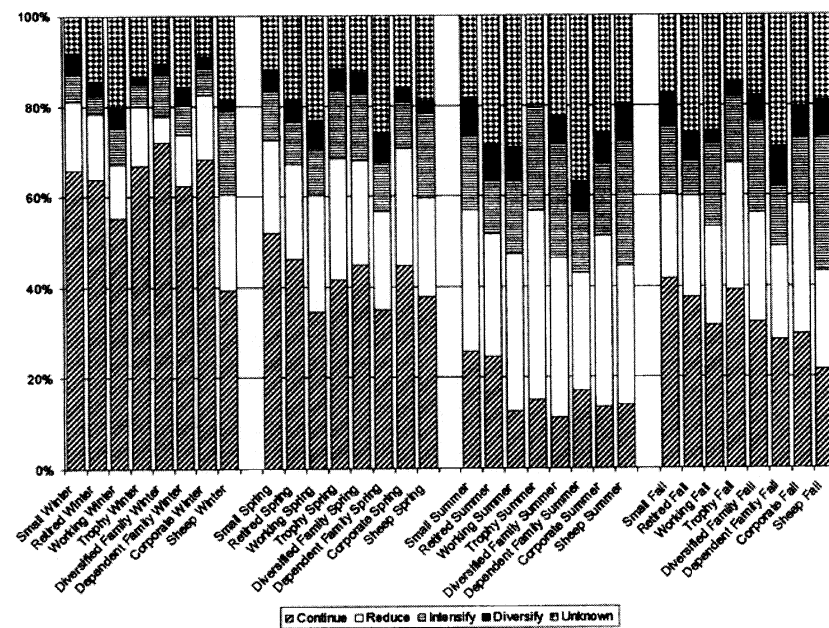

Fig. 5. Responses Response by group to elimination of a season of use.

appropriately described this choice. More specifically, in many locales across the West, extensification has become prohibitively expensive, and many in the focus groups felt that extensification would only be undertaken as a small step in the process of a larger intensification plan. Therefore, the above responses are assumed to constitute the entire choice set

facing ranchers under the policy change scenarios. These 3 broad policy change scenarios and their corresponding levels were selected because all of these scenarios and levels of change have been discussed in the public land grazing policy debate that has developed in the last several decades.

Ranchers in the first scenario were

asked how they would respond to percent reductions (25%, 50%, 100%) in their permitted AUMs (Fig. 3). In the second scenario, ranchers were asked how they would respond to 3 increases in the grazing fee ($2–$5, $5–$8, and >$8 AUM^{-1} increase) over the current level (Fig. 4). Finally, ranchers were asked how they would respond to the elimination of winter, spring, summer, or fall use (Fig. 5). The MANOVA analysis shows that the mean response to these questions is significantly different across clusters for all levels of all questions, except 1, the response to the smallest change in the grazing fee (Table 3).

It is difficult to draw broad conclusions about the data presented in Figures 3, 4, and 5. In fact, drawing broad conclusions defeats the purpose of this analysis. Instead, these figures indicate the percentage of individuals in that group that will undertake a given strategy in the face of policy change. Given the characteristics of a particular group of ranchers, their response can then be predicted. This information has direct applicability to economic impact modeling on the regional level by classifying ranchers and quantifying how they will react to policy changes.

With that said, some general conclusions do emerge. First, for a relatively small increase in the federal grazing fee, from $1.35/AUM to $2–$5/AUM, there is no significant difference between clusters (Table 3). Also, at this small level of change, the large majority of ranchers will continue their operations as is, absorbing the additional cost (Fig. 3). Another interesting result that emerges concerns selection of the diversification strategy. Across all scenarios and all levels, diversification is the least frequently selected strategy (Fig. 3, 4, and 5). By encouraging income diversification, the stability of those family ranches dependent on farm or ranch income could be increased in the face of policy uncertainty. In addition, as levels of change increase, the dependent family ranchers and the retired hobbyists select the unknown response more frequently. This degree of uncertainty deserves further examination. Perhaps the choice set does not fully reflect the strategies they face or they may feel they are simply backed into a corner with no hope for recovery in the face of such changes. The latter explanation may hold some merit for the dependent family ranchers because they ranked the SKILLS objective highest of any other group (Table 1). The SKILLS objective indicates feelings of being trapped in ranching because ranching is the only pro-

Table 4. Private acreage by cluster as reported by respondents and extrapolated to the population.

Cluster	Respondent Private	Westwide Westwide
	----------(acres)------------	
Hobbyists		
Small Hobbyist	160,798	3,212,597
Retired Hobbyist	461,071	9,211,778
Working Hobbyist	251,698	5,028,696
Trophy Rancher	701,409	14,013,512
Professionals		
Diversified Family Rancher	662,386	13,233,868
Dependent Family Rancher	770,918	15,402,238
Corporate Rancher	1,719,844	34,360,914
Sheep Rancher	653,349	13,053,317
Total	5,381,473	107,516,920

fession they feel qualified to pursue given their skill set. Finally, as the level of change increases, all groups move away from continuing as a strategy and move into reduction and intensification. However, no clear pattern emerges between groups concerning preferences for 1 particular strategy over another.

Conclusions

The groups emerging from this analysis represent a continuum of economic behavior ranging from consumption of ranching as a good to ranching for profit. Ranching for a profit is a difficult concept because even the dependent family and corporate ranchers value the consumption of ranching as a good. This fits with previous results that even large ranchers may act as economic satisficers, producing an income that is satisfactory, enough to pay the bills, while consuming ranching as a good (Smith and Martin 1972). These results also help to describe the heterogeneity of ranchers across the West by first grouping by socioeconomic and demographic attributes. Overall, it is interesting to note that hobbyists, those not dependent on ranching income, comprise 50.4% of all public land ranch operators in the West. This distinction is arbitrary and is made when the percent of income derived from on-ranch sources is below 50%. All but 1 group, the retired hobbyists are well below this mark. Conversely, 49.6% of all public land ranchers in the West are dependent, and in most cases heavily dependent, on ranching for their income.

In terms of policy implications, the selection of the intensification strategy has implications for the environment and selection of this strategy bears closer inspection. It is widely accepted that ranching and cattle grazing are less intensive than commercial crop production in terms of water usage, labor inputs, and chemical usage (Skaggs et al. 1994). As

ranchers are forced to move away from grazing because of federal grazing reductions, some ranchers, as indicated in Figures 3, 4, and 5, will intensify their agricultural operation on their private land. Likewise, ranchers may sub-divide and sell their ranch property to make up for the lost income caused by policy changes. Summing across all respondents and extrapolating to the entire population, public land ranchers control 14.21% of the total land base in the 11 western states (Table 4). The environmental impacts from the increased intensification need to be analyzed as well as the income impacts.

Currently, input/output models developed for rural areas in the West use ranch classifications based on ranch budgets developed by size classes. While this is acceptable during the development of the base model in software such as IMPLAN, these groups may not represent homogeneous groups when strictly divided by ranch size and when modeling reactions to policy changes. Instead, the clusters represented here could be used to map expenditure patterns in the face of policy changes across 8 distinct groups based on not only size, but other socioeconomic characteristics like income, income sources, motivations, and their stated preferences in the face of such changes. The use of this information would yield more accurate impact assessments because better information on rancher attributes and behavior are used.

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Rangeland management under uncertainty: A conceptual approach

AMITRAJEET A. BATABYAL AND E. BRUCE GODFREY

Authors are Arthur J. Gosnell Professor, Economics Department, Rochester Institute of Technology, Rochester, New York 14623-5604, and Professor, Economics Department, Utah State University, Logan, Ut. 84322-3530. At the time of the research, the senior author was Associate Professor, Economics Department, Utah State University, Logan, Ut.

Abstract

A conceptual approach is commonly needed to provide guidance for developing new strategies concerning the use and management of renewable resources such as rangelands. The theoretical model constructed in this paper captures the essential aspects of dynamic and stochastic issues associated with the management of rangelands. We discuss the connections between the model and range policy. Specifically, we point out scenarios in which there is a limited role for policy. This is compared to scenarios when policy has a significant role to play in ensuring the sustainable use of rangelands. Finally, we suggest 2 ways in which our approach might be extended and used in a practical application.

Key Words: dynamic, policy, resource, stochastic

Resumen

Comúnmente se necesita una propuesta conceptual como guía para desarrollar nuevas estrategias concernientes con el uso y manejo de los recursos naturales tales como los pastizales. El modelo teórico construido en este articulo captura los aspectos esenciales de problemas dinámicos y estocásticos asociados con el manejo de pastizales. Discutimos las conexiones entre el modelo y la política de los pastizales, específicamente puntualizamos escenarios en los cuales hay un papel limitado de esta política y esto es comparado con escenarios en los que la política tiene un papel significativo para asegurar el uso sustentable de los pastizales. Finalmente sugerimos dos formas en las cuales nuestra propuesta pudiera se extendida y utilizada en una aplicación práctica.

Rangelands are an important renewable resource. In addition to performing a number of salient ecological functions, rangelands provide humans with consumable products such as red meat, fiber and water, and non-consumptive services such as recreation and wildlife viewing. As such, it is no surprise that range managers have systematically attempted to manipulate "range components to obtain the optimum combination of goods and services for society on a sustained basis" (Holechek et al. 2001, p. 5). The management of rangelands is not easy because range managers rarely have complete information about the impact of actions that may be taken. This state of affairs is in part due to a lacuna in the range management literature. Although previous studies (Lambert and Harris 1990, Passmore and Brown 1991, McCluskey and Rausser 1999, Batabyal 2000, Batabyal et al. 2001) have studied aspects of range management in the presence of uncertainty, there are very few studies that have explicitly modeled the connections between uncertainty, the ecology, and the management of rangelands over time.

Given this state of affairs, a conceptual approach is needed to provide guidance for developing new strategies concerning policies that affect the use of rangelands. The model outlined below has 3 desirable features. First, the approach is consistent with an important ecological model of range behavior, namely, the state-and-transition model of Westoby et al. (1989). Second, the

approach expressly accounts for the role that uncertainty plays in the temporal evolution of managed rangelands. Finally, by exploring the *connections* between policy and range behavior, our approach defines the role that policy can play, and, on occasion, not play in ensuring the sustainable use of rangelands. The formal state-and-transition model outlined in the following section provides the basis for a discussion of the policy implications associated with the dynamic and the stochastic structure of rangelands. This discussion is followed by an extension of the model in 2 ways that are likely to be important and that are not captured in the basic model. The final section of the paper outlines areas for future research.

A "State-and-Transition" Model of a Rangeland

Preliminaries

As discussed but not formalized in Westoby et al. (1989), rangeland dynamics can be usefully described in terms of a discrete number of states and a set of transitions between these states. Range managers often use the term "condition class" to refer to these states. Moreover, as noted in Holechek et al. (2001), it is common to think of rangelands as existing in 1 of 4 possible condition classes such as excellent, good, fair, and poor. Consequently, we assume that rangelands can exist in 4 possible states, but the number of states could easily be extended, without any loss of generality, to any countable number of states.

Environmental factors such as fire and/or actions such as the alteration of the stocking rate result in rangeland transitions from 1 condition class to the other. To formalize this notion, suppose that our rangeland makes state transitions in accordance with a discrete-time Markov chain (Ross 1997, Perrings 1998). In other words, when in state i, $i = 1,..., 4$, the rangeland will make a transition to state j, $j = 1,..., 4$, with probability P_{ij}. From a management perspective, not all condition classes are equally desirable. In particular, it seems reasonable to think of excellent (state 1) and good (state 2) as constituting the desirable set of states, and fair (state 3) and poor (state 4) constituting the undesirable set of states of the rangeland. Formally, we have $D = \{Excellent\ (state\ 1),\ Good\ (state\ 2)\}$, and $U = \{Fair\ (state\ 3),\ Poor\ (state\ 4)\}$.

The goals of resource managers are to use the policies at their disposal (i.e., changing the stocking rate, burning, introducing plant populations) to keep the rangeland in the desirable set D for as long as possible. However, because resource managers cannot be certain about the appropriateness of a particular policy (say, all the positive and negative implications of a burn) and because state transitions occur not only because of managerial actions but also because of environmental factors, it is possible that despite the resource manager's best intentions, the rangeland will end up in a state in the undesirable set U. As such, resource managers would like to know 2 things. First, what is the *expected* amount of time ($\bar{U}$) that the rangeland spends in set U, given that it is currently in a state in U. Second, what is the *expected* amount of time ($\bar{D}$) the rangeland spends in set D, given that it is presently in a state in D. Let us now compute these 2 expectations.

Two Expectations

Let π_k, $k = 1,..., 4$, denote the stationary probabilities (see Ross 1997, pp. 172–182) of the rangeland. Now, for state $i\ \varepsilon\ D$ and state $j\ \varepsilon\ U$, the rate at which the rangeland enters state j from state i is $\pi_i P_{ij}$. From this it follows that the rate at which our rangeland enters state j from a state in the desirable set D is $\sum\limits_{i=1}^{2} \pi_i P_{ij}$. With these 2 pieces of information, we conclude that the rate at which our rangeland moves from the desirable to the undesirable set of states is $\sum\limits_{j=3}^{4} \sum\limits_{i=1}^{2} \pi_i P_{ij}$. Similarly, but now in

terms of the 2 expectations $\bar{D}$ and $\bar{U}$, the rate at which the rangeland moves from the desirable to the undesirable set of states is $1/(\bar{D} + \bar{U})$ Equating these last 2 expressions, we get

$$\sum_{j=3}^{4} \sum_{i=1}^{2} \pi_i P_{ij} = \frac{1}{\bar{D}+\bar{U}} \qquad (1)$$

To compute $\bar{D}$ and $\bar{U}$ explicitly, we need a second equation linking these 2 expectations. This equation can be obtained by noting 2 facts. First, the percentage of time that the rangeland is in the desirable set of states is $\sum\limits_{i=1}^{2} \pi_i$. Second, the proportion of time the rangeland spends in the desirable set of states is $\bar{D}/(\bar{D} + \bar{U})$. Combining these 2 facts, we get

$$\sum_{i=1}^{2} \pi_i = \frac{\bar{D}}{\bar{D}+\bar{U}} \qquad (2)$$

Now using equations (1) and (2), it is straightforward to verify that

$$\bar{D} = \frac{\sum\limits_{i=1}^{2} \pi_i}{\sum\limits_{j=3}^{4} \sum\limits_{i=1}^{2} \pi_i P_{ij}}, \quad \bar{U} = \frac{\sum\limits_{j=3}^{4} \pi_j}{\sum\limits_{j=3}^{4} \sum\limits_{i=1}^{2} \pi_i P_{ij}} \qquad (3)$$

Inspecting equation (3) and recalling the properties of the stationary probabilities of a Markov chain (Ross 1997), it is clear that although managerial actions can influence the expected amount of time that the rangeland spends in the desirable and the undesirable set of states, ultimately, it is the transition probabilities, i.e., the P_{ij}s, that should be the target of range policy. To see this clearly, consider the connections between alternate policies and the transition probability matrix, P, of our 4-state rangeland (Markov chain). P can be written as

$$P = \begin{bmatrix} P_{11} & P_{12} & P_{13} & P_{14} \\ P_{21} & P_{22} & P_{23} & P_{24} \\ P_{31} & P_{32} & P_{33} & P_{34} \\ P_{41} & P_{42} & P_{43} & P_{44} \end{bmatrix} \qquad (4)$$

In this matrix, the first row and column denote the excellent state (state 1), the second row and column denote the good state

(state 2), and so on. Thus, the probability of making a transition to the excellent state (state 1), given that the rangeland is currently in the poor state (state 4), is denoted by P_{41}. The other elements of the matrix P have similar interpretations. Now, although resource managers may have disparate policy goals, one reasonable goal is to ensure that the rangeland stays in the desirable set of states D, for as long as possible. This can be done by influencing the transition probabilities in the P matrix.

Inspection of equation (4) shows that from the standpoint of range policy, the matrix P can be usefully partitioned into 4 zones. These 4 zones correspond to the following 4 sub-matrices

$$P_1 = \begin{bmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{bmatrix}, P_2 = \begin{bmatrix} P_{13} & P_{14} \\ P_{23} & P_{24} \end{bmatrix}, P_3 = \begin{bmatrix} P_{31} & P_{32} \\ P_{41} & P_{42} \end{bmatrix}, P_4 = \begin{bmatrix} P_{33} & P_{34} \\ P_{43} & P_{44} \end{bmatrix} \quad (5)$$

If the rangeland is in P_1, then it is in the desirable set of states (1 or 2). As such, this is a zone in which no major policy initiatives are required to ensure the well-being of this rangeland. In contrast, when the rangeland is in P_4, it is in the undesirable set of states (3 or 4) and the probability of bringing it to the desirable set is 0. This means that in this zone, there is no role for policy. One such "no role" involves taking no action to improve the rangeland. Put differently, the rangeland is so degraded that it is either impractical or actually impossible to restore it to one of the desirable states. The 2 intermediate zones corresponding to P_2 and P_3 are of particular interest. This is where there is the greatest scope for policy. In other words, in these 2 zones, resource managers can, inter alia, change the stocking rate, remove noxious plants, keep livestock away from streamside areas, and introduce plant populations, in order to ameliorate the rangeland. Inspecting P_2, we see that the probabilities here involve moving from the desirable to the undesirable set of states. As such, it is clear that when in this zone, the objective of policy should be to take those actions that will minimize the probabilities in this sub-matrix and improve the rangeland resource. In contrast, inspection of P_3 tells us that the probabilities here involve moving from the undesirable to the desirable set of states. This means that when in this zone, policy should confine itself to those actions that maximize the probabilities in this sub-matrix and thereby improve the range. This way of looking at the task of range management provides a clear indication as to when there is a substantial role

and when there is a very limited role for managerial actions in ensuring the sustainable use of our rangeland. This conceptual approach is now demonstrated with a numerical example.

An Example

Suppose that the transition probability matrix in equation (4) is

$$P = \begin{bmatrix} 1/2 & 1/2 & 0 & 0 \\ 1/4 & 1/4 & 1/4 & 1/4 \\ 1/5 & 1/5 & 2/5 & 1/5 \\ 0 & 0 & 1/4 & 3/4 \end{bmatrix} \quad (6)$$

While the transition probabilities in equation (6) are illustrative, subject to data availability, they can be estimated using econometric techniques (Ethridge et al. 1985). In a practical setting, these probabilities are useful because they provide rangeland managers with information about how the interaction of managerial actions and environmental factors affect range condition. Let us compute $\bar{U}$ and $\bar{D}$. To perform this computation, we shall use a 3-step procedure. First, we observe that the stationary probabilities satisfy $\pi_1 = (1/2)\,\pi_1 + (1/4)\,\pi_2 + (1/5)\pi_3$, $\pi_2 = (1/2)\,\pi_1 + (1/4)\,\pi_2 + (1/5)\,\pi_3$, $\pi_3 = (1/4)\,\pi_2 + (2/5)\,\pi_3 + (1/4)\,\pi_4$, and $\pi_4 = 1 - \sum_{i=1}^{3} \pi_i$ (Ross 1997).These 4 equations can be solved to yield $\pi_1 = 4/21$, $\pi_2 = 4/21$, $\pi_3 = 5/21$, and $\pi_4 = 8/21$. Second, we use these stationary probabilities and the transition probabilities in equation (6) to determine the rate at which our rangeland moves from the desirable to the undesirable set of states, i.e., the denominator of the 2 expressions for $\bar{D}$ and $\bar{U}$ in equation (3). This rate equals 2/21. Finally, we compute $\bar{D}$ and $\bar{U}$ by using this rate (2/21), and the expressions in equations (3) and (6). We get $\bar{D} = 4$ and $\bar{U} = 6.5$.

What are the implications of these computations for range policy? These computations tell us that, on average, our rangeland resource moves from the desirable to the undesirable set of states 2/21 or approximately 10% of the time. The rangeland resource stays in the undesirable set for 6.5 units of time on average. This is followed by a time span, on average 4 units long, during which the rangeland is in the desirable set of states. This kind of rangeland behavior is entirely consistent with the state-and-transition model of Westoby et al. (1989). Further, note that in ecology, the stability concept known as

persistence refers to "how long a [resource] lasts before it is changed to a new value" (Pimm 1991, p. 14). In the context of this note, the expectations $\bar{D}$ and $\bar{U}$ can be interpreted as the persistence of, respectively, the desirable and the undesirable set of states. This means that when range use policy is directed to the maximization (minimization) of $\bar{D}$ ($\bar{U}$), society benefits in an economic and in an ecological sense.

Two Extensions

The discrete-time Markov chain model described above nicely captures the essential elements of dynamic and stochastic rangelands. However, the scope of this model is restricted by the presence of 2 features. First, range policy cannot alter the transition probabilities (the P_{ij} s) because these probabilities are stationary. Second, range policy also cannot change the amount of time the rangeland spends in a particular state because the discrete-time Markov chain spends 1 unit of time in each state before making a transition. How might we account for these 2 features in our model?

First, let us consider the case of non-stationary transition probabilities. In this case, the probability of making a transition from condition class i at time t-1 to condition class j at time t depends on t. To formalize this time dependence, we write $P_{ij}^{(t-1,t)}$ instead of P_{ij}. Similarly, the transition probability matrix in equation (4) will now have to be replaced by a sequence of transition matrices. In other words, instead of working with the single matrix P of equation (4), we now work with a sequence of matrices $[P_t]_{t=1}^{\infty}$. Once we specify an initial vector that gives a probability distribution over the states of the non-stationary Markov chain, we have completely described our rangeland. Then we can investigate the limiting behavior of the rangeland under study as time approaches infinity. This rangeland may or may not converge to a limiting vector. For instance, consider the 2-condition class rangeland with transition matrices

$$P_{2t-1} = \begin{bmatrix} 1 - \dfrac{1}{2t-1} & \dfrac{1}{2t-1} \\ 1 - \dfrac{1}{2t-1} & \dfrac{1}{2t-1} \end{bmatrix},\ P_{2t} = \begin{bmatrix} \dfrac{1}{2t} & 1 - \dfrac{1}{2t} \\ \dfrac{1}{2t} & 1 - \dfrac{1}{2t} \end{bmatrix},\ t=1,2,3,... \quad (7)$$

In this case, it can be shown, using the methods outlined by Isaacson and Madsen (1976) that this non-stationary Markov chain displays a kind of limiting behavior

known as weak ergodicity.

We now address the "unit time in a state before transition" feature. Ideally, we would like rangeland management policy to be conducted in a way that the rangeland resource under study is in the desirable (undesirable) set of states for relatively long (short) periods of time. One way to model this is as follows. We let the transition probabilities be stationary. However, instead of having all transition times be 1 unit long, we now let the amount of time spent in state i before making a transition to state j be a random variable with a general distribution function $F_{ij}(\bullet)$. With this change, we have converted our discrete-time Markov chain into a semi-Markov process. We can now investigate the limiting behavior of this semi-Markov process as time approaches infinity by analyzing its embedded Markov chain. Specifically, for a 3-condition class rangeland, if we denote the stationary probabilities of the semi-Markov process by P_i, $i = 1,2,3$, it can be shown, using the methods outlined by Ross (1997), that these stationary probabilities satisfy $P_i = \pi_i \mu_i / \sum_{j=1}^{3} \pi_j \mu_j$ $i = 1, 2, 3$, where π_i is the embedded Markov chain's stationary probability of being in state i and μ_i is the mean time the semi-Markov process (rangeland) spends in state i.

Conclusions

The conceptual approach presented above highlights the advantages of linking rangeland resource management policy to the dynamic and the stochastic structure of a rangeland. Specifically, our approach is consistent with the state-and-transition model of range behavior proposed by Westoby et al. (1989). This approach explicitly accounts for the fundamental role that uncertainty plays in the temporal evolution of managed rangeland resources. This approach also makes transparent the role that management policy can play, and, on occasion, not play, in ensuring the sustainable use of rangeland resources. Finally, the optimization of management policy objectives ($\bar{D}$ and $\bar{U}$) arising from this approach involves the simultaneous maintenance of ecological stability in the sense of persistence.

The state and transition model can be extended in a number of ways. Transition probabilities are an important component of all the Markov models. Consequently, it would be useful to follow the lead of

Ethridge et al. (1985) and estimate the transition probabilities of a Markov model of a parcel of rangeland. Knowledge of transition probabilities will enable a researcher to determine the practical merits of stationary versus non-stationary approaches to the study of dynamic and stochastic rangelands.

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Grazing impacts on litter and roots: perennial versus annual grasses

E. MAPFUMO, M. A. NAETH, V. S. BARON, A.C. DICK AND D. S. CHANASYK

Authors are Post-doctoral Fellow and Professor in Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada T6G 2H1, Research Scientist and research scientist with Lacombe Research Centre, Agriculture and Agri-Food Canada, 6000 C&E Trail, Lacombe, Alberta, Canada T4L 1W1, and Professor in Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada T6G 2H1.

Abstract

Soil carbon (C) and nitrogen (N) storage in grasslands is a function of litter and root mass production. Research on how annual grasses compare with perennials for above ground and below ground mass production, and contributions to the soil C pool under pasture management is scarce. The objective of this research was to evaluate grazing intensity effects on litter and root mass, C and N pools of perennial grasses, smooth bromegrass (*Bromus inermis* L.) and meadow bromegrass (*Bromus riparius* Rhem.), and the annual grass, winter triticale (X *Triticosecale* Wittmack). Litter mass and C pool for the perennial grasses were greater than those for triticale. Litter C and N pools generally decreased with increased grazing intensity. Root mass was greater for the perennial grasses than for triticale at all grazing intensities. Meadow bromegrass generally produced more root mass than smooth bromegrass. Root C and N pools for triticale were 31 and 27%, respectively, of that for the perennial grasses. Estimated total C contribution (roots and litter) to the resistant soil organic C pool was 1.5 times greater for light compared to heavy grazing. Total C (litter + root) contribution for perennial grasses was 2.7 times greater than that for triticale. Perennial grasses provided a larger litter base and root system that promote greater storage of C in the soil compared with triticale.

Key Words: annuals, organic C, perennials, total N, sequestration

Grazing has a major impact on litter, roots, and soil characteristics. Litter herein refers to all dead (standing and fallen) plant material above the soil surface (Naeth 1988). Litter reduces soil erosion by reducing runoff and improves soil structure and fertility through addition of organic matter (Naeth 1988). Bare soils are more susceptible to raindrop impact and aggregate break down which can lead to surface sealing and increased erosion. Litter is especially critical at snowmelt and during intense rainfall events that can potentially remove large amounts of surface soil and nutrients (Chanasyk and Woytowich 1987). The amount of litter in a pasture is a function of forage growth, senescence, harvest and decomposition (Coleman 1992). Grazing affects plant characteristics primarily via biomass and litter removal. Standing and fallen litter mass and vegetation ground cover generally decrease while amount of bare ground increases with increased grazing

Resumen

El almacenamiento de nitrógeno (N) y carbón © en los suelos de pastizal esta en función de la producción de mantillo y biomasa radical. Hay una escases de investigación respecto a como los zacates anuales, comparados con los perennes, producen biomasa aérea y subterránea y las contribuciones a la reserva de C del suelo bajo praderas menejadas. El objetivo de esta investigación fue evaluar el efecto de la intensidad de apacentamiento en el mantillo y la biomasa de raíces de los zacates perennes, "Smooth bromegrass" (*Bromus inermis* L.) y "Meadow bromegrass" (Bromus riparius Rhem.) y de la especie anual de triticales invernal. (X Triticosecale Wittmack) y en las reservas de C y N. La biomasa de mantillo y la reserva de C de los zacates perennes fue mayor que la del triticale. Las reservas de C y N del mantillo generalmente diminuyeron al aumentar la intensidad de apacentamiento. La biomasa de raices fue mayor para los zacates perennes que para el triticale, esto se registró en todas las intensidades de apacentamiento. El "Meadow bromegrass" generalmente produjo más biomasa de raíces que el "Smooth bromegrass". Las reservas de C y N de las raíces del triticale fueron 31 y 27%, respectivamente, de las reservas registradas en los zacates perennes.. La contribución total estimada de C (raices y mantillo) a la reserva de C del suelo orgánico resistente fue 1.5 veces mayor para el apacentamiento ligero que para el apacentamiento fuerte. La contribución total de C (mantillo + raices) de los zacates perennes fue 2.7 veces mayor que la del triticale. Los zacates perennes proveyeron una mayor base de mantillo y sistema radical lo que promueve un mayor alamcenamiento de C en el suelo comaprado con el triticale.

intensity (Naeth et al. 1991).

Grasslands have the ability to store substantial pools of soil C and N. Grasslands contain about 10% of the world C pool (Parton et al. 1995). In temperate regions grasslands may release as much as 40% of their C through respiration when they are cultivated and converted to grains and oilseeds (Burke et al. 1995). This narrows the soil carbon-to-nitrogen ratio (C:N) favoring the release of soil N through N mineralization processes (Wedin 1996). Perennial pastures and hay crops on the Canadian prairies are usually found as a 2 to 9 year sequence in a forage-cereal rotation (Entz et al. 1995). During this time they contribute to soil C and N pools and after being broken enhance yields of cereal crops (Campbell et al. 1990, Entz et al. 1995). The residue that remains goes into the litter pool and subsequently a portion is sequestered in soil. Initial break down results in large losses of organic C stored under grasslands and annual cultivation exacerbates the loss (Campbell et al. 1990).

The objective of this study was to quantify grazing management effects on litter and root mass, litter and root C and N pools in 2 perennial pastures, smooth bromegrass (*Bromus inermis* L.) and meadow bromegrass (*Bromus riparius* L.), and triticale (X *Triticosecale* Wittmack) when grazed at light to heavy grazing intensities.

Materials and Methods

Site Description and Meteorological Conditions

The study was conducted at Lacombe, Alberta (52°28'N; 113°45'W; 847 m), on a Typic Haplustoll derived from glaciolacustrine parent material. The upper 15 cm of soil averaged 15% clay, 34% silt, and 51% sand. Soil pH using distilled water was 5.4 and the sodium adsorption ratio was 0.2.

Total precipitation between April and October for 1993, 1994, 1995, and 1996 was 416, 530, 408, and 383 mm, respectively. The long-term normal annual precipitation (89-year average) was 362 mm. Mean air temperature between April and October ranged from 6.5 to 13.6° C in 1993, 7.7 to 17.1° C in 1994, 5.8 to 15.9° C in 1995 and 2.8 to 16.1° C in 1996. During the winter months (November to March) the total precipitation was 89 mm in 1993/1994, 30 mm in 1994/1995, 88 mm in 1995/1996, and 235 mm in 1996/97.

Experimental Design, Species and Grazing Treatments

Before being broken the site had been under extensive grazing management of 15-year old perennial grass pasture that was composed of smooth bromegrass (*Bromus inermis* L.), quackgrass (*Elytrigia repens* L.) and Kentucky bluegrass (*Poa pratensis* L.). Cultivation of the plot area commenced in summer 1992 so that new species could be established in 1993. Data collection was initiated in 1994.

The experimental field plots were a randomized complete block design with 3 grazing treatments, 3 forage species and 4 replications as blocks. Each plot was 33 × 9 m and was subjected to 1 of 3 grazing treatments (heavy, medium, light). The upper two experimental blocks were east-facing on a 4 to 6% slope, while the other 2 blocks were on flat land.

Three forage species, 2 perennials and an annual, with potentially differing abilities to produce litter were used. Carlton smooth bromegrass (*Bromus inermis* L.) and Paddock meadow bromegrass (*Bromus riparius* Rhem.) were the perennial species; Pika winter triticale (X *Triticosecale* Wittmack) was the annual species. Smooth bromegrass is a rhizomatous species whereas meadow bromegrass is a bunchgrass such that differences in root and litter masses could be expected. Prior to seeding the experimental area received a broadcast application of 8, 31, 31, and 5 kg ha^{-1} of N, P_2O_5, K_2O, and S, respectively. This was followed by a light cultivation and packing. Smooth bromegrass was seeded at 11.2 kg ha^{-1} and meadow bromegrass at 16.8 kg ha^{-1}. Spredor II alfalfa (*Medicago sativa* L.) was seeded with each grass at 1 kg ha^{-1}. Alfalfa had almost totally disappeared by the time measurements were taken in 1996. Perennial species were broadcast seeded with a Model HHBS-125 Handi-Spred Lawn and Garden Seeder-Spreader. Seeding was followed by one pass with a diamond tooth harrow and one pass with a crowfoot packer. Each spring 100, 50, and 50 kg ha^{-1} of N, P_2O_5 and K_2O, respectively were broadcast over the experimental area. Such amounts of fertilizer are not uncommon in intensively grazed pastures. Annual plots were rototilled to a depth of 10 cm and seeded to triticale at 135 kg ha^{-1} in 2 passes with row spacing of 12.5 cm. A herbicide, 2-methyl-4-chlorophenoxy-acetic acid (MCPA), was applied in spring each year at a rate of 600 g ai ha^{-1} in 1994 to 1996 and at a rate of 900 g ai ha^{-1} in 1997, to the triticale to control weeds. No herbicides were applied in perennial grass plots. Residue (all above ground plant material remaining after the last grazing of the previous season) was left in place until spring (end of April) seeding.

All plots were grazed with one-year old crossbred beef heifers. In 1993, unquantified light grazing was used to reduce forage biomass by approximately 50% on all plots. Beginning in 1994, up to 8 animals were placed on a treatment at one time, depending on the intensity of grazing desired. Water was constantly available to cattle so as not to disrupt grazing habits. Grazing events lasted usually less than 24 hours.

Forage height was used to define grazing intensity. Grazing started when forages reached a target maximum and ceased when a target minimum height was reached. Target heights varied among species and were set according to the species morphology, the desired amount of litter and the amount of bare ground deemed appropriate for that treatment.

Forage heights were determined using a diskmeter (Bransby et al. 1977) and the average of 10 disk heights was calculated. The diskmeter was used in this case to maintain consistency in assessing forage availability. For perennials, heavy, medium and light grazing was initiated at 13, 17, and 26 cm and stopped at 6, 5, and 7 cm, respectively when averaged over all grazing events within a year. Comparable figures for triticale were 11, 12, and 21 cm on entry and 3, 4, and 6 cm on exit of animals from heavy, medium and light intensity grazing. Perennials were grazed 7, 5, and 3 times and the annuals 4, 4, and 2 times for heavy, medium, and light grazings, respectively within the 3 study years. Averaged over 3 years the animal unit months per hectare (AUM ha^{-1}, based on approximately 450 kg animal) for perennials was 45.2, 24.4, and 19.6 AUM ha^{-1}, for heavy, medium and light grazing, respectively. For triticale this was 23.3, 13.5, and 9.8 AUM ha^{-1}, for heavy, medium, and light grazing, respectively.

Vegetation Sampling

Litter samples were collected in fall 1994, 1995, and 1996 and in spring 1995, 1996, and 1997. Spring sampling occurred in late April, prior to cultivation of annual plots when perennials had already begun growing. Fall samples were collected between end of September and early October, after the final grazing event each year. Samples were collected from 3 randomly selected sites within each plot in each replicate. All vegetation within a 0.05-m^2 quadrat was clipped at ground level and the surface soil was raked with a hand-fork to remove litter above the soil-mineral surface. All material collected was separated into live (any green material) and dead components before oven-drying at 60° C to determine litter mass (all dead material standing and fallen).

Carbon and Nitrogen Pools in Litter

Three litter samples taken from each plot were combined before determination of the carbon (C) and nitrogen (N) fractions in litter using the Leco Carbon Determinator (Model CN 2000, Leco Corp., St. Joseph, Minn.) and the Kjeldahl digestion method (McGill and Figueiredo 1993), respectively. The litter C and N pools were the product of litter mass (kg ha^{-1}) multiplied by percent C or N content. Litter C and N pools were compared among grazing levels, plant species, and years.

Root Sampling

Soil cores were taken in October 1996 and 1997 to a depth of 60 cm from 3 random locations in non-crown areas in each plot in each replicate using a hydraulically powered sampler with a 5.1-cm diameter probe. Soil cores were separated into depth segments of 0 to 5, 5 to 15, 15 to 30, and 30 to 60 cm and bulked by depth for each plot. Samples were transported from the field immediately, spread in shallow pans and dried at room temperature in a forced-air dryer. Roots were separated from soil with a hydropneumatic elutriation system (Smucker et al. 1982). No attempt was made to differentiate between live and dead roots. Root material was collected on a fine-mesh screen and transferred by washing on to Whatman No. 4 filter papers 9 cm in diameter. The papers and roots were dried in a forced air oven at 85° C for at least 24 hours and then weighed. Root mass per hectare for each sampling depth was calculated from the sample core size. Due to small sample sizes, the samples for each depth within each replicate were combined and ground through a cyclone mill (UDY Corporation, Boulder, Colo.) to pass a 0.5-mm screen. Total C and total N were measured with a Leco Carbon Determinator (Model CN 2000, Leco Corp., St. Joseph, Minn.) and the Kjeldahl digestion method (McGill and Figueiredo 1993), respectively. Root masses for the 0 to15 cm and 0 to 60 cm were examined to determine if there were differences among grazing levels and species in the total root mass (0 to 60 cm) and in the amount of roots found in the plough layer (0 to 15 cm).

Statistical Analyses

Statistical analyses was conducted using the SAS statistical package generalized linear models procedure (SAS Institute 1989). Analyses of litter mass, litter C pool, litter N pool, root mass, root C pool, and root N pool were conducted using a split-split-plot design repeated across years. Grazing intensity and species were main plot effects tested for significance using replicate within (grazing X species) as the error term, years were a subplot effect tested with replicate within years as the error term, and the interactions were sub-subplot effects tested with the residual error (Steel and Torrie 1980). Where the F-test indicated a significant (P ≤ 0.05) effect, means were separated by calculation of least significance difference (LSD) using the appropriate error mean squares (Gomez and Gomez 1984).
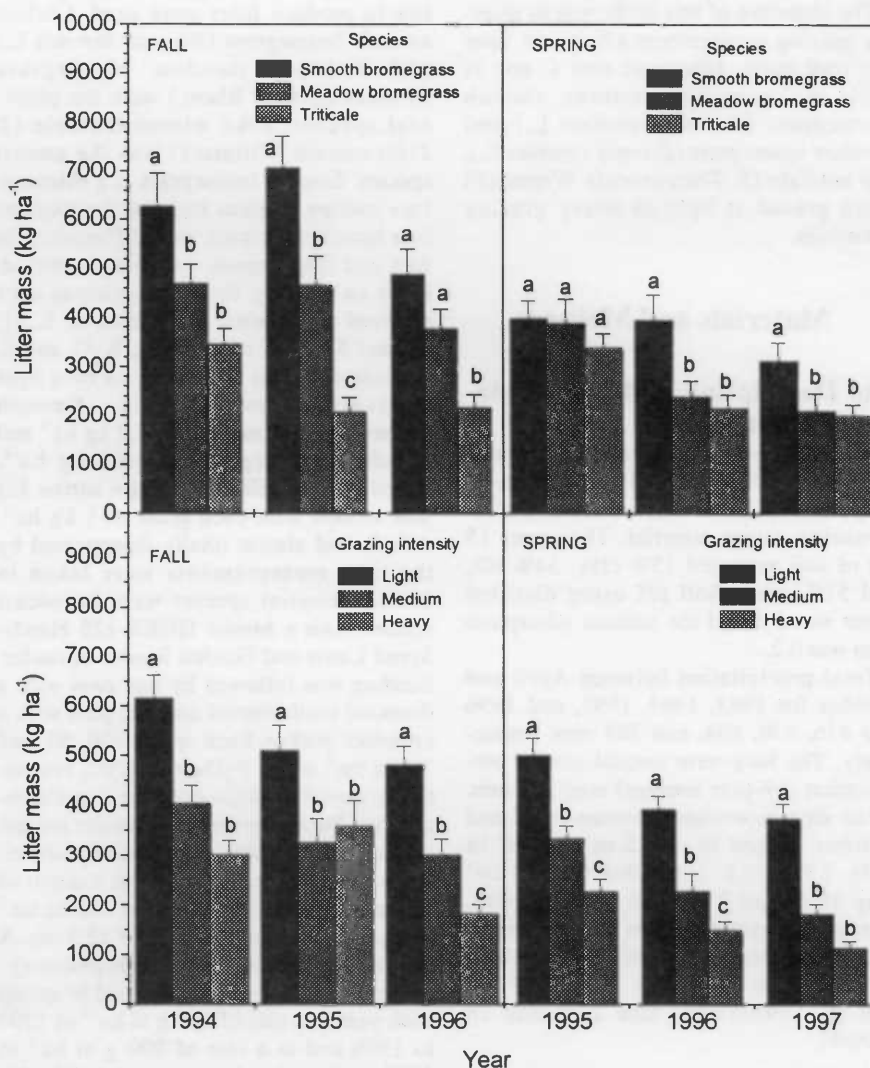
Fig. 1. Litter mass (kg ha⁻¹) in fall and spring under different species, years, and grazing intensities.

Results

Litter Mass, Carbon, and Nitrogen Pools

Litter mass in fall was greater for perennial grasses than for triticale whereas in spring litter mass for smooth bromegrass was greater than that for other species (Fig. 1). Averaged across years, litter mass in fall for triticale was only 48% that for perennials whereas in spring it was 78%. In both spring and fall, litter mass decreased with increasing grazing intensity (Fig. 1). Heavy and medium grazing had average fall litter masses 53 and 64% that for light grazing, respectively. However, in spring, litter masses for heavy and medium grazing were 39 and 59% that for light grazing, respectively.

Differences in litter C pool among species were evident in fall of all years. In all years the C pool in fall was greatest for smooth bromegrass and smallest for triticale whereas in spring litter C pool differences among species were low and inconsistent (Fig. 2). In spring, litter C for triticale across grazing intensities was 72% of that for perennials, and litter masses for heavy and medium grazing were, respectively, 36 and 57% of that for light grazing. In general, the litter C pool in both fall and spring decreased with increased grazing intensity (Fig. 2). In 4 out of 6 cases the C pool of the heavy grazing treatment was less than 50% of that for the light grazing treatment.

The litter N pool in 2 out of 3 years was greater for perennials than for triticale, with smooth bromegrass having the largest N pool of all forages and triticale having the smallest (Fig. 3). Litter N pool in spring for triticale was 71% of that for

perennials. In fall, the heavy grazed treatment had a smaller N pool in litter than the light grazed treatment whereas the N pool of the medium grazed treatment was intermediate. Furthermore, heavy and medium grazing litter masses were 41 and 62% of that for light grazing, respectively.

Litter C:N ratios ranged between 13:1 and 16:1 and were similar among forages in both fall and spring (Fig. 4). The litter C:N ratio in fall generally decreased with increased grazing intensity. For spring, litter C:N ratios for heavily grazed forages were lower than that for lightly grazed forages in 2 out of 3 years (Fig. 4).

Root Mass, Carbon and Nitrogen Pools

Trends among grazing intensities for accumulated root mass to 15 cm or 60 cm (Table 1) were similar. The majority of root material (52 to 60%) existed in the upper 15 cm. Root mass of triticale was always substantially less than that of the perennial grasses throughout the soil profile (Table 1). Root mass of the perennial grasses was 2.6 to 5.2 times that of triticale within grazing levels.

Grazing intensity affected root mass of the species differently (Table 1). Over the 60-cm depth and within the 0 to 15-cm depth root mass of triticale was unaffected by grazing intensity. Root mass of smooth bromegrass maximized at the medium grazing intensity for the 0 to 60-cm depth interval and decreased between medium and light grazing intensities for the 0 to 15-cm depth interval (Table 1). By contrast root mass of meadow bromegrass increased from medium to light grazing intensity for the 0 to 60-cm depth interval and for the 0 to 15-cm depth interval (Table 1).

Perennial grasses always had signifi-
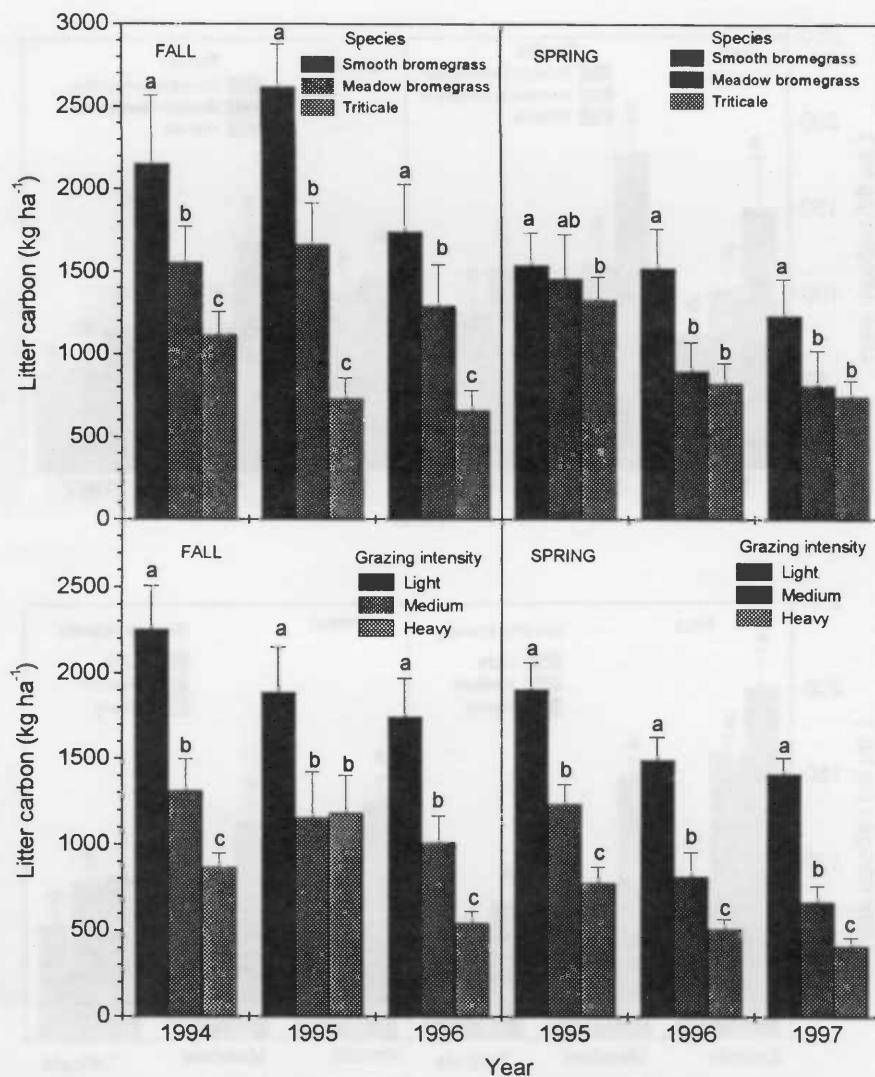
Fig. 2. Litter carbon (kg ha^{-1}) in fall and spring under different species, years and grazing intensities.

cantly higher root C and N pools than triticale (Table 2). Averaged over grazing level triticale had 25 to 30% of the root C and 28 to 32% of the root N pool size of perennial grasses. For smooth bromegrass the C and N pools to 60 cm depth were greatest in the medium grazing intensity. The root C pool for meadow bromegrass under heavy grazing intensity was 67% of that under light grazing intensity. The root N pool for meadow bromegrass increased up to the light grazing intensity with the heavy grazing intensity 75% of the light. The widest range among species for C and N pool size occurred at the light grazing intensity. At this grazing intensity, triticale and smooth bromegrass were 20 and 81%, respectively, of meadow bromegrass for the root C pool, and 28 and 85%, respectively, of meadow bromegrass for the root N pool.

Significant variation was observed among species and from year to year for root C:N ratio (data not shown). There

Table 1. Root mass (kg ha^{-1}) in the surface (0 to 15 cm) segment and for the whole profile (0 to 60 cm) under 3 grass species subjected to three grazing intensities averaged over 2 years.

Species	Grazing intensity		
	Light	Medium	Heavy
	---------------- Root mass (kg ha^{-1})---------------		
	Surface (0-15 cm)		
Smooth bromegrass	1390 ± 164 bB	2020 ± 280 aA	1720 ± 275 aA
Meadow bromegrass	2610 ± 402 aA	2090 ± 222 aB	1540 ± 382 aC
Triticale	530 ± 68 cA	800 ± 209 bA	480 ± 125 bA
	Total (0-60 cm)		
Smooth bromegrass	2840 ± 263 bB	3520 ± 243 aA	3120 ± 295 aB
Meadow bromegrass	4890 ± 539 aA	3730 ± 331 aB	3320 ± 728 aB
Triticale	940 ± 82 cA	1320 ± 246 bA	810 ± 133 bA

Values presented are means ± standard errors for 8 replicates.
Means within column and depth increment followed by different lower case letters indicate significant difference among species within grazing intensities (Least Squares Means, P ≤ 0.05).
Means within row and depth increment followed by upper case letters indicate significant difference among grazing intensities within species (Least Squares Means, P ≤ 0.05).
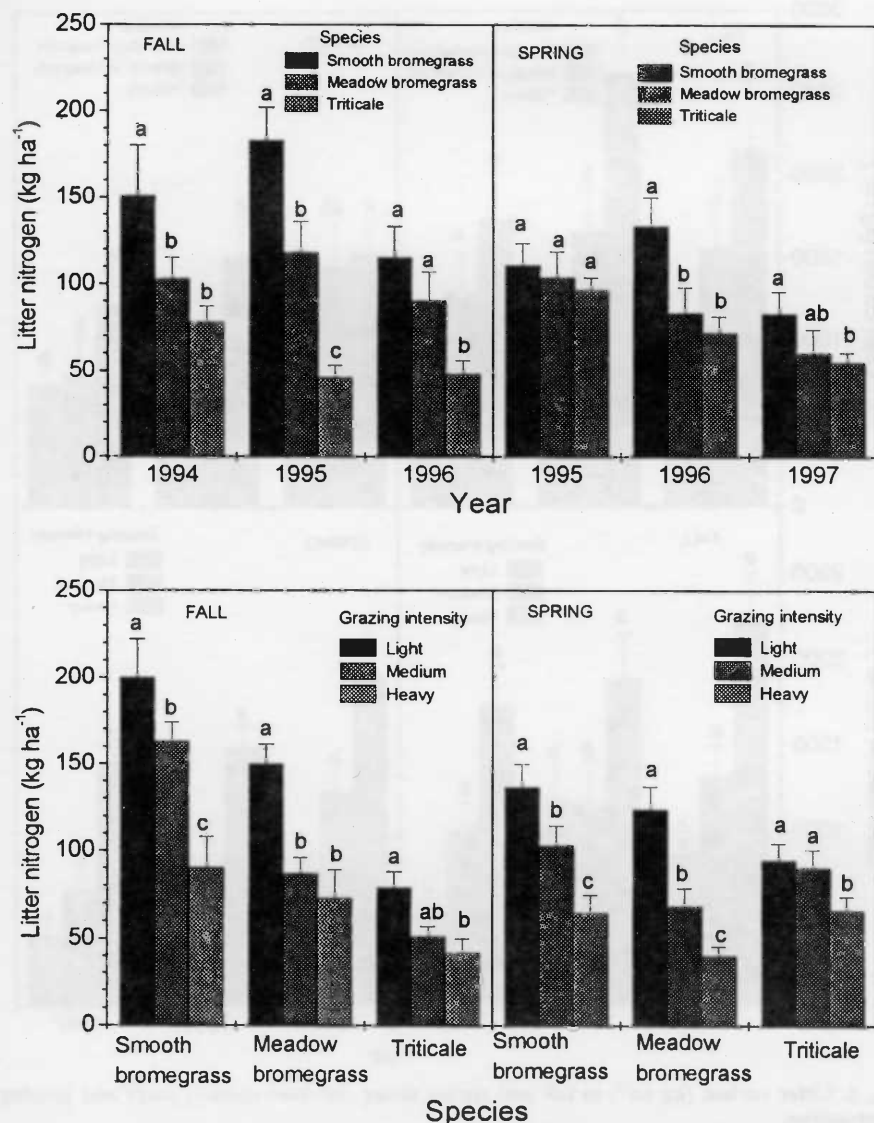
Fig. 3. Litter nitrogen (kg h^{a-1}) in fall and spring under different species, years and grazing intensities.

was a trend for triticale to have a lower C:N ratio than smooth and meadow

bromegrass, but the difference was only significant in 1997. The year-to-year dif-

Table 2. Carbon and nitrogen pools in roots of annual and perennial grasses subjected to light, medium and heavy grazing.

Species	Grazing intensity		
	Light	Medium	Heavy
	------------- Carbon pool (kg ha^{-1}) -------------		
Smooth bromegrass	1190 ± 117 bB	1490 ± 117 aA	1270 ± 123 aB
Meadow bromegrass	1960 ± 214 aA	1450 ± 107 aB	1320 ± 271 aB
Triticale	400 ± 34 cA	460 ± 86 bA	310 ± 51 bA
	---------------- Nitrogen pool (kg ha^{-1}) ----------------		
Smooth bromegrass	42.2 ± 3.7 bB	59.7 ± 8.3 aA	45.9 ± 3.9 aB
Meadow bromegrass	66.2 ± 7.7 aA	54.1 ± 8.6 aAB	49.8 ± 15.1 aB
Triticale	15.4 ± 1.6 cA	19.1 ± 3.6 bA	13.0 ± 1.7 bA

Values presented are means ± standard errors for 8 replicates.
For each pool means within each column followed by different lower case letters indicate significant difference among species within grazing intensity (Least Squares Means, P ≤ 0.05).
For each pool means within each row followed by upper case letters indicate significant difference among grazing intensity within species (Least Squares Means, P ≤ 0.05).

ferences in C:N ratio reflected variations in the root-N concentration. Overall the root C:N ratio ranged between 22:1 and 36:1.

Discussion

Litter mass, Litter C and N Pools

The benefits of litter through improved soil structure and infiltration as well as decreased raindrop impact, runoff and evaporation have been reported widely (Willms et al. 1986, Naeth et al. 1990). In our study, accumulations of litter were strongly influenced by grazing intensity as well as plant species and year. The reduced amount of litter on heavily grazed treatments compared to lightly grazed ones may be attributed to greater removal of green herbage through grazing. It is also possible that heavy grazing may have accelerated litter decay through trampling compared with medium and light grazing. This result has been reported for other grasslands (Rhoades et al. 1964) including grazed lands in Alberta (Naeth et al. 1990, Dormaar and Willms 1992).

Treatment differences in the C and N pool of litter were most clearly expressed in fall. Responses in litter C to grazing intensity were clear with light grazing always providing more C than heavy. The seasonal differences in the carbon content of litter under each grazing intensity may be partly due to freezing effects (loss of cell contents) over winter. Furthermore, a concurrent study conducted on the same plots indicated that annual runoff was dominated by snowmelt-induced runoff, averaging 98, 84 and 86% for the light, medium and heavy grazing, respectively (Gill et al. 1998). This implies that the physical loss of litter could have occurred during snowmelt in spring resulting in reduced litter and litter C pools compared with pools in fall of the previous year.

Quality of litter is reflected in the C:N ratio and lignin contents. Ultimately soil C and C:N ratio will reflect litter and root characteristics that influence decomposition rates (Wedin and Tilman 1990). Because the rate of microbial decomposition is related to the C:N ratio, it is expected that the proportion of C and N reaching the soil would be proportionately less than that indicated by C and N pools from litter. The lignin content controls the split of litter into structural and metabolic material. Most of the structural material (70%) with high lignin is stabilized in the soil while very little is found in microbial biomass (Parton et al. 1987).
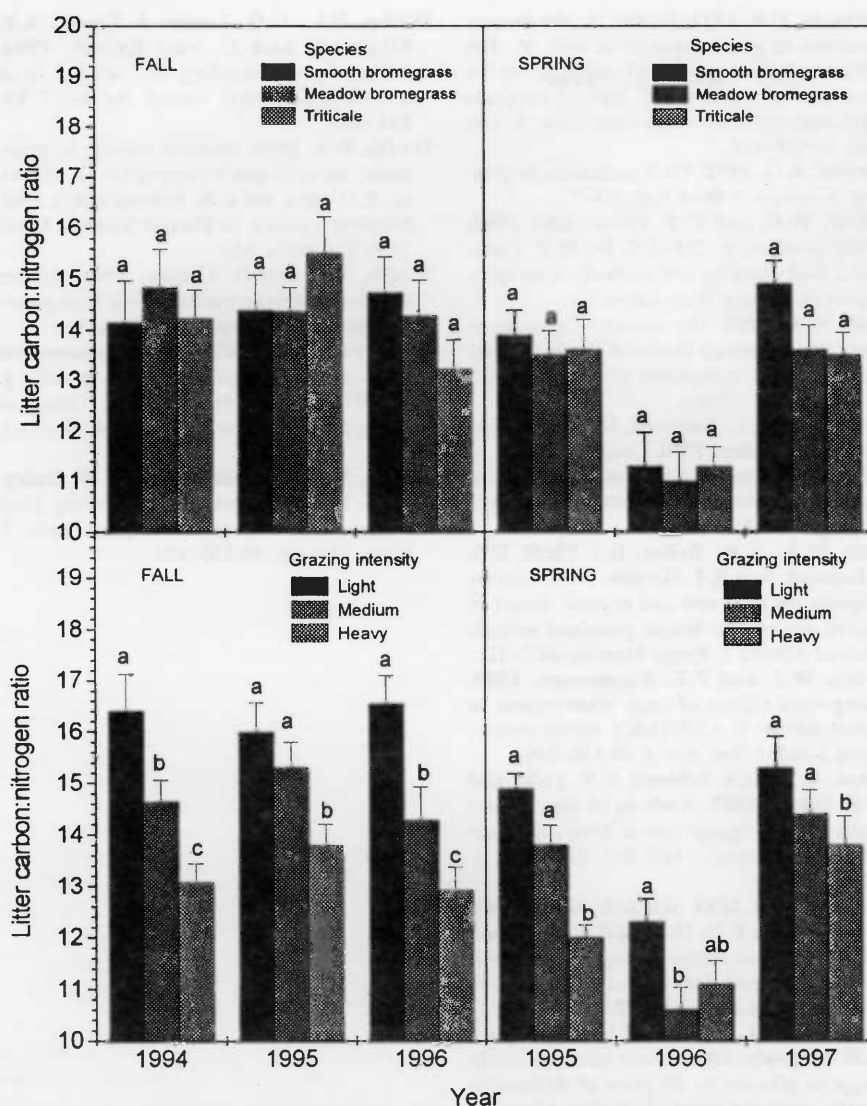
Fig. 4. Litter carbon:nitrogen ratio in fall and spring under different species, years and grazing intensities.

Root Mass, Root C and N Pools

Root mass is expected to decrease with increased grazing intensity (Briske 1991). Meadow bromegrass appeared to follow this trend for root mass with increased grazing intensity. However, smooth bromegrass under light grazing produced a lower root mass than that under moderate grazing. The difference in responses between the bromegrass species for grazing intensity is difficult to explain. Matches (1992) cited studies of other species where grazing intensity did not affect root mass (as for triticale) and Harker and O'Sullivan (1993) observed that quackgrass was stimulated to produce root material relative to untreated controls when thinned by herbicide application. Their conclusion was that rhizomatous species (like quackgrass and smooth bromegrass) might suffer from intraspecific competition for root development, when

allowed to grow uncontrolled.

In this study the perennials consistently had 3.7 times the C and 3.3 times the N pools in the root material compared with triticale, possibly because perennial roots include both live and dead roots whereas triticale had mostly live roots. Turnover of root material is an important consideration in determining the annual contribution of roots to the soil C and N pool. Roots of triticale were produced annually, and annual cultivation would increase the rate of decomposition of dead roots in the surface layer. The turnover of perennial grass roots is more difficult to assess because management level can influence lifespan of roots. Grazing, cutting, and fertilizer application, tends to shorten the average turnover period (Whitehead 1995). Lifespan of roots may vary from 4 to 6 weeks to up to several years in shortgrass prairie (Whitehead 1995). Decomposition

rates are greater in root material with low C:N ratios (Whitehead 1995). In a similar environment Walley et al. (1996) reported an average root turnover rate of 1 year for alfalfa and meadow bromegrass.

Litter and Roots Contribution to the Stable Soil C Pool

According to Van Veen and Paul (1981), 50% of the litter produced annually on native grassland enters the soil. In cereal grasses 80% of the litter that enters the soil is easily decomposed while the remaining 20% is more resistant to decomposition (Jenkinson 1977; Parton and Rasmussen 1994). An estimated 63% of the root C is easily degradable with the remaining 37% forming part of the resistant soil organic matter (Van Veen and Paul 1981). Using these percentages the estimated C contributions from litter and roots resulted in total C contributions to resistant organic C of 1,210, 1,550, and 1,810 kg C ha^{-1} for heavy, medium, and light grazing, respectively. Over the same period (i.e. 3 years), the total C contribution to resistant soil organic C was 2,608 kg C ha^{-1} for perennials compared to only 962 kg C ha^{-1} for triticale. However, these estimates are simplified because they did not take into account factors that make C contribution estimation more complicated, such as yearly cultivation of annual species and lignin concentration.

Within the top 30 cm, total soil organic C did not change significantly over the period of study (1994 to 1996) and was not affected by grazing treatments (Baron et al. 1999). Average soil total C concentrations over the 0 to 15-cm depth interval were 5.3% in 1994 and 5.4% in 1997, which is equivalent to 74 and 75 Mg ha^{-1} C, respectively. This observation is consistent with findings on Black Chernozems with high organic matter content (Campbell et al. 1991).

In conclusion, increased grazing intensity resulted in smaller litter C and N pools. A similar trend was observed for root C and N pools. Both litter and root mass, and litter C pool for perennials were greater than that for triticale. Thus growing perennials would provide a greater litter base, greater litter C and root C pools than annuals. Amidst concern about global warming, growing perennial species may potentially enhance C sequestration and reduce net emission of carbon dioxide from agricultural ecosystems.

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Windrow grazing and baled-hay feeding strategies for wintering calves

JERRY D. VOLESKY, DON C. ADAMS, AND RICHARD T. CLARK

Authors are repsectively Associate Professor, Agron. and Hort. Dept., Professor Anim. Science Dept., and Professor Agr. Econ. Dept., Univ. of Nebraska-Lincoln, West Central Res. and Ext. Center, 461 West University Drive, North Platte, Nebr. 69101.

Abstract

Management practices that lower livestock production costs are of interest to ranch enterprises. Windrow or swath grazing is a strategy where livestock directly graze windrow-stored forage, generally during a time when packaged hay or some other feed is provided. The objectives of this study were: 1) to quantify calf performance and forage intake and waste under windrow grazing (windrow) and bale-fed (bale) management strategies; 2) to quantify hay quality changes as affected by storage method and time; 3) to determine the effects of windrow coverage on subsequent meadow herbage yield and composition; and 4) to compare costs and returns associated with windrow and bale strategies. The forage source was wet meadow dominated by cool-season perennial species with alternating windrows baled and the remaining windrows left in place for direct grazing. Weaned steer calves were fed baled hay or grazed windrows during a November–January period each of 2 years. Windrow grazing calf gains were greater (P < 0.05) than bale-fed during the first year of the study but gains were similar during the second year. Greater weight gain for windrow calves during the first year was likely due to the presence of high quality regrowth that occurred after hay harvest. Diet samples collected from fistulated windrow animals in December contained 14.6% crude protein (CP) compared to 10.4% for hand-collected samples of windrows (P < 0.05). Crude protein content of windrow- and baled-stored forage was similar (10.6%, P > 0.05) during all sampling months (September–February). Crude protein content of standing (stockpiled) forage declined to 5.7% by February. Acid detergent fiber (ADF) and neutral detergent fiber (NDF) were similar between windrow and standing storage treatments during all months and higher than bales from November through February. Herbage yield was 20% less in the area directly covered by windrows the previous fall and winter compared to the control (P < 0.05). However, only about 9% of the total area of a pasture is affected by windrow-coverage when 1-m wide windrows are created 11 m apart, resulting in an overall herbage yield reduction of 1.5%. Total forage production costs for the bale-fed strategy were about $63 ha^{-1} (37%) higher than windrow grazing due to baling and bale moving costs. Feed costs averaged $0.16 head^{-1} day^{-1} for windrow and $0.30 head^{-1} day^{-1} for the bale strategy. When production data were applied to market prices for the previous 7 years, the mean net return ha^{-1} for windrow

Resumen

Las practicas de manejo que disminuyen lo costos de producción del ganado son de interes para muchas empresas ganaderas. El apacentamiento de heno cortado y dejado en hileras en el campo es una estrategia donde el ganado apacienta directamente el forraje de estas hileras, generalmente cuando el heno empacado o alguno otro alimento es suministrado. Los objetivos de este estudio fueron: 1) cuantificar el comportamiento productivo del becerro y el consumo de forraje y desperdicio en el apacentamiento de forraje almacenado en hileras y empacado, 2) cuantificar los cambios de calidad del heno debido al método y tiempo de almacenamiento, 3) determinar los efectos de la cobertura de las hileras del heno en el rendimiento de forraje y composición subsecuentes de la pradera y 4) Comparar los costos y la tasa de retorno asociados con las estrategias de almacenamiento en hileras y empacado. La fuente de forraje fue una pradera humeda dominada por zacates perennes de estación fría, las hileras de forraje se manejaron alternadamente empacando unas hileras y las otras dejadas en el terreno para apacentamiento directo. Durante 2 años, en el periodo de Noviembre a Enero, becerros machos destetados se alimentaron con heno empacado o apacentaron las hileras de forraje sin empacar. Durante el primer año la ganancia de los becerros apacentando el heno en hileras fueron mayores (P < 0.05) que la de los alimentados con heno empacado, sin embargo, las ganancias del segundo año fueron similares. La mayor ganacia obtenida en el primer año por los becerros apacentando heno en hileras proablemenre se debio a la presencia del rebrote de alta calidad que ocurre después de la cosecha del heno. Las muestas de la dieta colectadas de animales fistulados apacentando en heno en hileras contenia 14.6% de proteína cruda, comparado con el 10.4% de las muestras colectadas manualmente de las hileras (P <0.05). Durante todos los meses de muestreo (Septiembre – Febrero) el contenido de proteína cruda fue similar para el heno almacenado en hileras y el empacado (10.6%, P > 0.05) El contenido de proteina cruda del forraje almacenado en pie disminuyó a 5.7% en Febrero. La fibra ácido detergente (FAD) y la fibra neutro detergente (FND) fueron similares entre el forraje almacenado en hileras y el que se almaceno en pie durante todos los meses del estudio, y de Noviembre a Febrero fueron mayores que los del heno empacado. El rendimiento del área directamente cubierta por las hileras de heno fue 20% menos comparada con el control en el otoño e invierno previos (P < 0.05). Sin embargo, aproximadamente solo el 9% del area total de la pradera es afectada por la cobertura del heno en hileras, esto cuando el'ancho de las hileras es de 1 m y la separación entre ellas de 11 m, resultando en una reducción general del rendimiento de forraje de 1.5%. Los costos totales de producción del forraje para la estrategia de alimentación con forraje empacado fueron aproximadamente $63 dolares ha^{-1}

más altos que los costos del apacentamiento de heno almacenado en hileras, esto debido a los costos de empaque y movimiento de las pacas. Los costos de alimentación promediaron $0.16 cabeza⁻¹ día⁻¹ para el heno en hileras y de $0.30 cabeza⁻¹ día⁻¹ para el heno empacado. Cuando los datos de producción fueron aplicados a los precios de mercado de los 7 años previos, el retorno neto medio ha⁻¹ del heno en hileras excedio al retorno neto del heno empacado por aproximadamente $ 93 dolares y el retorno neto para una estrategia que vendió directamente el heno por $ 174 dólares.

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exceeded the net return for the bale strategy by about $93 and the net return for a strategy that directly sold the hay by $174.

Lowering production costs using efficient management practices is of interest to ranch enterprises. Using strategies that extend the normal grazing season for range livestock enterprises is one approach that can reduce costs. Adams et al. (1994) reported that grazing Sandhills wet meadows with cows with calves during May rather than feeding hay increased calf weaning weight and reduced feeding costs. Other strategies include use of complementary grazing of seeded forages (Lodge 1970, Nichols and Clanton 1987, Vallentine 1990), grazing of stockpiled forages (Ocumpaugh and Matches 1977), or any approach that places greater reliance on the grazing animal rather than machines for harvesting forages (D'Souza et al. 1990).

Another strategy to potentially lower harvest and feeding costs is the direct grazing of windrows or swaths in lieu of baling. The objective of this strategy is to produce windrow-stored forage that will match the nutrient requirements of a certain class of livestock. McCaughey (1997) reported that additional benefits include reduced machinery use for handling manure and that livestock are provided with exercise and a clean environment. Cows grazing windrowed oats maintained body condition and back-fat similar to cows fed a typical winter ration of haylage, straw, and barley grain (AAFRD 1998). Turner and Angell (1987) reported similar winter crude protein content of mountain meadow forage that was either baled or bunch-raked. Cows grazing the bunch-raked forage also gained 10 kg more body weight than those fed baled hay.

We initiated a 2-year study in 1997 to evaluate windrow grazing of meadow forage with weaned calves as an alternative to the conventional feeding of baled hay. Our approach was unique in that we harvested regrowth meadow hay in an attempt to provide a forage that would meet the nutrient requirements of a weaned calf. The objectives were: 1) to quantify calf performance, feed intake, and waste under windrow grazing and hay feeding management strategies; 2) to quantify hay quality changes as affected by storage method and time; 3) to determine the effects of windrow coverage on subsequent wet meadow herbage yield and composition; and 4) to compare costs and returns associated with windrow grazing and hay feeding strategies.

Materials and Methods

Study Area and Pasture Sites

The study was conducted from 1997 to 1999 at the University of Nebraska, Gudmundsen Sandhills Laboratory (GSL), 11 km northeast of Whitman, Nebr. (42° 04'N 101° 26'W, elevation = 1075 m). Mean annual precipitation at the site is 460 mm with about 75% occurring from April through September. The average January temperature is –6.2° C and the average July temperature is 22.3° C.

Experimental pastures were established on a subirrigated range site of a wet meadow that had primarily been used for hay production. Soils of the study pastures are Elsmere loamy fine sands (sandy, mixed, mesic Aquic Haplustolls) and Gannett-Loup fine sandy loam (coarse loamy, mixed, mesic Typic Haplaquoll) derived from an eolian sand parent material. Vegetation of the study pastures was dominated by cool-season species including smooth bromegrass (*Bromus inermis* Leyss.), redtop bent (*Agrostis stolonifera* L.), timothy (*Phleum pratense* L.), slender wheatgrass [*Agropyron trachycaulum* (Link) Malte], Kentucky bluegrass (*Poa pratensis* L.), and bluejoint reedgrass [*Calamagrostis canadensis* (Michx.) Beauv.]. Several species of sedges (*Carex* spp. and *Cyperus* spp.), rushes (*Scirpus* spp.), and spikerushes (*Eleocharis* spp.) were present at the site with slough sedge (*Carex atherodes* Spreng.) and Nebraska sedge (*C. nebraskensis* Dewey) being particularly abundant. Prairie cordgrass (*Spartina pectinata* Link) was the major warm-season species and minor amounts of big bluestem (*Andropogon gerardii* Vitman) and switchgrass (*Panicum virga-*

tum L.) were present. Red clover (*Trifolium pratense* L.), alsike clover (*Trifolium hybridum* L.) and white clover (*T. repens* L.) were minor components of the vegetation.

Three rectangular, 3.25-ha pastures were fenced during May 1997. Pastures were located on the edge of the meadow basin and extended about halfway to the center of the basin. Degree of soil wetness, duration of flooding, and proximity to water table increased down slope.

Grazing, Haying, and Livestock Management

Each of the 3 pastures were grazed by mature cows with calves at 96 animal-unit-days (AUD) ha⁻¹ during the last 2 weeks of May in 1997 and 1998. This stocking rate resulted in heavy utilization with nearly all of the available forage being removed. After grazing, pastures were fertilized at a rate of 65 kg N, 22 kg P, and 22 kg S ha⁻¹ , and allowed to grow the remainder of the summer. A sickle-bar mower was used to cut the forage in each pasture on 1 September 1997. Inclement weather delayed hay harvest until 22 September in 1998. Cut forage was raked into windrows that were approximately 1 m in width and 11 m apart. Alternate windrows were then baled (450 kg round), and bales removed. Remaining windrows were left in place. Within a pasture, windrow location was different each year to avoid covering the same area with a windrow 2 successive years.

The grazing and feeding trial began in mid-November and continued through January of each year. Forty-eight steer calves were randomly allocated into 3 replicate groups (8 head each) for the windrow grazing (windrow) treatment and 3 replicate groups for the bale-fed (bale) treatment. Calves were 1/4 Hereford, 1/4 Angus, 1/4 Simmental, and 1/4 Gelbviegh and had an initial weight was 203 kg. They were approximately 8 months of age and had been weaned in October. Calves did not receive implants prior to the trials. In each windrow pasture, temporary electric fencing was used to initially allocate about 0.5 ha to the calves. This size of area contained about 200 linear m of windrow and 800 kg total windrowed forage. Every 10 to 14 days, the temporary fence was advanced to allow access to an additional 0.5 ha of ungrazed windrow area. A back-fence was not used so calves had the opportunity to utilize previously grazed areas, but were observed to graze in the windrow area where they had most recently been given access. Bale-fed

calves were kept in dry-lot pens and fed hay packaged from the alternate windrows in the corresponding pastures. Each pen of 8 calves had free-choice access to a single bale placed in a circular, ring-type feeder. A new bale was added when remaining hay was no longer accessible from the feeder.

Both windrow and bale calves received supplemental salt and mineral on a free-choice basis. All calves were weighed at the beginning and end of the trial period. Intermediate weights also were taken during the first week of December and January of each year. Weighing took place after a 14-hour overnight fast from food and water.

Each year in February following the grazing period by calves, 145 head of mature, dry cows were used to remove additional forage from the windrow pastures. This single herd sequentially grazed each entire windrow replicate pasture for 2 days (107 AUD ha^{-1}) in the first year of the trial and for 3 days (161 AUD ha^{-1}) in the second year.

Hay Yield and Herbage Standing Crop

Hay yield in fertilized and control sub-plots was determined by hand-harvesting methods in the week before the mechanical hay harvest of each whole pasture. Three control sub-plots were established in each pasture by placing a 4 × 6 m tarp over the ground before the broadcast application of fertilizer. After the fertilizer application, the tarps were removed and sub-plot locations marked. Fertilized sub-plots were located adjacent to the control sub-plots. A hand-operated sickle-bar mower was used to cut three, 1 × 4.9 m strips in each control and fertilizer sub-plot. The mower was set to leave an approximate 6-cm stubble height. Cut forage was gathered and weighed. Sub-samples were collected from each strip and oven-dried at 60° C to a constant weight for dry matter determination.

Herbage standing crop before (mid-November) and after (late-January) the winter calf grazing period was determined by hand-clipping 20, randomly-located 0.25-m[2] quadrats in each windrow pasture. All herbage within a quadrat was clipped to ground level, bagged, and later oven-dried at 60° C to a constant weight. Because clipping was at ground level, this herbage included all growth that had occurred after the 1 September 1997 or 22 September 1998 hay harvest as well as any residual plant material that was below the 6-cm mowing height.

Forage Intake

Fecal output for estimation of forage intake was determined with 18 calves during December 1997 and 1998. Three calves from each windrow or bale replication were sampled. Each calf on the intake trial was orally dosed with an intraruminal continuous chromium (Cr)-releasing device[1] 5 days before a 6-day fecal collection period (Adams et al. 1991). Calves on the intake trial were observed each morning until they defecated and 300 to 500 g of feces collected. Forage intake was estimated by dividing fecal output by the indigestibility of the forage diet (Kartchner 1980).

Concurrent with the fecal collections for the windrow and bale calves, total fecal collections were made on 8 steer calves that were similar in weight and age to those under the windrow and bale treatments. These calves were dosed with the same intraruminal continuous Cr releasing device and fitted with fecal bags for total fecal collection to obtain a correction factor for total fecal output (Adams et al. 1991, Hollingsworth et al. 1995). Four of the calves were individually fed baled hay and 4 were individually fed hay collected from windrows. Bale and windrow forages were mixed collections from each of the 3 replications. Feces collected in the bag were weighed, mixed, and sub-sampled (300 to 500 g) daily during the 6-day collection period. Daily weights of forage fed, refusal, and feces were used in the calculation of in vivo organic matter digestibility.

Diet samples were collected on 8 December in windrow pastures each year using 3 esophageally fistulated cows per pasture. Cows were held off feed overnight and allowed to graze 30 to 40 minutes for sample collections. Diet extrusa samples were collected in screen-bottom bags.

All fecal and extrusa samples were stored frozen and then freeze-dried before chemical analyses. Samples were ground to pass through a 1-mm screen in a Wiley mill. Diet extrusa samples were analyzed for dry matter and organic matter using standard methods (AOAC 1990). Nitrogen content was determined using a LECO CHN-1000 Elemental Analyzer[2] and crude protein (CP) expressed as N × 6.25. Neutral detergent fiber (NDF) was determined according to Van Soest et al. (1991), and acid detergent fiber (ADF) by

the method of Van Soest (1963). Fecal samples were analyzed for chromium concentration by atomic absorption spectrophotometry using an air plus acetylene flame (Williams et al. 1962).

Forage Waste

Forage waste under the windrow treatment was estimated from pre- and post-grazing weights of 2-m linear sections of windrow. Three, 2-m sections of windrow were located randomly in the area of each pasture that was initially grazed during December. Windrow sections were cut at the 2-m beginning and endpoints and slid onto a sheet of plywood. After weighing on a platform scale, the undisturbed windrow sections were placed back in their original locations. Sub-samples were collected for dry matter determination. Windrow section weights were taken on the day before the calves were allowed access to the area of pasture that contained a marked windrow section. Post-grazing weights of windrow sections were taken 30 days later using the same procedures as described for the pre-grazing weights. Weights of windrow sections before cow grazing were considered the same as the windrow weights after calf grazing. Weights of windrow sections after cow grazing were measured in February of each year.

To estimate forage waste by calves under the bale treatment, pre- and post-feeding weights of 3 bales per pen were taken. Post-feeding measurements took place 1 day after the round-bale feeder had been removed and a new bale was brought into a pen. New bales were placed at different locations within the pen. Hay that was refused and trampled in and around the round-bale feeder was collected and weighed. Sub-samples of both pre- and post-feeding hay were collected for dry matter determination.

Effect of Time and Method of Storage on Forage Quality

To evaluate the effect of time and method of storage on forage quality, samples of windrow, baled, and standing (stockpiled) forage were collected after hay harvest (September) and each month through February. Standing forage samples were collected from a 5 x 30 m plot in each pasture that was not harvested for hay and excluded from any winter grazing. Standing forage was collected by hand-

[1]Captec Chrome manufactured by Captec Pty. Ltd., Australia; distributed internationally by NuFarm Ltd., Manu Street, P.O. Box 22-407, Otahunu, Auckland 6, New Zealand.

[2]LECO Corporation, 3000 Lakeview Ave., St. Joseph, Mich. 49085-2396.

clipping ten, 0.1-m² randomly-located quadrats at each sample date. The standing forage was clipped to leave a 6-cm stubble height. Windrows were sampled by hand-collecting forage (approximately 50 g portions) at 10 random locations throughout each pasture. Samples were always collected from windrows that had not been grazed; including the February samples that were taken from a 40-m length of windrow that had been specifically excluded from cow grazing. Bales were sampled using a 90-cm hay-probe. At each date, a total of 10 sample cores were taken from at least 5 different bales that represented each pasture's bale production.

Composites were made for all forage sub-samples for treatment (standing, windrow, or bale) by replication by date groups. Samples were oven-dried at 60° C to a constant weight and ground to pass through a 1-mm screen. Samples were analyzed for dry matter, organic matter, CP, NDF, and ADF using the same procedures as described for the diet extrusa samples.

Effect of Windrow Coverage on Subsequent Herbage Yield and Composition

Each year following the winter grazing period by calves and cows, 3 plots where windrows had been located, were randomly selected in each pasture. These plots (4 by 4 m), included the area covered by a 4–m length of windrow and the adjacent area not covered by a windrow (control). Fences were constructed to exclude grazing on these plots during the following spring. Sampling was conducted in mid-July of 1998 and 1999 by hand-clipping eight, 0.5 m² quadrats in each plot. Four of the quadrats were in the windrow-covered area and 4 were in the adjacent control area. All herbage was clipped at ground level and sorted into grass, sedge/rush, legume, and forb components and then oven-dried at 60° C to a constant weight.

Statistical Analysis

Data were analyzed using analysis of variance procedures (SAS Institute Inc. 1985). Pastures were considered experimental units for analyses of the effect of time and method of storage on forage quality, hay yield, and effect of windrow coverage on subsequent vegetation production and composition. Windrow grazing pastures or bale-fed pens were experimental units for analyses pertaining to calf performance, forage intake, and forage waste. Model components include year,

treatment, and replication. Year and treatment effects were tested using year X replication or treatment X replication as the error term. Year X treatment interaction effects were tested using the residual error term. Model components associated with the effect of time and method of storage on forage quality data included treatment, year, month, and replication. Treatment effects were tested using the treatment X replication interaction as the error term. Year and year X treatment effects were tested using the pooled year X replication and year X treatment X replication interactions as the error term. Month and all its interactions were tested using the residual error term. Treatment means of quality characteristics of standing, bale, and windrow stored forage were separated using Least Significant Difference (LSD) protected by a prior F-test (P < 0.05).

Economic Analysis

Partial budgeting techniques were used to compare the 2 strategies. Some costs common to both strategies were included to determine whether either strategy could be profitable over a range of calf prices. Fertilizer costs were included in both strategies and were based on the actual applications made to the study pastures as previously discussed. Other costs common to both were the market value of the calves at the beginning of the trials and interest on that value. Interest was charged at a 10% nominal rate for the days calves grazed windrows or were fed hay. The calves were priced into each strategy based on November prices for western Nebraska and eastern Wyoming (personal communication, Livestock Marketing Information Center). The only other costs included were those that were different and associated with either windrow or bale strategies. For purposes of comparison, a 40.5 ha field, typical of ranch-scale operations, was assumed. Fencing costs for windrow included a two-wire electric fence around the perimeter of the field and a single-wire, portable fence used for allocating windrows to calves. We charged depreciation and interest on the average value of the fence investment (including energizer). We estimated it would require about 0.42 hours ha⁻¹ of labor to erect the perimeter fence and move the internal fence to allocate windrows. Mowing, raking, baling and bale moving costs were based on custom rates for Nebraska (Jose and Miller 1998). The only difference in hay costs between the 2 strategies was the lack of baling and bale moving costs for

windrow. Hay yields were assumed the same.

The bale strategy required estimation of bale feeding costs. A budget for hay feeding was developed based on feeding round bales to an equivalent number of calves (410) as would graze 40.5 ha of windrows. We assumed that a 6-bale processor pulled by a 78 kW tractor would be used to feed the calves. Depreciation and interest on average investment value for the tractor and bale processor were charged as well as estimated fuel, lubrication and repair costs. We assumed a 10-year life with 0 salvage value for the bale processor, which would be used to feed 1000 Mg per year. We estimated that the tractor would be operated an average of 500 hours per year and would be traded after 7 years. Labor estimates for feeding hay were based on records kept by GSL staff for feeding cattle.

All costs including fertilizer and fuel, are for 1998, the mid-point of the research trials. Costs were calculated on a per hectare or per Mg basis depending on the feed source and then converted to a per head basis. The conversion was based on the intake estimates and feed records from the 2 years of the study.

Net returns from the retained ownership strategies were calculated by subtracting the costs described above from the gross revenue generated by multiplying appropriate feeder calf prices times the actual weights of cattle on the trials. Feeder calf prices for the average of January and February were used (personal communication, Livestock Marketing Information Center) since the calves finished trials near the end of January or early February. Note that the cost estimates do not include deductions for returns to land, management, or overhead. We assumed that those costs would be similar between strategies. We compared net returns for the 2 years of the study based on the livestock gains observed. We used 1998 costs but prices for 1997/1998 and 1998/1999. The November prices for the first year of each trial period (1997 or 1998) were used to calculate calf cost as it entered the strategies. Values for calves at the end of the trials were estimated using January/February prices for the succeeding year (1998 or 1999).

A final comparison of net returns was made for the option of selling hay. Hay was priced at the field, based on the average of "all hay" and "other hay" prices for the years 1992–1999 (Nebraska Agricultural Statistics Service 1999, 2000). Fertilizer and harvesting costs,

including bale moving, were used to estimate costs for the hay enterprise. Net returns from the hay enterprise were compared to net returns received from windrow and bale strategies using prices relevant for the years 1992-1999 and a projected gain of 0.23 kg day^{-1}. This series was chosen since prices have been reported by 50-pound increments since 1992 and this period covers a wide price range. Costs were held constant at 1998 levels since we were interested in price effects, which tend to be more variable than costs. Cattle gains were held constant at 0.23 kg day^{-1} since 2 years of data are inadequate for assessing production variability and calves under both strategies attained that level of performance each year of the trial.

Results and Discussion

Annual precipitation during 1997 and 1998 was 87 and 96% of the mean, respectively. Precipitation during the September through January sampling period was 104 and 119% of the mean (108 mm) during 1997–98 and 1998–99, respectively (Fig. 1). Snowfall during the mid-November through January grazing and feeding period each year was relatively light with a maximum of 63 mm recorded during a single-day event. Snowfall events of 152 mm (October 1997) and 127 mm (November 1998) occurred before the start of the grazing and feeding periods. Melting of the majority of snow from all events occurred within 2 to 4 days.

Hay Yield and Herbage Standing Crop

Despite a 3-week later harvest date in 1998 compared to 1997, hay yield from the wet meadow pastures was similar over years (P > 0.05) and averaged 4,460 kg ha^{-1}. Hay yield was 780 kg ha^{-1} higher in fertilized plots compared to the control (P < 0.10). Nichols et al. (1990), working on a similar wet meadow site, reported a hay yield of about 6,600 kg ha^{-1} when similar rates of fertilizer were applied in April and the hay harvested in July. Hay yield was about 1,800 kg ha^{-1} higher under fertilization compared to a control (Nichols et al. 1990). Although our observed hay yield was considerably less than that reported by Nichols et al. (1990), our management included grazing of the pastures in May (96 AUD ha^{-1}). We applied fertilizer in early June after the grazing period. Because these pastures were dominated by cool-season species, it is likely that fertilizer-use efficiency and yield response could have been

improved with an April application.

Herbage standing crop at the beginning of the windrow grazing period (mid-November) was greater (P < 0.05) in 1997 (1,400 kg ha^{-1} compared to 1998 (440 kg ha^{-1}). These estimates included all growth that occurred after the 1 September 1997 or 22 September 1998 hay harvest as well as any residual plant material that was below the 6-cm mowing height. The lower standing crop in 1998 was primarily attributed to the later cutting date and differences in fall growing conditions. The date of the first hard freeze (≤ -4° C) occurred on 12 October 1998 compared to 25 October 1997. Herbage standing crop after the calf windrow grazing period (late-January) also was greater during the first trial year (990 kg ha^{-1}) compared to the second year (400 kg ha^{-1}, P < 0.05). This equates to 28 and 9% disappearance of the herbage standing crop during the calf windrow grazing period during the first and second trial years, respectively.

Calf Weight Gain

There was a year by treatment interaction effect for calf weight gain (Table 1). During the first year of the trial, windrow calves gained 37 kg compared to 27 kg for bale calves. There was no difference in weight gain between treatments during the second year of the trial.

The greater weight gain for windrow calves during 1997–98 was likely due to the presence of high quality regrowth that occurred after haying. Diet samples collected from esophageal-fistulated cows on 8 December 1997 contained 14.6% CP compared to 10.4% CP for hand-collected samples of windrows (Table 2). Acid detergent fiber and NDF content of diets, windrow, and baled hay samples were similar (P > 0.05). During the diet collection period, the cows were observed to consume windrow-stored forage, but also spent considerable time selecting green plant material that was present in the areas between windrows. Some of the regrowth

Table 1. Body weights and gains of calves grazing windrows or fed baled, wet meadow hay.

| Trial year | Item | Treatment | | SEM[1] |
		Windrow grazing	Bale-fed	
1997–98	Initial weight, kg	204	203	1.90
	Final weight, kg	241[a]	230[b]	2.04
	Total gain, kg	37[a]	27[b]	1.31
	Daily gain, kg day^{-1}	0.53[a]	0.39[b]	0.02
1998–99	Initial weight, kg	201	204	1.80
	Final weight, kg	220	221	1.51
	Total gain, kg	19	17	1.44
	Daily gain, kg day^{-1}	0.26	0.24	0.02

[1]Standard error of the mean, N = 6.
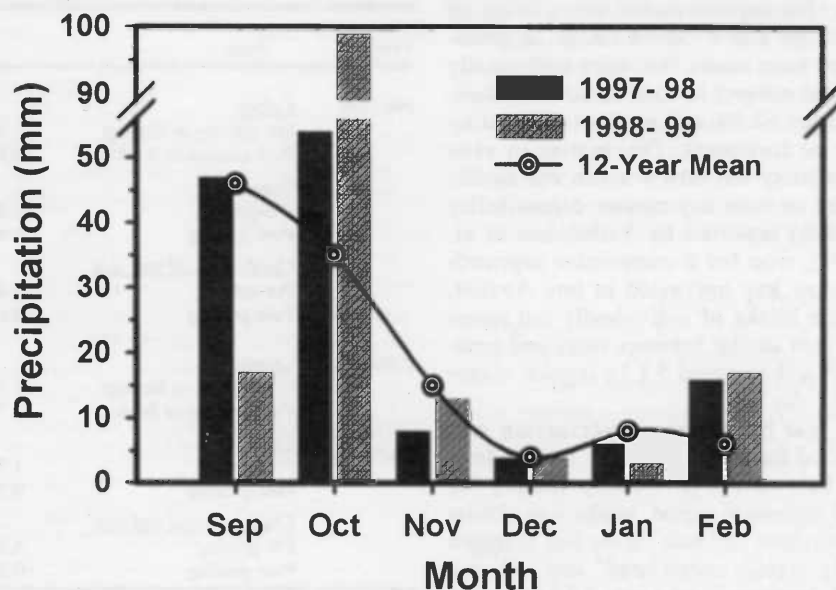[ab]Within rows, treatment means with unlike superscripts differ (P< 0.05).

Fig. 1. Monthly and 12-year means of precipitation during the trial period at the Gudmundsen Sandhills Laboratory near Whitman, Nebr.

Table 2. Percentage crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) of diets from esophageal-fistulated cows in windrow grazing pastures, grab-samples hand-collected from windrows, and core samples collected from bales[1].

Year	Treatment	CP	ADF	NDF
		------------ (%) ------------		
1997	Diets in windrow grazing pastures	14.6[a]	40.9	60.9
	Windrow grab samples	10.4[b]	39.5	62.2
	Baled hay samples	10.3[b]	40.3	60.4
1998	Diets in windrow grazing pastures	12.1	44.3	63.7
	Windrow grab samples	10.9	42.0	61.0
	Baled hay samples	10.5	42.8	61.2

[1]Organic matter basis. All samples were collected on 8 December each year.
[ab]Within year and quality component, treatment means with unlike superscripts differ (P< 0.05).

in the windrow pastures was observed to remain green as late as 20 December 1997. Calf weights taken in early December and January showed daily gains under windrow grazing were greater than bale-fed during November and December. Daily gains during January were similar between windrow and bale groups.We found no studies in the literature that evaluated calf weight gain under windrow grazing and bale-feeding strategies. However, Turner and Angell (1987) reported that by the end of the winter, cows grazing rake-bunched meadow forage were 10 kg heavier than cows fed meadow hay. In a 3-year trial in Saskatchewan, cows grazing windrowed oats during November to January gained an average of 0.42 kg day^{-1} while cows fed free-choice straw supplemented with oat silage and grain gained 0.28 kg day^{-1} (AAFRD 1998).

Forage Intake

In vivo organic matter digestibility of baled hay and windrow forage, as determined from steers that were individually fed and subject to total fecal collection, averaged 67.3% and was not affected by year or treatment. Dry matter in vivo digestibility was 60.4% which was similar to the in vivo dry matter digestibility (60.8%) reported by Villalobos et al. (1997), who fed a comparable regrowth meadow hay harvested in late August. Forage intake of individually fed steers was also similar between years and treatments and averaged 5.1 kg organic matter head^{-1} day^{-1}.

A year by treatment interaction was detected for forage intake by the windrow and bale calves (P < 0.05). During the 1997 collection period, intake was similar for windrow and bale calves and averaged 5.5 kg organic matter head^{-1} day^{-1}. During 1998, however, intake was 5.5 kg organic matter head^{-1} day^{-1} for windrow calves compared to 4.9 kg organic matter head^{-1}

day^{-1} for bale calves. The range of intake estimates given here corresponds to 2.3 to 2.6 kg/100 kg body weight day^{-1} for our calves. We expected intake of windrow calves to be higher in 1997 because of the greater weight gain (Table 1). From an analysis of steer gain and windrow and bale diets (NRC 1996), we postulated that windrow calf intake was likely over-estimated by the marker techniques in 1998. The NRC (1996) analysis showed that degradable intake protein and energy would support greater daily gains but gains were limited by metabolizable protein.

Forage Waste

Pre-grazing weight of windrow-stored forage averaged 4.21 kg linear m^{-1} and pre-feeding weight of bales was 450 kg (Table 3). Under our grazing management,

forage waste (refusal) by windrow calves averaged 29% and was higher than waste by bale calves (12.5%). Allowing cows to graze in the windrow pastures after the calf grazing period resulted in an additional 23% utilization of the windrow forage during the first year of the trial and an additional 75% utilization during the second year. Forage waste after the combined calf and cow grazing periods averaged 18% and 4% during the first and second year of the trial, respectively. The difference between years was largely due to the cow stocking rates that were applied. A single herd (145 head) sequentially grazed each windrow pasture for 2 days (107 AUD h^{-1}) during the first year of the trial and for 3 days (161 AUD ha^{-1}) during the second year.

Our estimate of round-bale feeding waste was higher than that reported by Smith et al. (1974), who estimated 4.7% waste by cows fed bales in rack feeders. Kallenbach (2000) reported 5.4% waste when using round bales and feeders. When round bales were spread or unrolled across a feed-ground, Kallenbach (2000) reported waste ranging from 12.3 to 43.0%, depending on the number of day's supply that was provided. There are also additional forage losses associated with round-bale packaging. Shrock and Fairbanks (1975) found that because of leaf shattering, greater forage loss occurred when using a round baler compared to a rectangular baler. Estimates of lost forage due to hay

Table 3. Mean pre- and post-grazing or feeding weights (± standard error) (dry matter basis) of windrows and bales and forage waste by cattle grazing windrows or fed baled hay[1].

Year	Item	Windrows		Bales	
		Weight	Waste	Weight	Waste
		- - (kg m$^{-1)}$) - -	- - (%) - -	- - (kg) - -	- - (%) - -
1997–98	Calves				
	Pre-grazing or feeding	3.49 ± 0.52	—	446 ± 2	—
	Post-grazing or feeding	0.88 ± 0.38	24[a]	54 ± 5	12[b]
	Cows				
	Pre-grazing	0.88 ± 0.38	—	—[2]	—
	Post-grazing	0.64 ± 0.23	77	—	—
	Combined calf and cow				
	Pre-grazing	3.49 ± 0.52	—	—	—
	Post-grazing	0.64 ± 0.23	18	—	—
1998–99	Calves				
	Pre-grazing or feeding	4.93 ± 0.25	—	452 ± 6	—
	Post-grazing or feeding	1.79 ± 0.80	34[a]	58 ± 5	13[b]
	Cows				
	Pre-grazing	1.79 ± 0.80	—	—	—
	Post-grazing	0.22 ± 0.06	25	—	—
	Combined calf and cow				
	Pre-grazing	4.93 ± 0.25	—	—	—
	Post-grazing	0.22 ± 0.06	4	—	—

[1]Trial years were different with respect to forage waste by cows and the combined calf and cow waste (P < 0.05).
[2]Cows were not allowed to utilize baled hay remaining after calves.
[ab]Bales and windrows were different with respect to forage waste by calves (P < 0.05).
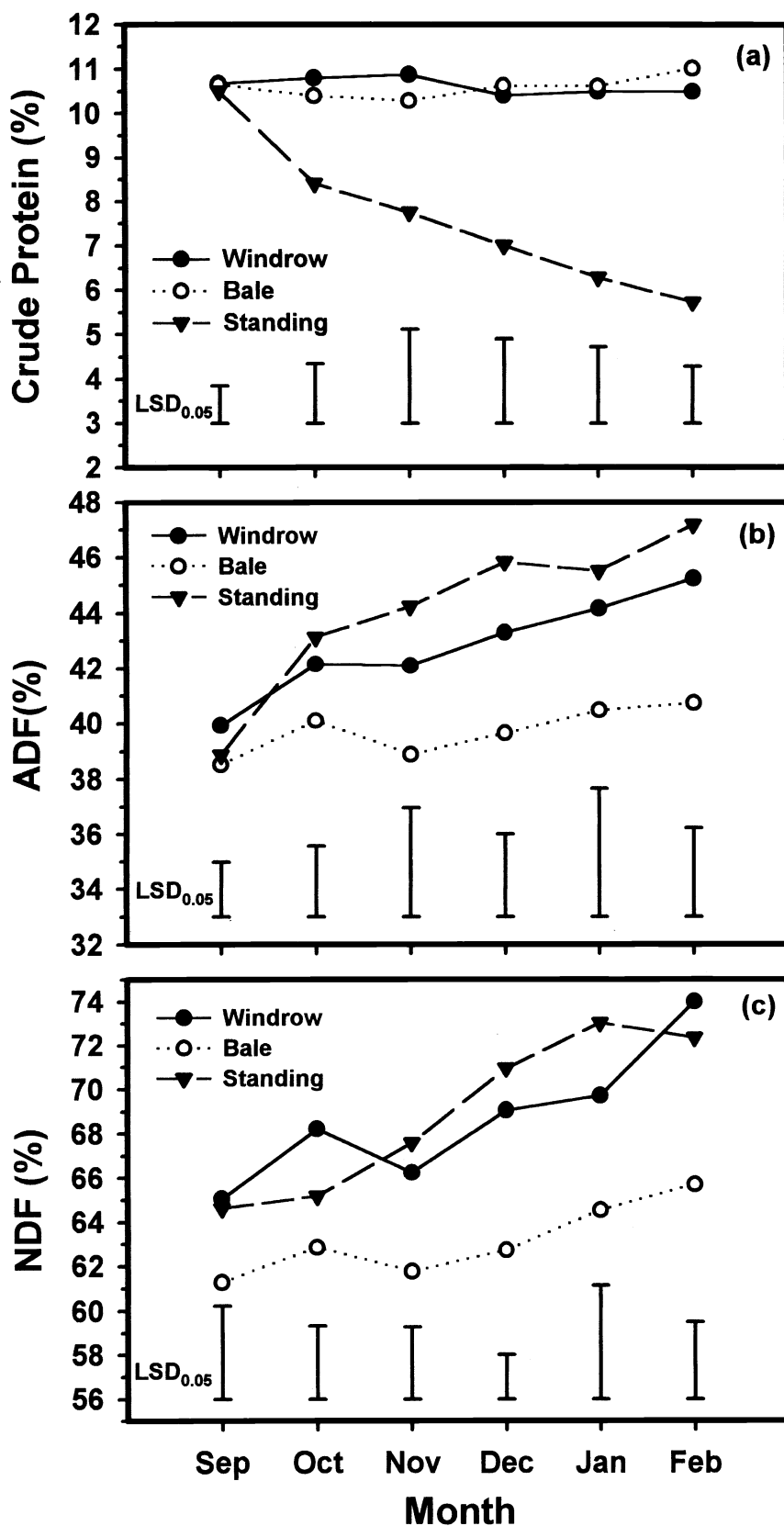
Fig. 2. Effect of time and method of storage on (a) crude protein, (b) acid detergent fiber (ADF), and (c) neutral detergent fiber (NDF) of wet meadow hay (organic matter basis), 1997–98 and 1998–99.

not being picked up by the baler, shatter during the packaging process, and losses during transport average 8% (Anderson and Mader 1984).

Effect of Time and Method of Storage on Forage Quality

Year did not affect crude protein (CP) content, acid detergent fiber (ADF), or neutral detergent fiber (NDF) of windrow, baled, or standing (stockpiled) forage (P > 0.05). A treatment by month interaction was detected for CP content. Crude protein content under windrow, baled, and standing storage treatments was similar in September (10.6%), but CP of standing forage declined to 5.7% by February (Fig. 2a). Crude protein content of windrow- and baled-stored forage was similar over all sampling months. Streeter et al. (1966), in a study using upland Sandhills hay (primarily warm-season), reported no differences in the winter crude protein content of hay that was either baled (small round), windrow-stored, or bunched in piles and stored. Crude protein content of forage that was left standing, however, declined by nearly 50% from summer to winter. Moxon et al. (1951) also reported higher CP content in windrow-stored forage compared to that left standing.

Acid detergent fiber (ADF) of windrow, bale, and standing forage was similar during September and averaged 39.1% (Fig 2b). There was a treatment by month interaction effect on ADF (P < 0.05). Acid detergent fiber of standing forage was greater than bale-stored forage from October through February. There was no difference in ADF between standing and windrow-stored forage during all sampling months. For these 2 treatments, ADF increased each month and averaged 46.2% in February. Neutral detergent fiber (NDF) was similar for windrow, bale, and standing forage treatments during September and averaged 63.6% (Fig. 2c). Similar to ADF, there was a treatment by month interaction effect on NDF, where NDF of standing and windrow-stored forage was higher than that of bale-stored forage from November through February. In February, NDF of standing and windrow-stored forage averaged 73.1% compared to 65.7% for bale-stored forage.

Several factors likely contributed to the decline in quality of our standing forage. Plant maturity is considered the major factor affecting plant morphology and determining forage quality (Nelson and Moser 1994). The plants in our study pastures (primarily cool-season) continued growth and advanced in maturity until hard-

freezes in October. After October, nutrient losses were probably due to leaching and leaf loss associated with weathering. Burzlaff and Clanton (1971) reported that in vitro dry matter digestibility (IVDMD) of upland Sandhills hay significantly declined with time when field-stored as bunches, windrows, or left standing. This is consistent with our results given the negative relationship between ADF and IVDMD (Van Soest 1987). Although they were not measured in our study, mineral and vitamin content as affected by storage method may be an important consideration. Streeter et al. (1966) reported little change in phosphorus content when storage treatments involved cutting the forage. Phosphorus in standing forage, however, declined significantly with time. Carotene, the vitamin A precursor, generally declines with time in all stored forages (Moser 1980), however, Streeter et al. (1966) found a slower decline under bale-storage compared to windrows, bunches, or standing forage.

Although yield was considerably less compared to management that uses a July harvest date without any prior grazing (Nichols et al. 1990), our management practice of grazing the wet meadow pastures in May likely enhanced the quality of forage harvested in September (Table 2, Fig. 2a, 2b, 2c). A large portion of the plants appeared to be vegetative when harvested in September suggesting that stage of maturity was a primary factor contributing to quality. Villalobos et al. (1997) reported a crude protein content of 15.3% for hay that consisted of regrowth harvested in late August after an initial June harvest. For meadow that was not grazed during May, Nichols et al. (1990) reported a CP content of 8.3% for hay harvested in July. Reece et al. (1994), working on a wetland meadow site, reported CP contents of 8.3, 6.0, and 5.8% when harvest dates were 15 June, 15 July, and 15 August, respectively.

Effect of Windrow Coverage on Subsequent Vegetation Production and Composition

In July of the growing seasons following windrow grazing, composition of wet meadow herbage averaged 63% grasses, 30% sedges and rushes, 6% legumes, and 1% forbs. Total herbage yield was 20% less in the area directly covered by windrows compared to the control (Table 4). This difference was due to 1,280 kg ha^{-1} less grass yield under the windrow covered treatment compared to the control. There were no treatment effects on yield of the sedge/rush, legume, and forb plant groups;

although the treatment effect on forb yield was approaching statistical significance (P = 0.12). Visual observations indicated that dandelion (*Taraxacum officinale* Weber) and common lambsquarters (*Chenopodium album* L.) were the most abundant forbs.

Table 4. Effect of windrow coverage on subsequent wet meadow herbage yield and composition, July, 1998 and 1999.

Plant group	Treatment Windrow covered	Control	SEM[1]
	- - - - - - (kg ha^{-1}) - - - - - - -		
Grasses	2,900[a]	4,180[b]	466
Sedges / rushes	2,020	1,990	434
Legumes	370	350	102
Forbs	230	90	53
Total	5,520[a]	6,610[b]	305

[1]Standard error of the mean, N = 9.
[a,b]Within plant group, treatments means with unlike superscripts differ (P < 0.05).

Although our data indicate a 20% reduction in total herbage yield in the area covered by windrows, only about 9% of the total area of a pasture is affected by windrow-coverage when 1-m wide windrows are created 11 m apart. Applying this percentage to our data shows that for the entire pasture, the net effect due to windrow coverage would be about 100 kg ha^{-1} or 1.5% less yield.

It is likely that the coverage by windrows contributed to individual grass plant death or at least reduced vigor. Vegetation during the previous fall exhibited etiolated growth when covered by windrows. Dormancy of plants under

windrows also may have been delayed because of protection from freezing temperatures. Etiolated growth occurred to a lesser extent in the spring when covered by residual, ungrazed windrow forage. Most plants appeared to grow through it in conjunction with decomposition of residual forage. Residual windrow forage appeared to decompose rapidly during the spring with only small amounts visible by early-June.

Economics

Estimated costs for producing and harvesting hay were about $63 ha^{-1} (37%) higher for the bale-feeding strategy compared to windrow grazing due to baling and bale moving costs (Table 5). The costs of feeding bales are a major addition to the bale-fed strategy and are just over $12 Mg^{-1} or about 33% of the costs for harvesting hay. Additional costs for windrow grazing are for fencing materials and labor to install the fence and move the temporary fence while grazing windrows. The resulting strategy feed costs were $0.16 head^{-1} day^{-1} for windrow grazing compared to $0.30 head^{-1} day^{-1} for the bale-fed.

During the 1997-1998 trial year, net returns for windrow grazing were $72.26 head^{-1} compared to $52.31 head^{-1} for the bale-fed strategy. This difference reflects both the lower costs and the fact that animals gained better under windrow grazing that year. Net returns during 1998–1999 were $62.96 head^{-1} for windrow grazing and $49.34 head^{-1} for bale-fed with the difference primarily due to strategy costs

Table 5. Costs of forage production and grazing or feeding for windrow grazing and bale-fed strategies.[1]

Item	Windrow grazing	Bale-fed
Forage production	- - - - - - - - - - ($ ha^{-1}) - - - - - - - - - -	
Fertilizer and application	79.87	79.87
Mow and rake	24.69	24.69
Bale (large round)	—	47.68
Move bales	—	15.14
Total	104.56	167.38
Grazing or feeding[2]		
	- - -($ ha^{-1}) - - -	- - ($ Mg^{-1}) - -
Hay cost	104.56	37.36
Feeding cost		
Labor	—	1.76
Bale feeder (depreciation, interest, repair)	—	5.58
Tractor (depreciation, interest, repair, fuel)	—	4.80
Fence	8.69	—
Labor	4.15	—
Total costs ha^{-1} or Mg^{-1}	$117.41 ha^{-1}	$49.50 Mg^{-1}
Feed cost head^{-1}	$11.60	$21.24
Feed cost head^{-1} day^{-1}	$0.16	$0.30

[1]Explanation of assumptions and cost derivations are provided in Material and Methods section.
[2]Costs for windrow grazing are dollars ha^{-1} and costs for the bale-fed strategy are dollars Mg^{-1}.

Table 6. Net returns per hectare under windrow grazing, bale-fed, and hay-sell strategies[1].

Year	Windrow grazing	Bale-fed	Hay-sell
	($ ha[-1])		
1992–93	335.85	243.32	69.87
1993–94	128.48	32.88	93.17
1994–95	177.03	82.34	108.25
1995–96	−125.10	−223.96	123.33
1996–97	506.74	417.14	152.12
1997–98	461.82	371.23	202.84
1998–99	573.58	484.20	94.54
Mean	294.06	201.10	120.59
Standard deviation	248.35	251.97	44.58
Coefficient of variation (%)	84	125	37

[1]Based on use or hay production from 40.5 ha fertilized wet meadow and a yield of 4.97 Mg ha^{-1} (as-fed basis), 410 calves (227 kg), a projected calf gain of 0.23 kg day^{-1} for both windrow grazing and bale-fed treatments, the average of the Nov.–Jan. and Nov.–Feb. calf sale prices each year, and a 72-day windrow grazing or bale feeding period. Hay prices were marketing year averages (1992–1999).

since animal gains were similar. These returns do not include costs for land, management, or overhead.

In an analysis that projected strategy net returns for the years 1992 through 1999, gain from the windrow grazing averaged $29.04 head[-1] compared to $19.86 head[-1] for bale-fed. This analysis was based on 1998 costs and steer calf prices during the given years. Animal gains were held constant at 0.23 kg day^{-1} so the year to year differences reflect only price changes. Net returns for bale-fed were more variable compared to the mean as reflected by the coefficient of variation of 125% compared to 84% for windrow grazing.

In another analysis, net returns were calculated on a ha^{-1} basis for windrow grazing, bale-fed, and a third strategy, selling hay (Table 6). The per head costs for both windrow and bale-fed strategies were converted to the ha^{-1} basis by the carrying capacity of a 40.5 ha wet meadow. That area would produce enough windrow grazing or bales to maintain 410 steer calves at the weights reflected in our study. We added the third option of selling the baled hay at prices relevant for the same years. Hay prices are for prices received by Nebraska producers for the marketing year (1 June to 31 May). The mean net returns for windrow grazing exceeded the net returns for the other 2 options by about $93 and $174 ha^{-1} for bale-fed and selling hay, respectively. In the 1995-1996 years, both retained ownership strategies lost money, but the hay selling strategy showed positive net returns. In fact, in 3 of the 7 years, selling hay would have generated more net returns than the bale-fed strategy. Net returns from selling hay exceeded those from windrow grazing in only one year. The coefficient of variation for selling hay was the lowest of the 3 options reflecting lower variation in net returns from year to year. A producer that is highly risk averse may choose this option to avoid losses such as those that occurred in 1995-1996.

Conclusions

Windrow grazing of meadow forage was an effective and feasible management strategy for wintering calves. The calves readily adapted to the strategy, however, winter grazing period conditions were mild during the 2 years of the study. Quality of windrow-stored forage remained relatively constant through the fall and into the winter months and resulted in adequate calf gains. Forage waste or refusal under windrow grazing is closely associated with grazing management. Strip grazing techniques that balance the supply and demand for 1- or 2-day periods may be more effective, but increase labor requirements. Our management practice of having cows graze at the end of the calf grazing period was also effective in reducing waste and results in additional savings in feed costs. We found that windrow coverage of the perennial vegetation reduced total herbage yield the following growing season. However, for the entire pasture, the net effect of reduced yield because of windrow coverage was minimal. Costs for windrow grazing were substantially less than those associated with the bale-fed strategy. Correspondingly, net returns per head and hectare were greater for windrow grazing compared to the bale-fed strategy. Highly risk averse producers may still prefer selling hay rather than windrow grazing or feeding bales since net return variation was the least for that strategy.

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Quality of forage stockpiled in Wisconsin

JANET L. HEDTCKE, DANIEL J. UNDERSANDER, MICHAEL D. CASLER, AND DAVID K. COMBS

Authors are Research Specialist, Agronomy Dept., University of Wisconsin, Madison, Wisc. 53706 (jlrieste@facstaff.wisc.edu)., Professors, Agronomy Dept., University of Wisconsin, Madison, Wis. 53706, and Associate Professor, Dairy Science Dept., University of Wisconsin, Madison, Wisc. 53706. At the time of research, senior author was Research Assistant, Agronomy Dept., University of Wisconsin, Madison, Wisc. 53706.

Abstract

Stockpiling forage is a commonly used method to extend the grazing season in the southern U.S.A. However, there is little data on stockpiled forage in the upper Midwest. This study was conducted to determine the quality changes of 7 stockpiled cool-season grasses [early and late maturing orchardgrass, *Dactylis glomerata* L., quackgrass, *Elytrigia repens* (L.) Desv. Ex. Nevski, reed canarygrass, *Phalaris arundinacea* L., smooth bromegrass, *Bromus inermis* Leyss., tall fescue, *Festuca arundinacea* Schreb., and timothy *Phleum pratense* L.], with and without N fertilizer, in Wisconsin. Forage was sampled at 3 offseason dates at 3 sites. To determine if N improved forage quality, 4 N-fertilizer treatments were imposed: 0 or 67 kg N ha^{-1} applied at start of stockpiling and 2 treatments totaling 168 kg N ha^{-1} applied in the fall and spring. Over winter, crude protein (CP) decreased from 116 to 107 g kg^{-1}, neutral detergent fiber (NDF) increased from 594 to 667 g kg^{-1}, acid detergent fiber (ADF) increased from 367 to 435 g kg^{-1}, and in vitro organic matter digestibility (IVOMD) fell from 734 to 655 g kg^{-1}. Nitrogen fertilizer improved CP in most environments but generally did not affect IVOMD, NDF, or ADF. Smooth bromegrass and quackgrass ranked highest in CP concentration and tall fescue ranked lowest. Timothy and late-maturing orchardgrass ranked highest in IVOMD while quackgrass and reed canarygrass consistently ranked lowest. Quality of all stockpiled forage studied can maintain livestock such as beef cattle or dry dairy cows over winter if the forage is accessible and adequate animal stocking density is maintained.

Key Words: Stockpiling, forage quality, winter grazing, cool-season grasses

Rotational grazing is an increasingly common and effective method used to reduce the amount of forage that must be mechanically harvested and stored. In a typical upper-Midwestern grazing system, pasture is generally available to the grazing animal from late April to late October. Beyond these months, grazing animals must be fed with stored forage. Combining stockpiling with rotational grazing may help producers manage pastures throughout the year and reduce winter feed costs, while efficiently utilizing pasture forage. Labor can be reduced to 25% of that for conventional wintering of beef cows (Van Keuren 1970).

By stockpiling pasture, feed can be provided to grazing animals well into December and possibly longer if ice and snow do not prevent grazing. Cattle and sheep can graze through as much as 0.5 m of fresh snow as long as there is a good supply of ungrazed forage below (Decker 1988). However, as winter progresses,

Resumen

El almacenamiento de forraje en pie es un método comúnmente utilizado para extender la estación de apacentamiento en el sur de Estados Unidos. Sin embargo, en la parte superior del Medio Oeste de Estados Unidos hay poca información sobre este método. Este estudio se condujo en Wisconsin para determinar los cambios en la calidad del forraje almacenado en pie de 7 especies de zacates de estación fría ["Orchardgrass", *Dactylis glomerata* L.(maduración temprana y tardía), "Quackgrass", *Elytrigia repens* (L.) Desv. Ex. Nevski, "Reed canarygrass", *Phalaris arundinacea* L., "Smooth bromegrass", *Bromus inermis* Leyss., "Tall fescue", *Festuca arundinacea* Schreb. y "Timothy" *Phleum pratense* L.] cultivados con y sin fertilización nitrogenada. El forraje se muestreo en 3 fechas fuera de la estación de crecimiento en 3 sitos de Wisconsin. Para determinar si el N mejoró la calidad del forraje se aplicaron 4 tratamientos de N: 0 or 67 kg N ha-1 aplicados al inicio de la etapa de almacenamiento del forraje y 2 tratamientos totalizando 168 kg N ha-1 aplicados en otoño y primavera. En el invierno la proteína cruda (PC) disminuyó de 116 a 107 g kg^{-1}, la fibra neuto detergente (FND)aumentó de 594 to 667 g kg^{-1}, la fibra ácido detergente (FAD) aumentó de 367 a 435 g kg^{-1} y la digestibilidad in vitro de la materia orgánica (DIVMO) diminuyó de 734 a 655 g kg^{-1}. La fertilización nitrogenada mejoró el contenido de protína cruda en la mayoría de los ambientes, pero generalmente no afecto la DIVMO, FND, o la FAD. El "Smooth bromegrass" y "Quakgrass" presentaron los mayores contenidos de PC y el "Tall fescue" el menor. El "Timothy" y el "Orchardgrass" de maduración tardía se mostraron los más altos porcentajes de DIVMO mientras que el "Quackgrass"y "Reed canarygrass" presentaron en forma consistente los mas bajos porcentajes. La calidad del forraje almacenado en pie que se estudio puede mantener durante el invierno al ganado, tal como los bovinos para carne o vacas lecheras secas, si el forraje es accesible y se utiliza y mantiene una densidad de carga animal adecuada.

grasses tend to lay down under the weight of the snow, ice, and wind, increasing leaf rot and decay and thus decreasing palatability and nutritional value.

Yield and intake of stockpiled forage was reported by Riesterer et al. (2000b). In contrast, quality of forage stockpiled in the upper Midwest has not been reported. The objectives of this study were to compare over-winter quality changes of several stockpiled cool-season grasses common to upper Midwest pastures, with and without N fertilization. This data will permit us to estimate the ability of different stockpiled forages to meet the nutritional needs for different animal classes out-wintered on pasture and will allow us to more accurately calculate the appropriate animal stocking density

Materials and Methods

Field research was carried out at the University of Wisconsin Agricultural Experiment Stations near Arlington (43° 18' N, 89° 21' W), Lancaster (42° 50' N, 90° 47' W), and Marshfield, Wisc. (44° 39' N, 90° 8' W), during 1995 to 1998. The soil types were Plano silt loam (fine-silty, mixed, mesic, Typic Argiudoll) at Arlington, Rozetta silt loam (fine-silty, mixed, mesic, Typic Hapludalf) at Lancaster, and Withee silt loam (fine-loamy, mixed, frigid, Aeric Glossaqualf) at Marshfield.

Soil samples were taken once each spring to a 15-cm depth at each site. Soil samples were analyzed for pH, organic matter, available P, and extractable K by the University of Wisconsin Soil and Plant Analysis Laboratory using the procedures of Schulte et al. (1987). Soil tests at the Arlington site indicated a soil pH near 6.5, organic matter content of 3.9%, P levels at 49 mg kg^{-1}, and K levels at 155 mg kg^{-1}. Lancaster soil tests revealed a slightly higher pH of 6.8, organic matter content of 3.2%, P levels at 28 mg kg^{-1}, and K levels at 105 mg kg^{-1}. Soils at Marshfield had a pH of 7.0, organic matter content of 3.5%, P levels at 32 mg kg^{-1}, and K levels at 125 mg kg^{-1}.

Seven cool-season grasses, 'AC Nordic' (late maturity) and 'Benchmark' (early maturity) orchardgrass [Dactylis glomerata L.], 'Roseau' quackgrass [Elytrigia repens (L.) Desv. Ex. Nevski], 'Palaton' reed canarygrass [Phalaris arundinacea L.], 'Alpha' smooth bromegrass [Bromus inermis Leyss], 'Barcel' tall fescue [Festuca arundinacea Schreb], and 'Colt' timothy [Phleum pratense L.] were established at these 3 sites in the spring of 1995. Land was prepared with a soil digger followed by a culti-packer. Grass seed was drilled in seven, 15-cm rows within the plot at the Lancaster and Arlington sites, and in five, 15-cm rows at the Marshfield site (using a Tool Carrier 2700 Wintersteiger drill[1], Salt Lake City, Ut.). Plot size was 1.2 x 3.7 m at Arlington and Lancaster and 0.9 x 6.1 m at Marshfield. A border of 'Martin' tall fescue was planted around each plot of quackgrass to reduce the potential of interplot contamination by rhizome spreading (Casler and Goodwin 1998). At planting and again on 1 August, plots received 67 kg N ha^{-1} from NH$_4$NO$_3$ applied with a drop spreader. All stands

had nearly 100% ground cover at the beginning of the study.

Four N treatments were imposed (Table 1). Plots received 1 of 2 fertility treatments in late summer, either a control, 0 (F0), or 67 [F67(1)] kg N ha^{-1} on 1 August, which coincided with the start of stockpiling. Two other fertility treatments were applied in the spring and at the start of stockpiling in late summer. The F168(2) treatment was an application of 101 kg N ha^{-1} after the first spring cut (late May) and 67 kg N ha^{-1} on 1 August. The F168(3) treatment was a split application of 45 kg N ha-1 applied before the first spring cut (early April) and 56 kg N ha^{-1} applied after the first spring cut, as well as 67 kg N ha^{-1} on 1 August. The effect of the spring N treatments on seasonal yield distribution and carry over to fall stockpiling is reported in Riesterer et al. (2000a,2000b).

During the 1996 and 1997 growing seasons, all plots were mechanically harvested to an 8-cm stubble with a flail chopper when the tallest plots reached a 30-cm height, ending on 1 August. Forage accumulated after 1 August was primarily leafy, vegetative material that was harvested as three stockpiling treatments during the off-season: 1) near the first killing frost, 2) mid-December, and 3) late March or early April (Table 2), these treatments are hereafter referred to as the October, December, and March harvest dates, respectively.

Grasses were harvested at Arlington and Marshfield using a rotary (lawn) mower with an attached bag to collect forage from a 1.5 x 0.5 m area from the center of the plot. First plots were cut to an 8-cm height and then to a 2.5-cm stubble by adjusting mower-blade height, and the quality was calculated as a weighted average from both cutting heights. Two cutting heights were taken to measure the change in proportion of dry matter in each height over winter as discussed in Riesterer et al. (2000b). A composite of both cutting heights was used to estimated quality because it was assumed that animals would likely graze to 2.5 cm if forage was a challenge to find under snow. At Lancaster, 3 randomly selected 0.2 m^2 subsamples per plot were clipped before grazing to a 2.5-cm stubble.

All samples were dried in a 55° C forced-air oven for 1 week. Due to soil contamination in the samples from the low cutting heights and offseason harvest dates, all forage quality was reported on an organic matter (OM) basis. Dry samples were ground in a Wiley mill through a 2-mm screen. Ground samples were then scanned with a near infrared reflectance spectrophotometer (NIRSystem, Inc.1, Silver Spring, Md., model number 6500) to predict the following quality parameters: crude protein (CP), neutral detergent and acid detergent fibers (NDF and ADF), in vitro organic matter digestibility (IVOMD), and OM. After all samples

Table 1. Rates and schedules of 4-fertilization treatments.

N-fertilization treatment[1]	Late summer[2]	Early spring[3]	Late spring[4]
	-------------------(kg ha^{-1})--------------------		
F0	0	0	0
F67(1)	67	0	0
F168(2)	67	0	101
F168(3)	67	45	56

[1] Each N treatment shows the total kg N ha-1 and the number of applications in parenthesis.
[2] 1 Aug. 1996 and 1997.
[3] 15 Apr. 1997 and 8 Apr. 1998.
[4] 1 Jun. 1997 and 20 May 1998.

Table 2. Dates of first killing frost and harvest schedule at Arlington, Marshfield, and Lancaster, Wisc. in 1996 and 1997.

Year	Site	Killing frost	Harvest date		
			1st	2nd	3rd
1996					
	Arlington	3 Oct.	8 Oct.	13 Dec.	31 Mar.
	Marshfield	3 Oct.	1 Oct.	1 Dec.	10 Apr.
	Lancaster	3 Oct.	9 Oct.	17 Dec.	24 Mar.
1997					
	Arlington	15 Oct.	20 Oct.	3 Dec.	30 Mar.
	Marshfield	25 Oct.	9 Oct.	1 Dec.	3 Apr.
	Lancaster	26 Oct.	3 Nov.	28 Dec.	30 Mar.

were scanned, the data was centered and then approximately 10% of the samples were selected for wet chemistry analysis. Equations were calibrated from existing pasture equations and modified with the wet chemistry results.

Wet chemistry performed on the selected samples followed the procedures outlined in the Forage Analysis Procedures of the National Forage Testing Association (Undersander et al. 1993). Acid detergent fiber was determined according to the Association of Official Analytical Chemists (AOAC 1990b), CP was determined using the macro copper catalyst Kjeldahl method (AOAC 1990c), and OM was determined by ashing samples in a muffle furnace for 8 hours at 550° C (AOAC 1990a). Neutral detergent fiber analysis followed Goering and Van Soest (1970) and Van Soest et al. (1991) methods modified by Mertens (1992). In vitro organic matter digestibility was determined according to the methods of Tilley and Terry (1963).

Metabolizable energy for maintenance requirements of ruminants was calculated from in vitro organic matter digestibility (IVOMD) in a series of equations. First, total digestible nutrients (TDN, %OM) was assumed to be equal to IVOMD since ether extract is low in forages and ash has been removed (Van Soest 1994). Digestible energy (DE, Mcal kg^{-1} OM) was calculated using the equation from Swift (1957) as follows:

$$DE = TDN(\%) * .04409 \quad (1)$$

Metabolizable energy (ME, Mcal kg^{-1} OM) was calculated with an equation from Moe and Tyrrell (1976):

$$ME = -0.45 + 1.01 \, DE \quad (2)$$

Increased maintenance energy requirements needed in environments below animal's lower critical temperature were calculated with the following equation (NRC 1981a):

$$ME^* = A(LCT - T)/I \quad (3)$$

where,
ME* = additional maintenance energy (Mcal day^{-1})
A = body surface area (m^2),
    note: (A = .09BW0.75, BW = body weight in kg)
LCT = lower critical temperature (°C)
T = ambient temperature (°C)
I = total insulation of animal [°C (Mcal m^2 day)$^{-1}$]

The experimental design was a strip-split-plot in complete blocks with 4 replicates (Gomez and Gomez 1984). The vertical factor was fertility treatments, the horizontal factor was harvest dates, and the sub-plot factor was grass species and cultivars. The experimental design was chosen for convenience and to place maximum precision on interactions involving harvest dates and fertility treatments (Milliken and Johnson 1998). The initial analysis of variance (ANOVA) used the model in Table 3 with the addition of years as a split-plot-in-time factor (Steel et al. 1996). Results from the initial ANOVA generally showed year by treatment interactions to be non-significant and few changes in ranking of treatments between years. Therefore, years were averaged and data were analyzed by the ANOVA model in Table 3. Occasional missing data values were estimated by SAS Proc GLM and inserted without adding degrees of freedom (SAS 1985, Steel et al. 1996). Lancaster data were analyzed separately from Arlington and Marshfield because of differences in defoliation methods. The location effect for Lancaster was excluded from the former model, and the year effect was included as a split-plot-in-time factor (Steel et al. 1996). All effects in both ANOVA models were assumed to be fixed, except for blocks. Comparison between means was made using Fisher's LSD at P < 0.05.

Results

Crude Protein

Crude protein (CP) levels of stockpiled forage, averaged over all factors, were surprisingly low in October at 115 g kg^{-1} (ranging from 88 to 142 g kg^{-1} across all sites) (Table 4). Previous research has shown that CP of stockpiled forage ranges from 70 to 220 g kg^{-1}, averaging about 140 g kg^{-1} (Bryan et al. 1970, Gardner and Hunt, 1955, Matches et al. 1973, Taylor and Templeton 1976, Wedin et al. 1966). In our study, CP concentration was based on the entire plant above a 2.5-cm stubble, which likely increased the proportion of old, brown, and senesced leaf material and leaf sheaths vs. younger greener leaves above this height. Although complete harvest details were not always given in previous studies, we speculate that the combination of a lower cutting height and freezing temperatures in Wisconsin which may have accelerated cell leaching, both likely contributed to the lower CP levels in our study compared to other research.

The Marshfield site ranked the highest in CP, followed by Lancaster, and then Arlington, averaging 120, 110, and 95 g kg^{-1}, respectively, across offseason harvests (Table 4). Crude protein concentration of stockpiled forage did not change throughout the winter at Arlington, perhaps due to the initial low values (Table 4). Crude protein concentration declined at both Marshfield and Lancaster in late autumn by 16.3 and 17.1%, respectively. Crude protein levels did not decline further beyond December at Lancaster while increases of 12.1% in late winter were measured at Marshfield.

October to December declines of CP concentration occurred in all species at both Marshfield and Lancaster but only in quackgrass and smooth bromegrass at Arlington (Table 4). Crude protein levels of tall fescue declined from 121 g kg^{-1} in October to 92 g kg^{-1} in November in Virginia (Brown et al., 1963). Losses in CP concentration from October to December were about 10% for tall fescue and both varieties of orchardgrass, and almost 20% for quackgrass and smooth bromegrass, averaged over all sites. Crude protein concentration of timothy and reed canarygrass also declined rapidly after October, the latter species in agreement with Bryan et al. (1970).

Crude protein estimates were higher for all species in March than December at Marshfield. Tall fescue, timothy and both orchardgrass varieties had CP-concentration increases up to 21.1% in late winter. An early study in Europe reported little or no decline in CP concentration of timothy and orchardgrass from October to January

Table 3. Form of analysis of variance for standing forage dry matter at 2 locations.

Source of variation	df	F-test denominator
Location (L)	1	—
Blocks/L	6	—
Harvest date (H)	2	Error(a)
L x H	2	Error(a)
Error(a)	12	Error(c)
Fertility treatments (F)	3	Error(b)
L x F	3	Error(b)
Error(b)	18	Error(c)
H x F	6	Error(c)
L x H x F	6	Error(c)
Error(c)	36	Error(d)
Species (S)	6	Error(d)
S x L	6	Error(d)
S x H	12	Error(d)
S x L x H	12	Error(d)
S x F	18	Error(d)
S x L x F	18	Error(d)
S x H x F	36	Error(d)
S x L x H x F	36	Error(d)
Error(d)	432	

Table 4. Mean crude protein concentration of 7 stockpiled grasses on 3 offseason harvest dates at Arlington, Marshfield, and Lancaster, Wisc. Means are averaged across 4 N treatments, 2 years, and 4 replicates.

Location	Species	Harvest date October	December	March	Mean
		-----------------(g kg^{-1})-----------------			
Arlington					
	Orchardgrass, late	99	94	98	97
	Orchgardgrass early	97	95	99	97
	Quackgrass	103	95	96	98
	Reed canarygrass	95	93	87	92
	Smooth bromegrass	104	96	101	100
	Tall fescue	88	90	89	89
	Timothy	96	93	99	96
	LSD (0.05)[1]	4	4	4	2
	Mean	97	94	95	
Marshfield	Orchardgrass, late	126	109	132	122
	Orchardgrass, early	124	110	128	121
	Quackgrass	137	115	125	126
	Reed canarygrass	137	110	120	122
	Smooth bromegrass	142	113	124	127
	Tall fescue	116	97	113	108
	Timothy	125	102	120	116
	LSD (0.05)[1]	4	4	4	2
	Mean	129	108	123	
Lancaster					
	Orchardgrass, late	122	108	110	114
	Orchardgrass, early	126	111	108	115
	Quackgrass	137	103	110	116
	Reed canarygrass	123	101	94	106
	Smooth bromegrass	134	106	109	116
	Tall fescue	106	95	98	100
	Timothy	115	92	100	103
	LSD (0.05)[1]	6	6	6	4
	Mean	123	102	104	

[1]LSD for harvest x location mean over species is 3 at Arlington & Marshfield, and 5 at Lancaster.

(Hughes, 1954). High organic matter losses over winter as reported by Riesterer et al. (2000b) likely accounted for this increase, as CP did not increase per se.

Species generally ranked the same at all sites and at each harvest date. Smooth bromegrass and quackgrass ranked highest in CP concentration, followed by both varieties of orchardgrass. All species ranked higher than tall fescue and timothy. Similarly, reed canarygrass was higher in CP than tall fescue in Iowa (Bryan et al., 1970, Wedin et al., 1966), and orchardgrass ranked higher than timothy in Scotland (Corbett 1957).

The addition of 67 kg N ha^{-1} on 1 August improved CP concentration by an average of 10.5% averaged over sites. However, the earlier-season N treatments [F168(2) and F168(3)] had no effect on CP content (data not shown). The influence on N on CP concentration was variable across sites, only notable in October at Arlington, while its effect at Lancaster

and Marshfield was evident only during December and March. Dry soil conditions at Lancaster in addition to late-autumn leaf senescence at Marshfield may explain the 'deferred' response to N.

Addition of N generally increased the CP concentration of most species at all sites (Table 5). There was no significant fertilizer by harvest date interaction. Smooth bromegrass and quackgrass ranked first or second under all N treatments and all sites, while timothy, reed canarygrass, and tall fescue ranked the lowest in CP concentration.

Fiber

Both neutral detergent fiber (NDF) and acid detergent fiber (ADF) of stockpiled forage increased by 10.8 to 15.6%, respectively, over winter across sites (Tables 6 and 7) similar to previously reported results in Ohio (Penrose et al. 1994). The majority of the NDF increase over winter

(7.8%) occurred from October to December while the majority of ADF increase (11.3%) occurred after December.

Neutral detergent fiber and ADF increased from October to December in most species at each site (Tables 6 and 7). Reed canarygrass increased the most by about 12.0% from October to December, while all others increased from 5.3 to 7.6% during this time over all sites.

Species generally ranked the same in fiber across harvest dates at Arlington and Marshfield while there was some inconsistency at Lancaster (Tables 6 and 7). Timothy consistently ranked first or second with lowest NDF and ADF, with Lancaster as a major exception. Quackgrass and reed canarygrass usually ranked last with the highest NDF and ADF at all harvest dates across sites with the major exception of quackgrass at Lancaster.

Neutral detergent fiber and ADF response to added N was inconsistent across sites (Table 8). Similar to what Collins (1991) found with tall fescue in Kentucky, N application decreased NDF by 2.3% and ADF by 6.7% at Arlington. However, there was no significant change in either NDF or ADF at Lancaster or Marshfield. Generally, the spring-and-fall-applied N treatments [F168(2) and F168(3)] were not different than the fall-only N treatment [F67(1)], therefore, all 3 added-N treatments were averaged together in the fiber tables.

Neutral detergent fiber values of individual species were generally similar over all N treatments (Table 8). Small NDF decreases at Arlington of 2.7 to 3.8% for the late-maturing orchardgrass, quackgrass, timothy, and smooth bromegrass were due to added N. Less differences were found at Lancaster and Marshfield. There have been no other reports on NDF values of stockpiled forage besides tall fescue, and for this species, NDF was not affected by N fertilization (Collins 1991).

All species responded to N at Arlington with decreased ADF contents (Table 8). Decreases in ADF ranged from 4.7% for tall fescue up to 9.2% for the late-maturing orchardgrass. However, quackgrass was the only species at Marshfield to respond to added N with decreased ADF. No species responded to N at Lancaster. Species ranked similarly on all N treatments at Arlington and Marshfield.

Table 5. Mean crude protein concentration of 7 stockpiled grasses on 4 N treatmentsat Arlington, Marshfield, and Lancaster, Wisc. Means are averaged over 3 offseason harvest dates, and 4 replicates.

Location	Species	N treatment[1]			
		FO	F67(1)	F168(2)	F168(3)
		----------------(g kg^{-1})----------------			
Arlington & Marshfield					
	Orchardgrass, late	98	103	110	106
	Orchardgrass early	96	105	109	106
	Quackgrass	97	108	114	109
	Reed canarygrass	97	99	103	105
	Smooth bromegrass	101	108	111	112
	Tall fescue	90	95	98	94
	Timothy	94	104	104	102
	LSD (0.05)[2]	4	4	4	4
	Mean	96	103	107	105
Lancaster					
	Orchardgrass, late	91	109	104	101
	Orchardgrass, early	90	110	107	103
	Quackgrass	93	99	102	100
	Reed canarygrass	86	93	94	98
	Smooth bromegrass	91	106	106	109
	Tall fescue	87	93	91	92
	Timothy	82	95	93	86
	LSD (0.05)[2]	7	7	7	7
	Mean	89	101	99	98

[1]FO = no N; F67(1) = 67 kg n ha^{-1} was applied 1 Aug.; F168(2) = 101 kg n ha^{-1} was applied on 1 Jun. and 67 kg N ha^{-1} was applied on 1 Aug.; F168(3) = 45 kg N ha^{-1} was applied 10 Apr., 56 kg N ha^{-1} was applied on 1 Jun., and 67 kg N ha^{-1} was applied on 1 Aug.
[2]LSD for fertility means over species is 2 at Arlington and Marshfield and 3 at Lancaster.

Table 6. Mean neutral detergent fiber concentration of 7 stockpiled grasses on 3 offseason harvest dates at Arlington, Marshfield, and Lancaster, Wisc. Means are averaged over 4 N treatments, 2 years, and 4 replicates.

Location	Species	Harvest date			Mean
		October	December	March	
		------------------(g kg^{-1})------------------			
Arlington					
	Orchardgrass, late	612	670	703	661
	Orchardgrass early	620	671	707	666
	Quackgrass	665	702	725	698
	Reed canarygrass	640	700	738	693
	Smooth bromegrass	644	688	712	681
	Tall fescue	619	679	713	670
	Timothy	602	659	709	657
	LSD (0.05)[1]	10	10	10	6
	Mean	629	681	715	
Marshfield					
	Orchardgrass, late	625	637	674	645
	Orchardgrass, early	641	632	683	652
	Quackgrass	625	659	681	655
	Reed canarygrass	595	661	691	649
	Smooth bromegrass	612	649	693	651
	Tall fescue	645	635	701	660
	Timothy	608	632	688	643
	LSD (0.05)[1]	10	10	10	6
	Mean	621	645	689	
Lancaster					
	Orchardgrass, late	526	595	587	569
	Orchardgrass, early	547	609	599	585
	Quackgrass	540	582	568	563
	Reed canarygrass	517	632	612	587
	Smooth bromegrass	524	590	592	569
	Tall fescue	523	613	623	586
	Timothy	554	610	601	588
	LSD (0.05)[2]	13	13	13	8
	Mean	533	605	597	

[1]LSD for comparing location-harvest means over species is 10 at Arlington and Marshfield and 14 at Lancaster.

Digestibility

Stockpiled forage remained highly digestible throughout the winter, with an average of 655 g kg^{-1} in March (Table 9). In vitro organic matter digestibility (IVOMD) declined from October to March by 10.8% across all sites, similar to declines noted in Missouri (Ocumpaugh and Matches 1977). The largest IVOMD losses occurred from December to March across all sites with the largest declines at Lancaster (7.8%) and Marshfield (11.1%). Increased ADF and NDF contents over winter in this study support this digestibility decline.

All species declined in IVOMD from October to December at Arlington and Lancaster, and all but tall fescue and both varieties of orchardgrass declined at Marshfield (Table 9). Quackgrass declined the least from October to December across sites with a 1.5% decrease in IVOMD while reed canarygrass declined the most with a 7.0% decrease. Continued growth and maturation of reed canarygrass stems in early autumn likely contributed to its quick decline in IVOMD.

In vitro organic matter digestibility of smooth bromegrass, reed canarygrass, and quackgrass did not decline beyond December at Arlington, but IVOMD for all other species-site combinations declined from December to March. In vitro organic matter digestibility of reed canarygrass declined the least from December to March (5.2%) while early-maturing orchardgrass declined the most (8.4%).

Species generally ranked the same in IVOMD at all 3 sites and harvest dates (Table 9). Timothy and late-maturing orchardgrass generally ranked the highest for all harvest dates at Arlington and Marshfield, followed by early-maturing orchardgrass. In contrast, at Berkshire, UK, IVOMD of stockpiled tall fescue was 3.0% higher than stockpiled orchardgrass (Baker et al., 1965). There were less obvious differences in IVOMD at Lancaster, with the exception that quackgrass and reed canarygrass generally ranked lowest in IVOMD. Both Bryan et al. (1970) and Wedin et al. (1966) found tall fescue to be more digestible than reed canarygrass, but there are no other reports on digestibility of stockpiled timothy, smooth bromegrass or quackgrass.

In vitro organic matter digestibility was not affected by N treatment (data not shown). Some researchers have reported small digestibility increases in stockpiled forage of 1 to 4% with the addition of 60 kg N ha^{-1} (Archer and Decker 1977,

Table 7. Mean acid detergent firber concentration of 7 stockpiled grasses on 3 offseason harvest dates at Arlington, Marshfield, and Lancaster, Wisc. Means are averaged over 4 N treatments, 2 years, and 4 replicates.

| Location | Species | Harvest date | | | |
		October	December	March	Mean
		------------------(g kg^{-1})------------------			
Arlington					
	Orchardgrass, late	388	427	478	431
	Orchardgrass early	400	416	474	430
	Quackgrass	440	452	514	469
	Reed canarygrass	408	434	502	448
	Smooth bromegrass	431	447	497	459
	Tall fescue	371	405	462	413
	Timothy	374	409	480	421
	LSD (0.05)[1]	12	12	12	7
	Mean	402	427	487	
Marshfield					
	Orchardgrass, late	385	377	431	398
	Orchardgrass, early	389	371	425	395
	Quackgrass	385	388	438	404
	Reed canarygrass	371	388	434	398
	Smooth bromegrass	384	391	448	407
	Tall fescue	380	352	420	384
	Timothy	366	368	434	390
	LSD (0.05)[1]	12	12	12	7
	Mean	380	377	433	
Lancaster					
	Orchardgrass, late	324	372	386	361
	Orchardgrass, early	326	375	389	363
	Quackgrass	328	366	377	357
	Reed canarygrass	307	374	400	360
	Smooth bromegrass	324	371	385	360
	Tall fescue	298	345	377	340
	Timothy	321	385	390	365
	LSD (0.05)[2]	6	6	6	4
	Mean	318	370	386	

[1]LSD for location-harvest mean is 14 for Arlington and Marshfield and 6 at Lancaster.

Balasko 1977), while some authors found no increase (Eck et al. 1981).

Generally, IVOMD of each species was not affected by N treatment with the exception that quackgrass and smooth bromegrass were 2.2 to 4.4% higher in IVOMD with the addition of N, averaged across Arlington and Marshfield (Table 10). In West Virginia, responses of tall fescue to added N were over 3.0% (Balasko 1977, Kroth et al. 1977) but smaller increases of 1.0% were noted in Maryland (Archer and Decker 1977).

Discussion

Quality Changes

Forage yields were highest at Marshfield and lowest at Lancaster, as previously reported (Riesterer et al. 2000b). Different environments can affect quality components. Soil-water limitations at Lancaster may have decreased the amount of photosynthate delegated to cell wall while more was stored as cell contents. Extended snow cover at Marshfield may have provoked senescence of a higher proportion of old leaves vs. young leaves resulting in higher CP. Corbett (1957) suggested that cool-season grasses maintain a fairly constant level of CP in the winter because many older leaves decompose or are blown away leaving a higher percentage of newer growth. However, in less severe winter conditions of the south, over-winter declines in CP levels have been cited with approximate losses of 25% from October to February (Ocumpaugh and Matches 1977, Taylor and Templeton 1976).

Generally, lower yielding grasses have lower fiber levels. Lancaster had the lowest NDF and ADF throughout the winter. The largest NDF increase of 11.9% in late autumn was here. This may reflect the initially low NDF values, in addition to higher temperatures than at the other 2 sites.

Cellular differences among grasses can influence quality. The early decline in IVOMD of reed canarygrass may have resulted from a higher degree of leaching of cell solubles upon freezing unlike orchardgrass which has an increased tolerance to freezing conditions (Premachandra et al. 1993). In Iowa, soluble carbohydrate percentage was maintained in tall fescue over the fall sampling period but was substantially reduced in reed canarygrass during this time (Wedin et al. 1966). In Kentucky, soluble carbohydrates in tall fescue increased from October to December (Dougherty 1981, Taylor and Templeton 1976). Furthermore, green fractions of tall fescue exhibited a high, but slowly declining, sugar content beyond December while brown fractions were consistently low in sugar (Taylor and Templeton 1976).

Due to early decline in quality, early-autumn grazing of quackgrass, smooth bromegrass, reed canarygrass, and timothy is suggested to obtain maximum quality intake. Stockpiled orchardgrass and tall fescue are suitable for grazing any time. It would be beneficial for producers to seed some pasture into orchardgrass or tall fescue which can be grazed later in winter when other pasture species have poor nutritional value. An alternative to reseeding pasture is to reserve stockpiled reed canarygrass, smooth bromegrass or quackgrass for low maintenance livestock.

Stockpiled Forage Quality vs. Animal Requirements

Feed requirements of livestock depend on maintenance needs and production levels of the animals. Nutrient content of the forage must match the energy, fiber and protein requirements of the animal. Several classes of livestock can obtain at least some, if not all, of their nutrient requirements from stockpiled forage under most winter conditions, assuming adequate stocking rate is maintained. Additionally, animals should have good body condition before outwintering. Stocking rates can be calculated from yields of stockpiled forage (Riesterer et al. 2000b).

Crude protein levels of stockpiled forage in our study averaged 108 g kg^{-1} over the entire winter. In October, stockpiled forage with CP levels of 116 g kg^{-1} is marginally low to meet the requirements of dairy heifers larger than 250 kg and gaining up to 0.8 kg day^{-1}, as well as late-lactation dairy cows and dry dairy cows, all of which require levels of CP at 120 g

Table 8. Mean neutral detergent firber (NDF) and acid detergent (ADF) fiber concentration of 7 stockpiled grasses on 2 N treatments at Arlington, Marshfield, and Lancaster, Wisc. Means are averaged over 3 offseason harvest dates, 2 years, and 4 replicates.

| | | NDF | | ADF | |
| | | N treatment[1] | | N treatment[1] | |
Location	Species	No N	N	No N	N
		------(g kg^{-1})------		------(g kg^{-1})------	
Arlington					
	Orchardgrass, late	676	656	465	422
	Orchardgrass early	673	664	453	425
	Quackgrass	715	693	500	463
	Reed canarygrass	700	691	473	443
	Smooth bromegrass	702	675	491	452
	Tall fescue	674	669	429	409
	Timothy	670	652	439	417
	LSD (0.05)[2]	11	11	13	13
	Mean	687	671	464	433
Marshfield					
	Orchardgrass, late	633	647	385	387
	Orchardgrass, early	634	646	385	381
	Quackgrass	673	658	413	391
	Reed canarygrass	658	664	400	392
	Smooth bromegrass	661	661	412	401
	Tall fescue	636	652	367	368
	Timothy	638	644	379	377
	LSD (0.05)[2]	11	11	13	13
	Mean	647	653	392	385
Lancaster					
	Orchardgrass, late	567	563	365	356
	Orchardgrass, early	571	587	364	364
	Quackgrass	543	563	355	357
	Reed canarygrass	566	588	359	361
	Smooth bromegrass	552	567	362	358
	Tall fescue	581	584	340	341
	Timothy	573	589	360	367
	LSD (0.05)[2]	15	15	7	7
	Mean	565	577	358	358

[1]The 3 added-N treatments were not different and have been averaged.
[2]LSD for comparing NDF and ADF location-fertility means over species is 6 and 8 at Arlington and Marshfield respectively, and 7 and 3 at Lancaster respectively.

kg^{-1} (NRC 1989). Dairy heifers younger than six months of age would not receive their required 160 g kg^{-1} CP from stockpiled forage (NRC, 1989). However, throughout winter, CP levels of stockpiled forage will generally satisfy the requirements of dry beef cows, gestating beef heifers, lactating beef cows (producing less than 14 kg milk day^{-1}), and ewes, all of which require 60 to 120 g kg^{-1} crude protein depending on stage of gestation and lactation (NRC 1984, NRC 1985). Crude proteins levels remained above 90 g kg^{-1} throughout winter, the critical dietary level to satisfy microbial N requirement (Waghorn and Barry 1987).

Stockpiled forage from this study would have provided sufficient energy for several classes of cattle. Energy content of our stockpiled forage averaged 2.82 Mcal ME kg^{-1} OM in October, 2.69 Mcal ME kg^{-1} OM in December, and 2.47 Mcal ME kg^{-1}

OM in March. Energy remains available for growing beef cattle at weight gains up to 0.9 kg day^{-1} as well as pregnant and nursing beef cows in most winter conditions (NRC 1984). In a study in Ohio, pregnant beef cows grazing a mixture of stockpiled tall fescue, orchardgrass, Kentucky bluegrass (*Poa pratensis*) and white clover (*Trifolium repens*) through December gained of 0.8 kg head^{-1} day^{-1} and gained from 0.3 to 0.9 points in body condition (Turner et al. 1998). Beef cattle gained from 0.4 to 1.3 kg head^{-1} day^{-1} while grazing tall fescue and -0.1 to 1.0 kg head^{-1} day^{-1} while grazing orchardgrass (Baker et al. 1965).

Energy in stockpiled forage of the current study would have met the maintenance energy requirement of grazing adult sheep weighing up to 70 kg. Stockpiled forage would also have supplied adequate energy to growing lambs of 30 kg gaining

0.05 kg body weight day^{-1}. Lambs grazing timothy pasture from December through mid-March showed no animal weight change over winter and the animals overwintered in healthy and thrifty condition (Griffith and Hutton 1936). However, ewes in late gestation would require energy supplementation as it is common for ewes to give birth to 2 or 3 lambs. Ewes pastured over winter on stockpiled tall fescue pasture in Ohio scored slightly below average in milking ability and gained 4.1 kg head^{-1}, only one-third the weight gained by silage-fed ewes (Parker and Van Keuren, 1967). Lambs born to winter-pastured ewes were strong at birth and comparable in birth weight and 30-day weight to the conventionally fed group.

Additional energy will be needed when animals are subjected to extreme winter conditions but levels of energy will vary according to class of livestock and environmental conditions (Table 11). As ambient temperatures fall below the lower critical temperature (LCT) of the animal, insulative and behavioral responses are inadequate to maintain core body temperature. Below the LCT, animals must increase metabolic heat production to maintain homeothermy which increases energy requirement of the animal. Increased intake of 30% can be expected as temperatures approach –15° C, assuming conditions are dry, but intake depression of 5 to 30% can accompany temperatures below –25° C with extensive precipitation and muddy conditions (NRC 1981b). In climates with rainy, wet winters, and extremely severe winter conditions, animals should have access to a covered shelter and a wind break since intake will not meet additional energy requirements.

Fiber levels of stockpiled forage in October were typical of grasses in the growing season (367 g kg^{-1} ADF and 594 g kg^{-1} NDF) but levels increased to 392 and 667 g kg^{-1} ADF and NDF, respectively, by March. Animals at maintenance generally can obtain adequate energy from grass diets in most winter conditions without NDF restricting intake. Additionally, animals at maintenance have slower passage rates allowing digesta to be more completely fermented by ruminal microbes. The maximum NDF concentration of the diet that will not restrict intake for mature beef cows ranges from 750 to 850 g kg^{-1} DM (Mertens 1985). Extra energy in the form of grain should be fed to animals on stockpiled pasture when temperatures fall below –25° C. In severe weather, it is likely that the high NDF val-

Table 9. Mean in vitro organic matter digestibility of 7 stockpiled grasses on 3 offseason harvest dates at Arlington, Marshfield, and Lancaster, Wisc. Means are averaged over 4 N rates, 2 years, and 4 replicates.

		Harvest date			
Location	Species	October	December	March	Mean
		------------------(g kg^{-1})------------------			
Arlington					
	Orchardgrass, late	759	725	698	727
	Orchardgrass early	745	717	686	716
	Quackgrass	697	674	678	683
	Reed canarygrass	696	643	651	6633
	Smooth bromegrass	744	712	705	720
	Tall fescue	744	701	677	707
	Timothy	780	741	710	744
	LSD (0.05)[1]	12	12	12	7
	Mean	738	702	686	
Marshfield					
	Orchardgrass, late	743	736	641	707
	Orchardgrass, early	736	733	637	702
	Quackgrass	701	673	617	664
	Reed canarygrass	710	657	608	658
	Smooth bromegrass	738	711	643	698
	Tall fescue	736	739	643	706
	Timothy	757	738	648	715
	LSD (0.05)[1]	12	12	12	7
	Mean	732	713	634	
Lancaster					
	Orchardgrass, late	764	712	664	713
	Orchardgrass, early	742	707	652	700
	Quackgrass	674	692	627	664
	Reed canarygrass	709	667	621	666
	Smooth bromegrass	749	728	657	711
	Tall fescue	751	692	647	697
	Timothy	739	713	656	702
	LSD (0.05)[2]	13	13	13	7
	Mean	733	701	646	

[1]LSD for location-harvest mean over species is 10 at Arlington and Marshfield and 9 at Lancaster.

ues of stockpiled forage will restrict intake before adequate energy is obtained, similar to the effect of high levels of NDF on intake of high producing dairy cows (Van Soest 1994).

High producing dairy cows require intake levels up to 25 kg DM day^{-1} to meet their energy demand for milk production (NRC, 1989). These animals cannot obtain this level of intake on stockpiled forage due to physical constraints of the rumen from high NDF. Furthermore, the high passage rate of digesta reduces the amount of microbial cell wall digestion and potential energy is lost to the animal. Therefore stockpiled forage should not be fed to high producing dairy cows as the main source of forage.

Conclusions

Stockpiling forage in late summer until the end of the growing season is an effective way to extend grazing while providing adequate-quality forage for many classes of livestock. Maintaining animal body condition is dependent on energy and protein content of the forage assuming intake is not limited.

Quality of stockpiled forage in Wisconsin decreased over winter but remained at adequate levels for several classes of livestock such as beef cows, dry dairy cows and sheep. In vitro organic matter digestibility remained high over winter at levels near 700 g kg^{-1}. Quality of reed canarygrass decreases rapidly in late autumn with more accelerated increases in fiber and higher losses in IVOMD than any other species. Therefore, reed canarygrass should be utilized early if maximum quality is the goal. Otherwise, reed

canarygrass should be allocated to the lowest maintenance group. Both orchardgrass varieties are excellent choices for stockpiling due to a relatively high CP and IVDOM throughout winter. Tall fescue and timothy would require the most protein supplementation, both maintaining the lowest level of CP while smooth bromegrass and quackgrass continued to be highest in CP. Addition of N generally improved CP concentration but did not affect digestibility or fiber levels.

Any of the 7 stockpiled grasses have adequate quality for animal classes with low nutrient requirements such as dry beef cows and sheep. However, animals with higher nutrient requirements will require protein and energy supplementation beyond December. Stockpiled forage should not be fed to lactating dairy cows as the sole source of forage as the fiber

Table 10. Mean in vitro organic matter digestibility of 7 stockpiled grasses on 2 N treatments at Arlington, Marshfield, and Lancaster, Wisc. Means are averaged over 3 offseason harvest dates, 2 years and 4 replicates

		N treatment[1]	
Location	Species	No N	N
		--(g kg^{-1}) --	
Arlington			
	Orchardgrass, late	729	727
	Orchardgrass early	719	714
	Quackgrass	683	684
	Reed canarygrass	670	662
	Smooth bromegrass	693	729
	Tall fescue	706	708
	Timothy	740	744
	LSD (0.05)[2]	14	14
	Mean	706	710
Marshfield			
	Orchardgrass, late	712	724
	Orchardgrass, early	726	711
	Quackgrass	645	675
	Reed canarygrass	647	657
	Smooth bromegrass	680	707
	Tall fescue	720	726
	Timothy	717	723
	LSD (0.05)[2]	14	14
	Mean	693	703
Lancaster			
	Orchardgrass, late	716	712
	Orchardgrass, early	705	695
	Quackgrass	670	662
	Reed canarygrass	663	665
	Smooth bromegrass	702	710
	Tall fescue	693	697
	Timothy	714	695
	LSD (0.05)[2]	15	15
	Mean	695	691

[1]The 3-added-N treatments were not different and have been averaged.
[2]LSD for location-fertility mean over species is 6 at all sites.

Table 11. Estimates of additional energy requirements for different classes of cattle in environments below their lower critical temperatures.[1]

Class of livestock	Additional energy required					
	°C			°C		
	−10	−20	−30	−10	−20	−30
	- - (Mcal ME day^{-1}) - -			- - (kg grain day^{-1}[2]) - -		
Beef						
Adult, lactating (500) kg						
dry, low wind	0	0	2.97	0	0	0.9
no shelter, 10 mph wind	0	0	5.70	0	0	1.7
Adult, Dry (500 kg)						
dry, low wind	0	0	5.34	0	0	1.6
no shelter	1.07	7.08	12.69	0.3	2.1	3.7
6-month old steer or heifer (100 kg)						
dry, low wind	0	0.42	1.82	0	0.1	0.5
no shelter, 10 mph wind	5.57	8.37	11.17	1.6	2.4	3.2
Yearling steer or heifer (300 kg)						
dry, low wind	0	0	0	0	0	0
no shelter, 10 mph wind	0.25	5.25	10.25	0.1	1.5	3.0
Newborn (40 kg)						
dry, low wind	3.30	5.17	7.04	—	—	—
Dairy						
Dry (650 kg)						
dry, low wind	0	3.48	9.28	0.	1.0	2.7
no shelter, 10 mph wind	9.86	18.15	26.43	2.9	5.3	7.7
Yearling steer or heifer (250 kg)						
dry, low wind	1.32	5.70	10.08	0.3	1.7	2.9
no shelter, 10 mph wind	7.98	13.68	19.38	2.3	4.0	5.6

[1]Adapted from NRC 1981. Lower critical temperature of the animal is at which point basal heat production is not enough to maintain homeothermy.
[2]Grain refers to cracked corn with 3.44 Mcal ME kg^{-1} DM.

concentration will limit intake and therefore energy.

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Soil erosion as affected by shrub encroachment in north-eastern Patagonia.

BERNARDO PARIZEK, CESAR M. ROSTAGNO, AND ROBERTO SOTTINI

Authors are Range Ecologist, Vector Argentina S.A, Mendoza, Argentina, (at time of the research B. Parizek was a Research Assistant, Universidad Nacional de la Patagonia SJB, Puerto Madryn), Soil Scientist, Centro Nacional Patagónico, CONICET, Bvard. Brown s/n, 9120, Puerto Madryn, Chubut, Argentina, and Hydrologist, Instituto Nacional de Limnología, CONICET, J. Maciá 1933, 3016 Santo Tomé, Santa Fe, Argentina.

Abstract

Soil erosion is the primary cause of irreversible loss of soil productivity on most rangelands. In northeastern Patagonia, the increase in soil erosion has been closely associated with the increase in shrub cover in the grass or shrub-grass steppes. We used rainfall simulation to compare infiltration and sediment production from patches of grass, shrub-grass, and shrub steppes of the Punta Ninfas range site. Bare soil and gravel covers were higher and litter cover was lower in the shrub steppe than in the shrub-grass and the grass steppes. In the shrub inter-spaces of the shrub steppe, bulk density was greater and macroporosity and soil organic matter were lower (P ≤ 0.05) than in the mounds beneath shrubs and in the grass and shrub-grass areas. Infiltration rate was 60 to 65% lower in the shrub steppe than in the grass and shrub-grass steppes, respectively. On the contrary, total sediment production and concentration were higher (P ≤ 0.05) in the shrub steppe as compared to the grass and the shrub-grass areas. Gravel cover was the variable that best predicted infiltration and sediment production. The organic matter content of the sediment, mostly litter, in the shrub and the shrub-grass steppes were similar and greater (P ≤ 0.05) than in the grass steppe. Runoff litter removal may represent one of the processes that drive the transition from shrub-grass to shrub steppes. High rates of sediment removal, mainly litter, from the shrub interspaces of the shrub steppe may limit the natural recovery of the soil physical and hydrological properties. These degraded patches fail to capture incident rainfall and restrict the possibilities for the recovery of perennial grasses favoring the dominance of shrubs.

Key Words: vegetation, litter, gravel cover; shrub, grass, shrub-grass steppes, organic matter removal, rainfall simulator, infiltration rate.

Shrub encroachment and soil erosion have been identified as the main degradation processes in semi-arid grazing rangelands (Friedel 1991). Both processes can be closely related and in general erosion follows shrub invasion (Buffington and Herbel 1965). Schlesinger et al. (1990) suggest that overgrazing results

Resumen

La erosión de los suelos es la causa principal de las pérdidas irreversibles del potencial productivo de los suelos en la mayoría de los pastizales naturales. En el nordeste de Patagonia, el aumento de la erosión de los suelos ha estado estrechamente asociado al aumento de la cobertura de arbustos en las estepas herbáceas o arbustivas-herbáceas. Nosotros empleamos lluvia simulada para determinar la tasa de infiltración y la producción de sedimentos en parches de estepas herbáceas, arbustivas-herbáceas y arbustivas del sitio ecológico Punta Ninfas. Las coberturas de suelo desnudo y de gravas fueron mayores y la cobertura de mantillo menor en la estepa arbustiva respecto a las estepas arbustiva- herbácea y herbácea. En los espacios entre arbustos de la estepa arbustiva, la densidad aparente fue mayor y la macroporosidad y la materia orgánica fueron menores (P ≤ 0.05) que en los montículos debajo de los arbustos y en las estepas arbustiva-herbácea y herbácea. La tasa de infiltración fue un 60 y un 65% mas baja en la estepa arbustiva que en las estepas herbácea y arbustiva-herbácea, respectivamente. Por el contrario, la producción total y la concentración de sedimentos fueron mas altas (P ≤ 0.05) en la estepa arbustiva comparado con las estepas herbácea y arbustiva-herbácea. La cobertura de gravas fue la variable que mejor predijo la tasa de infiltración y la producción de sedimentos. El contenido de materia orgánica de los sedimentos, mayormente mantillo, fue similar en la estepa arbustiva y la arbustiva-herbácea y en ambas mayores (P ≤ 0.05) que en la estepa herbácea. La remoción de mantillo por el escurrimiento superficial posiblemente represente uno de los procesos que provocan la transición de la estepa arbustiva-herbácea a la estepa arbustiva. Las altas tasas de remoción de sedimentos, principalmente mantillo, de los espacios entre arbustos de la estepa arbustiva pueden limitar la recuperación natural de las propiedades físicas e hidrológicas de los suelos. Estos parches degradados no pueden captar las lluvias incidentes, limitando así las posibilidades de recuperación de los pastos perennes y favoreciendo la dominancia de los arbustos.

in the redistribution of organic matter and nutrients and is the primary agent responsible for the current conversion of previously productive grasslands to unproductive mesquite (*Prosopis glandulosa* Torr.) shrublands.

In most of the Patagonian rangelands, grazing appears to have modified the vegetation and accelerated soil erosion processes (Soriano et al. 1983, Ares et al. 1990). Changes in vegetation include the increase of low forage quality shrub species such as neneo (*Mulinum spinosum* (Cav.) Pers.) and quilenbai (*Chuquiraga avellanedae* Cav.) (Bertiller 1993, Beeskow et al. 1995) in some originally productive grassslands.

In a range site of northeastern Patagonia, Beeskow et al. (1995) identified 3 stable states following the state and transition model proposed by Westoby et al. (1989). These states represent stable plant communities along a degradation gradient, with grass, shrub-grass, and shrub steppes representing a good, fair, and poor condition from a forage production perspective. However, no information exists on how well these plant communities protect the site against accelerated erosion. Recently, the Task Group on Unity in Concepts and Terminology (1995) proposed the concept of Desired Plant Community. The Desired Plant Community refers to any managed plant community that has the capability to protect the site against accelerated erosion. In this study we used rainfall simulation to assess how different plant communities on a range site of northeastern Patagonia influenced infiltration and interrill erosion.

Materials and Methods

Study Area

The study was conducted in the upper part of a flank pediment that extends from the plateau border to a playa lake in the Punta Ninfas area, 70 km east of Puerto Madryn in the NE portion of the Chubut province (43:00'S, 64:30'W) (Fig. 1). It is an undulating plateau dissected by coastal valleys and interrupted by numerous depressions with playa lakes. The climate is arid and temperate. Mean annual precipitation is 254 mm (1955–1992). Most of the rainfall occurs during the cold season from April to September. Mean annual temperature is 12.5°C. The mean annual wind velocity at 10 m above ground level is 4.6 m sec^{-1} (Barros 1983). Dominant soil in the flank pediment area is a Xeric Calciargids. This soil is shallow, with a loamy sand A horizon 10–15 cm thick, and a sandy loam B2t horizon 15–20 cm thick, underlain by a calcic horizon. A gravelly sand to sandy clay alluvium 50 to 80 cm thick forms the soil substratum. This deposit of Holocene age rests on tertiary sediments.

Southern extreme of South America with Argentina and the Chubut province.

Fig. 1. Location of the study area.

The study area is located in the ecotone between the Patagonian and Monte phytogeographic provinces. Principal species representing the first province are quilenbai and colapiche (*Nassauvia fuegiana* (Speg.) Cabrera), and coiron (*Stipa speciosa* Trin. and Rupr.). The cool season grasses flechilla (*S. tenuis* Phil.) and flechilla negra (*Piptochaetium napostaense* (Speg. Hackel ap Stuckert.)) are the main species of the Monte province.

Dominant plant physiognomy is a shrub-grass steppe although patches of grass steppe and shrub steppe are present. These physiognomic patches have been described as stable states (Beeskow et al. 1995). Within the grass and grass-shrub steppe patches a stable soil is present; in the shrub steppe, shrubs are associated with mounds and are distributed in a matrix of eroded soil with desert pavement and a low vegetation cover.

Sheep grazing for wool production was introduced in the area at the beginning of the last century. Continuous grazing is practiced extensively in pastures exceeding 2,500 ha. The mean stocking rate is 0.25 sheep ha^{-1}.

Experimental Procedures

We selected 3 homogeneous areas, 10 x 10 m each representing, the grass, shrub-grass, and shrub steppes. Inside these areas, 10 plots measuring 0.63 x 1.60 m (1 m^{-2}) were located in each plant community. Slope was homogeneous across the 3 areas with an average of 7.2%. Sheet metal frames were dug into the perimeter of the plots to channel the runoff generated by the simulated rainfall. Runoff leaving the lower border of the plots was channeled through a 5 cm diameter pipe connected to 5 liter containers. In December of 1994 and 1995, simulated rainfall was applied with a full cone, single nozzle rainfall simulator (Rostagno and Garayzar 1995) at an intensity of 100 mm hour^{-1}, during 30 minutes. This rainfall simulator produces a rainfall with a kinetic energy equivalent to 66% of the kinetic energy of a natural rainfall at the same intensity. In the study area, high intensity rainfall can occur from December to March. A rainfall event with the intensity and duration of the simulated rainfall occurs about once per 100 years (Vicenty et al. 1984). Runoff was collected at 1 and 2 minutes after rainfall initiation, and then at 5 minutes intervals in separate containers and determined by volume. Time to runoff was recorded for each plot. Infiltration rate was calculated for each interval as the difference between the applied rainfall and the runoff collected for each interval. Total runoff was passed through a 44 μm sieve. The sediment coarser than 44 μm was recovered dried at 105° C for 24 hours and weighed. The weight of the sediment < 44 μm was calculated using 50 ml aliquot. After drying and weighing, the total sediment <44 μm was calculated considering total runoff volume, then it was added to the > μ4 mm sediment and converted to kg ha^{-1}.

Previous to simulated rainfall application, ground cover (vegetation, litter, bare soil, and gravel) was determined using the point quadrat method (Goodall 1953). A metal frame with holes every 5 cm was placed on the plot and 66 points were measured in each plot. The slope of the plots was determined using the same frame as for ground cover.

A 130 cm^{-3} soil core (0 to 5 cm) was sampled for bulk density, root, and gravel content determinations from an area adja-

cent to each plot. Roots were separated by hand, washed, dried at 105° C and weighed; gravel was separated with a 2 μm sieve. Soil samples from this same depth were collected and analyzed for texture by the pipette method (Day 1965), and organic matter by the loss on ignition method (Davies 1974). Total porosity was calculated as: (1-bulk density/particle density) considering a particle density of 2.65 g cm^{-3} and macroporosity as the difference between water content at saturation and at field capacity (Helalia 1993). Field capacity (moisture equivalent) was estimated by centrifuging saturated samples (30 min; 2440 rpm).

Data Analysis

Data were analyzed using correlation (Pearson) to assess the linear association of the variables and stepwise multiple regression to identify the variables that best predicted infiltration and sediment production. Analyses of variance were performed on the terminal infiltration and sediment (mineral and organic) production data using the SPSS package. Mean separation with the protected LSD was used to compare infiltration and sediment production in each plant community. Significant levels were determined at $P \leq 0.05$.

Results and Discussion

Surface characteristics

Soil surface characteristics and plant cover for each plant community are presented in Table 1. Total vegetation cover presented the highest value in the shrub-grass steppe and the lowest in the shrub steppe, respectively. In the shrub steppe, the main changes relative to the shrub-grass community were decreased litter and herbaceous vegetation cover and increased gravel cover. In the shrub steppe where erosion has been more intense than in the other plant communities, the A horizon remaining beneath the shrubs as well as the accumulation of wind blown and splashed material give rise to small mounds associated with the shrubs, mainly quilenbai. However, the increase in bare soil cover in the shrub steppe was less than 2% compared to the grass steppe.

Soil characteristics of the grass and the shrub-grass steppes were similar and differed greatly with those of the shrub steppe (Table 2). The 2 contrasting surface conditions present in the shrub steppe (mounds beneath the shrubs and desert pavement covered areas in the shrub interspaces) were also different in term of soil characteristics. Sand, organic matter, and root content were significantly lower; gravel and bulk density were higher in the eroded shrub interspaces of the shrub

Table 1. Average canopy and ground cover (%) characteristics (standard deviation) for each plant community at the Punta Ninfas range site, Patagonia.

	Grass Steppe	Shrub-Grass Steppe	Shrub Steppe
	----------------------------------- (%) -----------------------------------		
Shrubs	0	23.0 (10.8)	28.4 (9.8)
Perennial Grasses	24.4 (1.1)	19.0 (8.4)	5.6 (4.4)
Perennial Dicot	7.4 (3.5)	1.8 (1.2)	0.2 (0.4)
Annuals	12.8 (3.0)	11.4 (8.1)	3.8 (1.3)
Bare Soil	18.8 (2.9)	15.2 (5.0)	20.6 (6.6)
Gravel	11.8 (1.9)	11.6 (3.4)	32.8 (12.8)
Litter	24.0 (3.7)	16.9 (5.7)	6.4 (4.4)

Table 2. Average soil characteristics (standard deviation), 0 to 5 cm soil depth, for each plant community and 2 microsites in the shrub steppe at the Punta Ninfas range site, Patagonia.

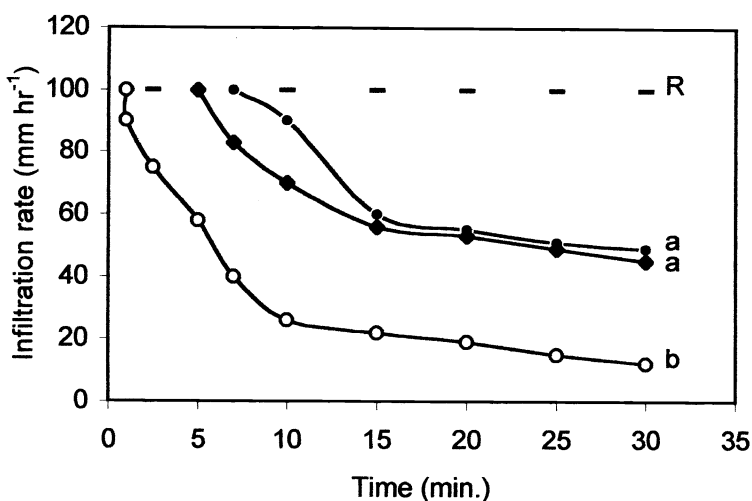|	Grass Steppe	Shrub-Grass Steppe	Shrub Steppe	
	Steppe	Steppe	SI	Mounds
Bulk Density (Mg m^{-3})	1.06 (0.07)	1.10 (0.11)	1.36 (0.15)	1.07 (0.05)
Macroporosity (%)	31.9 (1.2)	30.1 (3.2)	17.1 (2.3)	33.1 (1.8)
Gravel Content (%)	17.4 (9.2)	17.1 (8.4)	31.7 (14.5)	5.3 (3.6)
Sand (%)	73.0 (3.8)	75.0 (5.1)	61.2 (6.4)	83.1 (2.9)
Root Content (g m^{-2})	145.6 (31.1)	134.2 (28.6)	20.3 (9.3)	380.0 (83.0)
Organic matter (%)	2.49 (0.29)	2.67 (0.36)	1.46 (0.19)	2.23 (0.31)

SI= shrub interspaces

Fig. 2. Average infiltration rate across the 30 minute simulated rainfall for the soils of the shrub-grass (●), grass (◆), and shrub (○) steppes at Punta Ninfas range site, Patagonia. R is applied rainfall intensity. Plant community means with the same letter are not significantly different (P ≥ 0.05).

steppe as compared to the soil of the other plant communities. These differences were greater with respect to the soils beneath the shrubs (mounds) of the shrub steppe.

Infiltration Characteristics

Infiltration curves for each plant community are presented in Fig. 2. In the grass and the shrub-grass communities, runoff started at 5 and 7 min after rainfall initiation, respectively. This difference can be a result of the higher water interception/retention of the shrub canopy in the shrub-grass community. In these communities, the infiltration curves were similar after 15 min of the rainfall initiation. In the shrub steppe, runoff started at less than 1 min after rainfall initiation. In this plant community, the infiltration rate decreased abruptly the first 10 min; after which it decreased more slowly until the end of the simulated rainfall.

Terminal infiltration rate in the grass and shrub-grass steppes were similar and significantly higher than in the shrub steppe. Stepwise regression analysis using the variables presented in Table 1 as independent variables, gave us the following predictive model for infiltration rate (IR) at 30 min:

IR = 39.4 - 0.79 Gravel cover + 1.33 Annuals; $R^2 = 0.69$ (P = 0.001)   (1)

Our results produced a negative relationship between gravel cover and infiltration rate (r = -0.74). Similar results were found in a degraded shrub steppe with a Typic Torriorthent soil (Rostagno 1989). However, field-plot data on the relationship between coarse fragments cover and

runoff (or infiltration rate) are contradictory (Poesen 1992). Mehan (1986) showed that coarse fragments on the soil surface of rangelands tended to increase infiltration rates. It appears that as more soil surface was exposed, more of the soil surface develops a crust thus reducing infiltration rates.

In our study, gravel cover integrated soil and soil surface characteristics which were considered to negatively affect the soil infiltrability. Thus, in the shrub interspaces of the shrub steppe, where the higher gravel cover was found, gravel is well embedded in a surface crust. Valentin (1994) found a reduction in infiltration rate with increasing cover of embedded rock fragments. Equally, the shrub interspace soil presents a higher bulk density (Table 2) as compared to the soils of the shrub-grass and the grass communities as well as the mound soils. The increase in bulk density of the shrub-interspace soil of the shrub steppe represents a proportional decrease in macroporosity (Table 2). Because of their texture (loamy sand and sandy loam), the soils of the study area are susceptible to crust formation (Poesen 1988). However, a crust develops only in the shrub interspaces of the shrub steppe, probably related to the low organic matter content and low litter and grass cover of this soil.

The cover of annual plants was selected as the second variable of importance by the regression analysis. Annual cover was negatively related to gravel cover (r = -0.56) and integrated other soil surface variables considered to positively affect

the soil infiltration (i.e., perennial grass and litter cover).

To assess the differences in infiltration capacity of the degraded soils of the shrub interspaces and the mounds beneath shrubs in the shrub steppe, we determined their infiltration capacity separately by means of 15 cm diameter cylinders. Average (and standard deviation) infiltration rates for the first 10 minutes were 8.3 (3.5) and 175 (14.0) mm hour[-1] for the shrub interspace and the mound, respectively. In the grass steppe the average infiltration rate was 103.7 (22.0) mm hour[-1]. Although measurements of infiltration capacity using cylinder infiltrometers tend to exceed the true (vertical) infiltration capacity (Tricker 1978), our results show the large hydrological contrast between the crusted soil of the shrub interspaces and the mounds. It is interesting to notice that the infiltration rate of the soil beneath the shrub (mound) was also significantly higher than in the soil of the grass steppe. Thus, although the quilenbai positively affected the infiltrability of the soil under its canopy, the patches where quilenbai is dominant had the lowest infiltration.

Sediment Production

Sediment production in the grass and the shrub-grass steppes were similar and significantly lower than in the shrub steppe (Fig. 3). In the shrub steppe the sediment concentration was also significantly higher than in the other communities. Sediment concentration may provide a better measure of the erodibility of each soil surface condition. However, sediment concentration was low, 2.4, 1.7, and 1.8 g liter[-1] for the shrub, shrub-grass, and grass steppes, respectively. Sediment concentrations as high as 40 g liter[-1] were recorded in a shrub steppe with a Typic Torriorthent soil with a natural rainfall event (Rostagno et al. 1999). The low bare soil cover in the grass, shrub grass, and shrub steppes (<21%) and the low kinetic energy of the simulated rainfall (66% of a natural rainfall event of the same intensity) may have limited sediment detachment by raindrop impact.

Stepwise regression analysis using the variables presented in Table 1 as predictors produced the following predictive model for sediment production (SP): SP (g m^{-2}) = 11.6 + 3.0 Gravel cover (%); $R^2 = 0.46$ (P = 0.005), indicating that sediment production increased as gravel cover increased. This result is apparently contradictory, as gravel cover has been shown to decrease interrill erosion in most cases
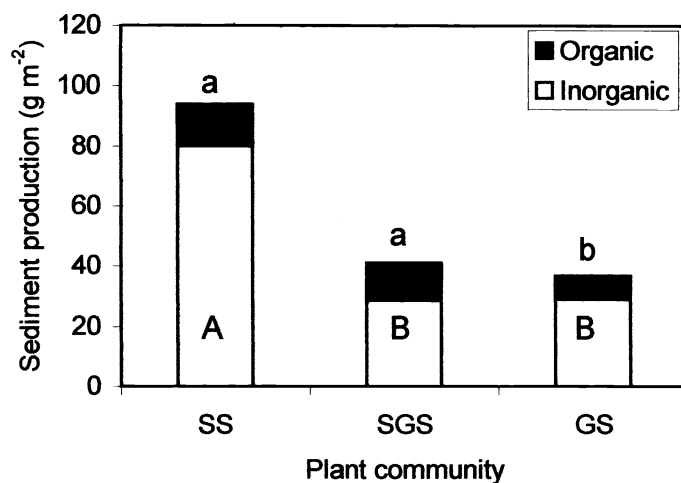
Fig. 3. Inorganic and organic sediment production for the shrub, shrub-grass, and grass steppes at the Punta Ninfas range site, Patagonia. Plant community means with the same lowercase and uppercase letters are not significantly different (P ≥ 0.05) for the organic and inorganic sediment production, respectively.

(Poesen et al. 1994). In the study area, gravel cover was negatively associated to herbaceous vegetation (r = –0.61) and litter cover (r = –0.68). The highest value of gravel cover was present in the shrub interspaces of the shrub steppe where a soil surface condition of low infiltrability and high runoff production dominates. Although gravel cover may decrease sediment production, it seems to be less effective than vegetal (Wilcox and Wood 1989) and litter cover (Benkobi et al. 1993) to protect the soil from erosion. For example, Benkobi et al. (1993) found that the litter and gravel cover necessary to reduce soil loss to 50% of bare ground was 60% and 85%, respectively. While both gravel and litter decrease sediment detachment by raindrop impact proportional to their cover, litter more effectively absorbs the erosive and transport energies of overland flow, reducing flow velocities, and increasing deposition.

Sediment Organic Matter Content

The organic matter content of the sediment was significantly higher in shrub and in the shrub-grass communities than in the grass community (Fig. 3). Although a high proportion of organic matter in the sediment was plant residues, organic matter content in the sediment was inversely proportional to litter cover. In the shrub steppe where litter cover was much lower than in the other plant communities, the high amount of runoff generated in this community may explain the higher amount of organic matter in the sediment. The decrease in litter cover following the decrease of grass cover may increase the

erodibility of these soils. In the grass community, litter cover accounted for 26% of the ground cover and decreased to 6.4% in the shrub steppe. Decline in the production of litter because of the low herbaceous cover in the shrub interspaces and the high potential for litter removal by runoff from these areas may increase the hydrological and physical differences between the communities. In the shrub steppe, the litter produced by shrubs (leaves, twigs, and inflorescence) accumulates beneath the shrubs and very little, if any, is spread beyond the shrub canopy. This decrease in vegetation and litter cover in the shrub steppe is reflected in the lower organic matter content of the shrub interspace soil (Table 2). A mechanism by which litter may enter the shrub interspaces of the shrub steppe is the deposition of litter carried by runoff generated from the surrounding grass or shrub-grass communities. In the shrub-grass steppe, the sediment organic matter content was also higher than in the grass steppe, and proportionally higher (percent of mineral sediment) than in the shrub steppe.

Shrub Encroachment, Soil Erosion, and Sustainable Production

Although the main cause of the decline in herbaceous vegetation producing the change from shrub-grass to shrub steppes in shrub invaded areas (i.e., shrub competition, intense grazing, etc.) is not clear, it is clear that past erosion in the shrub steppe has changed the characteristics of the soil and the distribution of soil resources. The positive feedback between past erosion and present erosion rate may

further increase the differences between the grass or grass-shrub and the shrub-dominated communities. This will also tend to increase the contrast between soils beneath shrubs and the soils of the shrub interspaces. Schlesinger et al. (1990) considered the increase in soil heterogeneity in shrub invaded areas as an indicator of rangeland degradation.

It is important to notice that differences in total plant cover between the grass and shrub steppes were small (i.e., < 5%). It seems that more important than total plant cover as causative factor in interrill as well as rill erosion, is plant cover distribution (Weltz et al. 1998). Thus, while in the grass steppe plant cover was homogeneously distributed, in the shrub steppe it was concentrated in small patches. Plant cover distribution determines the size of the patches of bare soil (or of gravel covered and crusted soil). De Soyza et al. (1998) defined a bare patch index (bpi = mean size of bare patches x proportion of bare soil) as a desertification indicator for the Chihuahuan Desert. They found that sites with high percentage of shrubs and sites near livestock watering points had the greatest bare patch index.

Equally important is the connection among bare patches. In the shrub steppe, the degraded shrub interspaces connect each other allowing the runoff to leave the local plant community (i.e., the shrub steppe patch) and eventually the range site. Under present land use (i.e., continuous grazing) an increase in the size and numbers of shrub steppe patches (degraded patches) can be expected, as shrubs are little affected by grazing. The grass steppe can be considered the Desired Plant Community (Task Group on Unity in Concept and Terminology 1995) for the site as it best meets forage production objectives. However, both, the grass and the shrub-grass steppes have the capability to protect the site against accelerated erosion.

In this range site where erosion dramatically changes the hydrological properties of the soil, the application of shrub control techniques (i.e. prescribed fire) that effectively help to restore the grass cover should be applied in the first stages of shrub invasion (i.e., in the shrub-grass steppe state). In areas close to the study site accidental fires have temporarily reversed shrub-dominated communities back to grass steppes. It is also probable that a grazing scheme that includes spring rest might favor perennial grasses in the shrub-grass steppes, slowing or reversing shrub cover increase. Bork et al. (1998) found in a sagebrush steppe that grazing

during the spring increased live shrubs and decreased perennial grasses cover as compared to a fall-grazed treatment. In the shrub steppe where degradation has severely affected the soil characteristics, it is less probable that herbaceous vegetation cover may be restored and sustainable management be achieved, unless a technique of water conservation is applied. However, because of drastic changes in soil properties, this plant community may persist and represent a different ecological site.

Conclusions

Soil surface characteristics as well as soil infiltrability and sediment production differed significantly in shrub dominated and grass or grass-shrub dominated plant communities on the same range site. In the Punta Ninfas range site, a continuous grass cover may coexist with a shrub cover of approximately 25%. Although the shrub-grass steppe is undesirable from a forage production perspective because the main shrubs have a very low forage value, soil conservation is not different from the grass steppe. On the contrary, the shrub-dominated community represents a poor condition from a forage production and a soil and water conservation perspective. Although the development of a dense desert pavement in the eroded shrub interspaces of the shrub steppe may limit sediment detachment, and thus, sediment production, the high runoff production from these areas keep the erosion rate of the shrub steppe above the erosion rates of the other communities.

The high rate of organic matter (mainly litter) and water losses from the shrub steppe may limit the natural recovery of the soil physical and hydrological properties and the possibilities for the re-establishement of the perennial grasses, and favor the dominance of shrubs.

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Seasonal grazing affects soil physical properties of a montane riparian community

MELINDA A. WHEELER, M.J. TRLICA, GARY W. FRASIER AND J.D. REEDER

Authors are former Graduate Research Assistant and Professor, Rangeland Ecosystem Science, Colorado State University, Fort Collins, Colo. 80523, and Research Scientists, respectively, USDA-ARS, Crops Research Laboratory, 1701 Center Street, Fort Collins, Colo., 80526.

Abstract

The effects of seasonal grazing treatments (early spring and late summer) on soil physical properties were studied in a montane riparian ecosystem in northern Colorado. Infiltration rates and bulk density were used as primary indicators of responses to a 1-time heavy grazing event on previously protected paddocks. Soil bulk density, porosity, gravimetric water content, organic carbon concentration and texture were measured at 0–5 cm, 5–10 cm, and 10–15 cm depths to determine how these parameters affected infiltration rates. Assessment of initial changes and subsequent recovery of the soil properties in response to the grazing treatments was conducted by measuring these parameters before each grazing event and at 4 time periods following the grazing event. Few differences between spring or late summer grazing periods on soil physical properties were found. A stepwise multiple regression model for infiltration rate based on soil physical properties yielded a low R^2 (0.31), which indicated much unexplained variability in infiltration. However, infiltration rates declined significantly and bulk density increased at the 5–10 cm depth and 10–15 cm depth in grazed plots immediately following grazing, but the highly organic surface layer (0–5 cm) had no significant compaction. Infiltration rates and soil bulk densities returned to pre-disturbed values within 1 year after grazing events, suggesting full hydrologic recovery. This recovery may be related to frequent freeze-thaw events and high organic matter in soils.

Key Words: Compaction, infiltration, soil bulk density, porosity, recovery

Use of mountainous riparian zones has been under increased scrutiny because of heightened awareness of their economical and ecological importance, as well as increased multiple use conflicts (Johnson et al. 1985). Improper management of many riparian areas has resulted in degradation of habitat for fish, wildlife and vegetation (Armour et al. 1994). Chaney et al. (1990) indicated that most of the degradation has been caused by improper cattle management. Livestock grazing in Western riparian zones has

Resumen

Se estudiaron los efectos de tratamientos de apacentamiento estacional (inicios de primavera y fines del verano) en las propiedades físicas del suelo de un ecosistema ribereño montano del norte de Colorado. Las tasas de infiltración y densidad aparente se utilizaron como indicadores principales de la respuesta a un evento de apacentamiento fuerte realizado una vez en potreros previamente protegidos. La densidad parente del suelo, la porosidad, el contenido gravimétrico de agua , la concentración de carbón orgánico y la textura se midieron a profundidades de 0–5 cm, 5–10 cm y 10–15 cm para determinar como estos parámetros afectaron las tasas de infiltración. La evaluación de los cambios iniciales y la recuperación subsecuente de las propiedades del suelo en respuesta a los tratamientos de apacentamiento se condujo midiendo estos parámetros antes y después de cada evento de apacentamiento y en 4 periodos de tiempo después del evento de apacentamiento. Se encontraron pocas diferencias en las propiedades del suelo entre los periodos de apacentamiento de primavera y finales verano. El modelo de regresión múltiple para la tasa de infiltración, basado en las propiedades físicas del suelo, produjo una R^2 baja (0.31), la cual indico mucha de la variabilidad inexplicada en la infiltración. Sin embargo, inmediatamente después del apacentamiento, en las parcelas apacentadas, las tasas de infiltración disminuyeron significativamente y la densidad aparente se incrementó en las profundidades de 5–10 cm y 10–15 cm, pero la capa superficial altamente orgánica (0–5 cm) no tuvo una compactación significativa. Las tasas de infiltración y la densidad aparente regresaron a los valores pre-disturbio dentro de un año después de los eventos de apacentamiento, sugiriendo una recuperación hidrológica total. Esta recuperación puede estar relacionada a los frecuentes eventos de congelación-descongelación y al alto contenido de materia orgánica de los suelos.

led to degradation of soil physical characteristics (Clary 1995), which in turn can lead to altered hydrologic properties (Bryant et al. 1972), increased sediment production (Warren et al. 1986b), and a decline in vegetation productivity and vigor (Dadkhah and Gifford 1980, Leininger and Trlica 1986).

Although some literature is available on the effects of cattle trampling on soil compaction and infiltration for upland rangelands (Warren et al. 1986a,1986b, Abdel-Magid et al. 1987a, 1987b), riparian soils generally possess more organic matter than upland soils and may therefore react differently to grazing. Little

quantitative information is available describing how soils and infiltration in riparian areas respond to activities in different seasons (Tierney 1992), or on how quickly soils recover from changes that result from grazing livestock (Bohn and Buckhouse 1985, Warren et al. 1986b, Tierney 1992, Clary 1995). Specifically, timing of grazing and length of rest periods have been indicated as areas where further investigation is needed to help determine best management practices (Gifford and Hawkins 1978, Warren et al. 1986a). A major concern is how season of grazing, with variations in soil conditions, can affect water infiltration. If infiltration is adversely affected, consequences may include altered groundwater recharge (Gifford and Hawkins 1978), increased surface runoff and evaporation (Gamougoun et al. 1984), and reduced vegetation production and vigor (Leininger and Trlica 1986).

The objectives of this study were to determine how cattle grazing during different seasons might affect hydrological and physical characteristics of riparian soils. Knowledge gained should help to develop strategies to reduce grazing impacts and provide additional information as to the time required for riparian soils to recover from previous grazing. If recovery rates of soil properties after grazing are known, then better management techniques for these areas might be developed to reduce physical impacts that large animals have on these riparian ecosystems.

Methods and Materials

Study Location and Site Description

The study area was along Sheep Creek, a C1 stream (Rosgen 1994) that is located 80 km northwest of Fort Collins, Colo. The area is within the Roosevelt National Forest at an approximate elevation of 2,500 m. The area had been severely overgrazed in the early part of the century, and was excluded from livestock grazing in 1956 by the Forest Service for resource recovery as well as research reasons. The major soil in the study area is a Fluvaquent, located in flood plains, low terraces and bottom lands in the area. The water table is commonly at a depth of less than 30 cm immediately following the spring melt. Gravimetric water content was often greater than 100% at the study site. The texture of the surface and underlying layers are extremely variable as a result of repeated flooding and range from sandy loam to clay loam. The soil profile

is commonly stratified with thin layers of sand or clay. There was often a highly organic peat layer over 20 cm thick in sedge riparian communities. The vegetation community consisted of willows (primarily *Salix planifolia,* Pursh) that dominated the overstory, with Kentucky bluegrass (*Poa pratensis,* L.) water sedge (*Carex aquatilus,* Wahlenberg), beaked sedge (*Carex rostrata,* Boott), tufted hairgrass (*Deschampsia caespitosa,* (L)) and dandelion (*Taraxacum officinale,* G.H. Weber) as major components of the herbacious understory (Schulz and Leininger 1990, Popolizio et al. 1994). Similar riparian areas have been described in Montana (Marcuson, 1977), Oregon (Roath and Kruger 1982), Utah (Platts and Nelson 1989), and Wyoming (Costello 1944).

Experimental Design

A randomized complete block design with a factorial arrangement of treatments was used. Treatments involved 2 grazing strategies (grazed and control) and 2 seasons of grazing (early spring and late summer). Three replicated plots (paddocks) approximately 1/4 ha in size for each grazing treatment and season of grazing were selected for similar traits of aspect, slope, vegetation community composition and soil type. The treatments were randomly applied to paddocks in a one-time, seasonal heavy grazing event where 60 to 75% of the herbacious vegetation was utilized (Pelster et al. 1996). Three ungrazed paddocks within the study area were used as a control. Six steers were put on the spring grazed plots beginning 30 June 1995, and grazing began on 8 September 1995 for summer grazed plots. The steers grazed in the plots for 4 to 5 days to reach the desired level of utilization.

Three random samples of soil bulk density were obtained and infiltration rates measured along 12 m transects within each of the 4 treatment combinations. Treatments were repeatedly sampled for 5 sampling periods (immediately before grazing, immediately after grazing, 2 weeks after grazing, 4 weeks after grazing, and 1 year after grazing).

Data were statistically analyzed with SAS programs (SAS 1996). Two analysis of variance (ANOVA) tests were used to determine if differences ($p < 0.10$) existed among grazing strategies, seasons of grazing, and repeated sample collections through time and all of their interactions. Soil bulk density and infiltration rates were the response variables. Data for the first time period were used as a covariate in an ANOVA model for infiltration and

adjusted for the variability in initial conditions of the study because the first sample period before grazing began could not be included in the model as a grazing treatment effect. The use of the first time period as a covariate for the ANOVA model for bulk density was not appropriate because a significant time of sampling x grazing treatment interaction existed. Additionally, to determine immediate effects of grazing, an ANOVA was conducted to determine if differences existed for infiltration rates and bulk density between pre-grazed conditions and immediately after grazing. An ANOVA was also used to determine if differences were evident in infiltration rates and bulk density between pre-grazed conditions and soil conditions 1 year later to ascertain whether recovery occurred.

Stepwise multiple regression analyses were performed to determine if some easily measured soil physical properties might be used as predictors for changes in bulk density and infiltration rates. These properties included gravimetric water content, organic carbon concentration, soil texture, and time of sampling as possible predictors for bulk density. These same properties at 3 soil depths, plus bulk density and porosity were used as possible predictors for infiltration rates.

Soil Parameters

Soil characteristics of bulk density, infiltration rate, porosity, aggregate stability and gravimetric water content were assessed before steers were introduced into paddocks. Samples from soil depths of 0–5, 5–10 and 10–15 cm were individually analyzed for all parameters except infiltration rate. Soil organic C and N and soil texture were also assessed at the 3 depths for each plot to determine how these parameters might affect water infiltration rates and bulk density. Data for porosity, gravimetric water content, bulk density, aggregate stability and infiltration were collected again after animals had been removed from each plot. Samples from control plots were collected simultaneously with the grazed plots. Sampling was repeated after 2 weeks, 1 month, and 1 year after the grazing treatments to assess recovery of various soil characteristics.

Sample Collection

Soil samples were collected by the core method (Blake and Hartge 1986) to determine bulk density, porosity, gravimetric water content and aggregate stability at random locations on each of three, 12 m

transects within each paddock on each sampling date. Three soil samples per paddock (1 sample per transect) were taken at each depth increment (0–5, 5–10, and 10–15 cm) for evaluation of bulk density, porosity and gravimetric water content. Two additional soil samples were collected along each transect and composited by depth increment for aggregate stability determination.

Infiltration rate was measured with a double ring falling head infiltrometer, which has been shown to give good comparative information for an area (Branson et al. 1981, Bouwer 1986). The inner ring was 25 cm in diameter, while the outer ring had a diameter of 50 cm to provide a hydraulic barrier to create one-dimensional flow. The outer ring was 3 mm thick and made of steel, while the inner ring was PVC pipe with a beveled cutting edge to minimize disturbance to the soil surface. Infiltration rates were assessed at 0, 15, 30, 45, 60, 75, and 90 min. intervals. Equilibrium infiltration rates were derived from the last 15 min. interval (Smith and Leopold 1941) and used to approximate saturated hydraulic conductivity for statistical analysis. Infiltration measurements were determined at 2 random locations along each of the 3 transects within each paddock.

All statistical analyses of infiltration rates are reported on log transformed data for this study. However, non-transformed adjusted means for infiltration rates are shown on graphs and tables to facilitate comprehension. Standard diagnostic tests on all models used did not reveal any gross violations of statistical assumptions.

Lab Analysis

The wet sieve method was used to measure aggregate stability for a more detailed assessment of the soil structure (Kemper and Rosenau 1986). Determination of both bulk density and gravimetric soil water content were made from the same sample
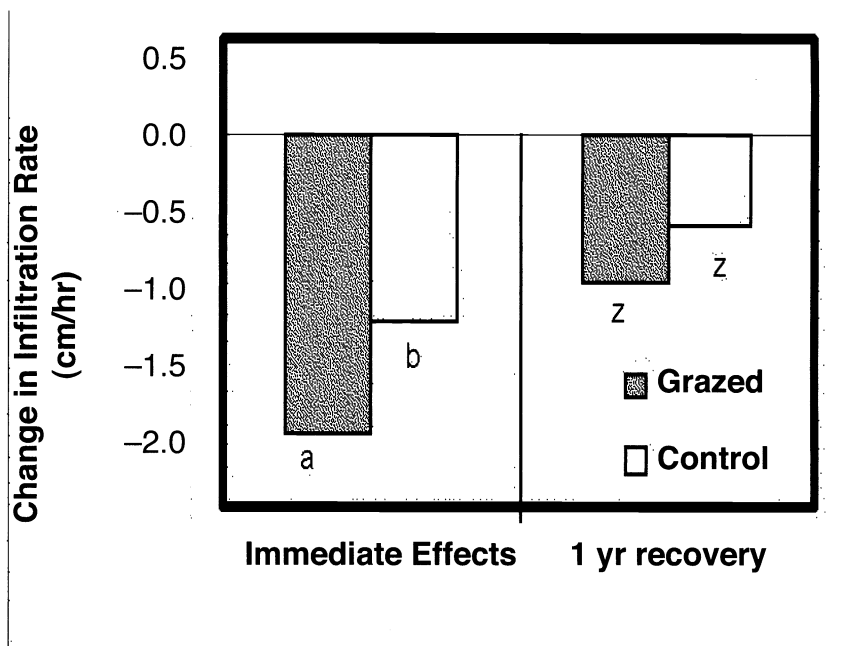
Fig. 1. Immediate effects of grazing and recovery on infiltration rates following a heavy grazing event in a montane riparian community. Different letters at the beginning of the alphabet represent statistical differences (p < 0.10) for immediate effects, whereas different letters at the end of the alphabet represent statistical differences (p < 0.10) in recovery after 1 year between grazed and control plots.

by the method outlined by Gardner (1986). Porosity was derived from particle density and bulk density as outlined by Danielson and Sutherland (1986). Soil organic C and N were determined by dry combustion (LECO 1993), and soil texture was assessed by the hydrometer method (Gee and Bauder 1986).

Results and Discussion

Infiltration

Infiltration rates ranged from 0.4 cm hr^{-1} to 13.1 cm hr^{-1}. Means of infiltration rates are shown in Table 1. The high variance in infiltration data was caused an abnormal distribution of residual errors. Large variability in soil, vegetation and hydrologic

characteristics is typical of data found both within and between riparian ecosystems (Swanson 1989, Clary 1995). Therefore, all infiltration data were log transformed to meet statistical assumptions of ANOVA and multiple regression.

Immediate Effects of Grazing

Analysis of variance was used to examine the differences in mean final infiltration rates before grazing and immediately after grazing. A significant grazing treatment effect (p = 0.03), and a seasonal effect of grazing (p = 0.10) was found, but not an interaction effect of season of grazing (spring vs. summer) x grazing treatment (grazed vs. ungrazed). Grazed plots had approximately a 1.6 cm hr^{-1} decrease in final infiltration rates immediately after grazing, whereas final infiltration rates in control plots declined by only about 1.0 cm hr^{-1} during the same time period (Fig. 1). Soils were wetter in the summer (74% gravimetric water content) when compared to the spring (59% gravimetric water content) in this study, and greater reductions in infiltration rates as a result of wetter soils in the summer were found.

Longer Term Effects and Recovery of Soil Properties

Analysis of covariance, which adjusted the final infiltration rates for the last 4

Table 1. Means ($\bar{x}$) and standard errors (SE) for infiltration rates (cm/hr) as affected by grazing treatment, season and time of sampling for a montane riparian ecosystem.

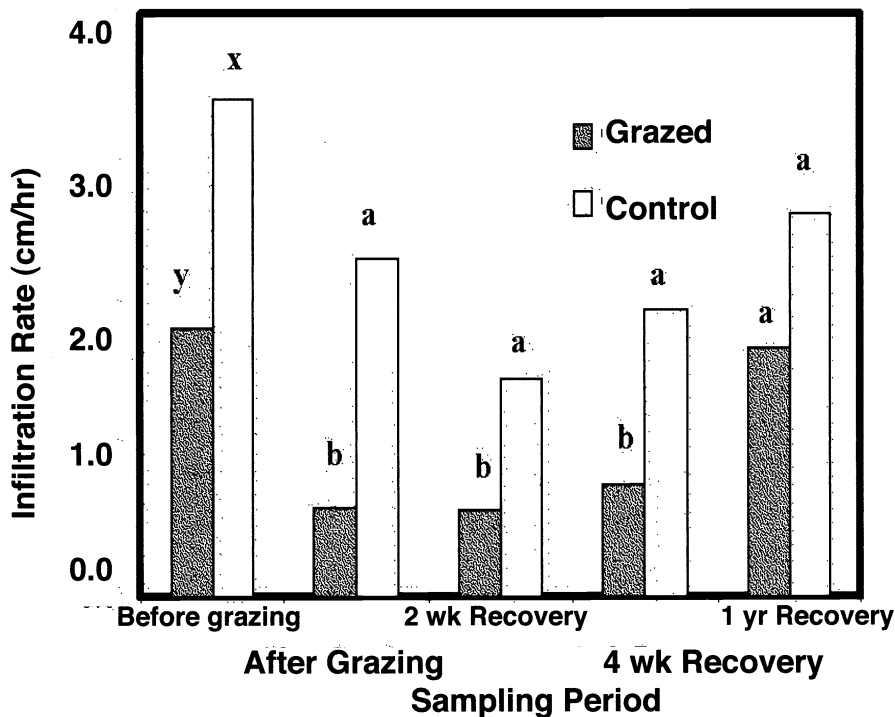|	Spring		Summer	
	Grazed	Control	Grazed	Control
Time of sampling	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE
			(cm/hr)		
Before grazing	1.1 ± 0.3	2.2 ± 0.3	3.1 ± 0.3	5.3 ± 0.3
After grazing	0.5 ± 0.4	2.4 ± 0.3	0.6 ± 0.3	3.1 ± 0.3
2 wk recovery	0.4 ± 0.3	2.3 ± 0.3	0.6 ± 0.2	1.5 ± 0.4
4 wk recovery	0.6 ± 0.3	4.0 ± 0.3	0.7 ± 0.2	1.4 ± 0.3
1 yr recovery	1.4 ± 0.3	3.7 ± 0.2	1.3 ± 0.3	2.7 ± 0.3

Fig. 2. Infiltration rates in grazed plots vs. control plots from immediately after grazing until 1 year later, when recovery of pre-disturbance infiltration rates were observed. Different letters above the bars represent statistical differences (p < 0.05) between grazed and control plots within each time period. Different letters at the end of the alphabet represent statistical differences (p < 0.05) between grazed and control plots before grazing was introduced.

time periods with pre-disturbance infiltration rates, yielded a significant grazing treatment (grazed vs. control) effect (p = 0.03), a significant season of grazing (spring vs. summer) effect (p = 0.08), and a significant time of sampling effect (p < 0.01). Interactions of season of grazing or grazing treatment with sampling periods did not significantly affect the final infiltration rates.

After adjusting for differences in pre-treatment infiltration rates, significant grazing treatment effects were seen in the average final infiltration rate of 0.6 cm hr^{-1} for grazed plots after the grazing event, as compared with the average infiltration rate for ungrazed control plots of 2.7 cm hr^{-1} (Fig. 2). Grazed plots continued to have lower infiltration rates than control plots throughout the study until 1 year after the grazing event, which signified hydrologic recovery within a year.

Seasonal changes in water table depth along streams are inevitable, as well as overland and underground flow as a result of seasonal fluvial patterns and precipitation events (Mitsch and Gosselink 1986). These hydrologic changes influence the water content of soils adjacent to the

stream (Kramer 1983), which in turn affect infiltration rates, bulk density, and plant growth. Interactions between livestock use and seasonal variations in soil conditions (Warren et al. 1986a) can further cause changes in soil hydrological properties following intensive grazing.

The combination of changes in environmental conditions, along with releases of water from the upstream reservoir in this study, may partially explain the significance of the sampling date (time) in the infiltration ANOVA model. The variable nature of the riparian zone was reflected in a relatively low multiple R^2 value (0.31) in the multiple regression analysis for final infiltration rates. Although several parameters are normally effective in prediction of infiltration rates, no single parameter in the model explained more than 8% of the variability in infiltration rates. Amount of clay in the top 5 cm, moisture at the 5-10 cm depth, and bulk density at the 5-10 cm depth were the strongest predictors of infiltration rate, but together only accounted for 23% of the variability in the final infiltration rates.

Other studies have demonstrated interactions of soil moisture, plant growth, and

hydrological recovery. Warren et al. (1986a) found evidence of some hydrological recovery 56 days after grazing during the growing season, but not after the same period of rest after grazing in a drier season. Bohn and Buckhouse (1985) found a trend of hydrological recovery in a riparian community in Oregon over a 5-year period in excluded areas. The quantitative evidence for hydrological recovery within 1 year after a heavy grazing event in this riparian ecosystem is significant new information.

Abundant soil moisture and high-seral vegetation at a study site may stimulate active root growth. In addition, freeze-thaw action in the soils during fall and spring aid in restoring native soil characteristics (Gamougoun et al. 1984). Moreover, sedges are thought to be especially resistant to grazing because of their rhizomatous growth habit. The impressive growth rate of *Carex spp.* in this fertile system after grazing (personal observation) should provide an abundance of macropores (Manning et al. 1989). The interaction of vegetation with the macropore network (Logue and Gander 1986, Naeth et al. 1991) is important for maintaining infiltration rates, yet there has been little quantitative information on these interactions.

Studies have been conducted to determine relationships between various soil moisture conditions and soil hydraulic properties after grazing (Edmond 1962, Warren et al. 1986b). It is believed that there is a greater chance for compaction in wet soils than in dry soils. Infiltration rates in the spring season averaged 1.8 cm hr^{-1} at the Sheep Creek site, whereas infiltration rates were about one half of this in the summer season (0.9 cm hr^{-1}). This is consistent with significantly lower gravimetric water content in the spring (59%) than in the summer (74%). Although soils were wetter in the summer, infiltration rates were not significantly affected by the difference in moisture, as evidenced by the lack of significant interactions between season of grazing and grazing treatment in the ANOVA model.

Confirming or refuting the interpretation that wet soils are more likely to exhibit compaction was an objective of this study. However, because of high soil moisture from a record wet year and water releases from an upstream reservoir, differences in soil moisture between spring and summer were not great enough to see a significant difference in compaction or a reduction in infiltration, and did not allow for any explicit conclusions to be drawn about wet vs. dry soil effects.
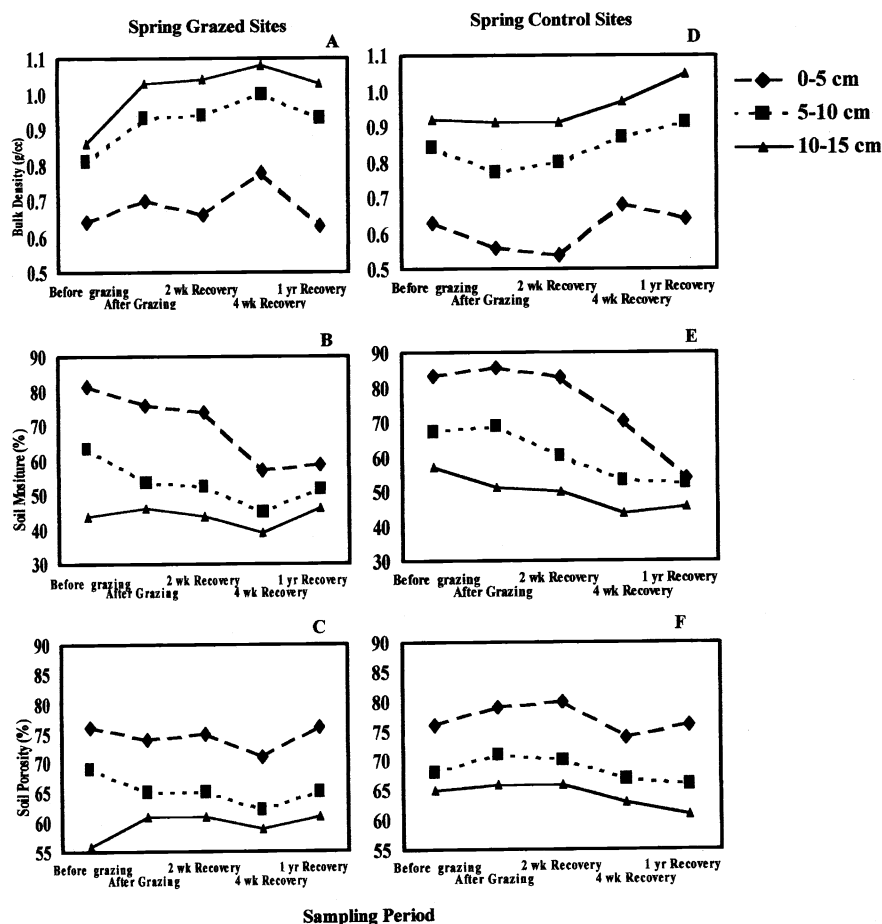
Fig. 3 Trends in soil bulk density (A,D), moisture (B,E), and porosity (C,F) for spring grazed and control paddocks at 5 sampling periods.

Bulk Density and Porosity

High organic matter contents in the surface layers within these *Carex spp.* communities resulted in low bulk density values. For the 3 soil depths sampled, mean values ranged from 0.60 g cm^{-3} for the surface layer (0–5 cm) to 0.91 g cm^{-3} for the 10-15 cm depth. Cooper et al. (1995) found similar values for bulk density in the top layer of an organic soil in New Zealand. Naeth et al. (1991) showed that some soil mixtures of organic matter and litter had water holding capacities as much as 216% of their dry weight. Figures 3 and 4 show trends in soil bulk density, porosity and moisture for both seasons of grazing and grazing treatments (grazed vs. control). Soils located deeper in the profile had greater bulk density than those closer to the surface and generally had lower water contents (Figs. 3 and 4).

A decline in soil moisture at all soil depths through the spring season was noted (Fig. 3). However, soil moisture remained high through the summer season as a result of upstream water release from Eaton Reservoir, which caused water to

flow from Sheep Creek into the stream banks (Fig. 4). Greater soil moisture during the summer was reflected in bulk density and porosity values. As soil moisture increased, bulk density declined and porosity increased. Regression analysis consistently revealed a significant negative correlation (p < 0.01) between bulk density and soil moisture in each of the soil depths sampled. As the soil became saturated, it expanded the organic matter which resulted in lower bulk density.

Given the unusually heavy dependence of bulk density on soil moisture found in this study, the average gravimetric water content in the spring (59%) compared with summer (74%) translated into higher average bulk density values in the spring (0.84 g cm^{-3}) as compared with the summer (0.70 g cm^{-3}). Porosity was inversely related to bulk density and was significantly higher in the summer (74%) than in the spring (68%).

Immediate Effect of Grazing

Increased soil bulk density and

decreased porosity immediately after the grazing event are shown in Figures 3a, 3c, 4a and 4c. Bulk density was significantly increased immediately after grazing at the 5–10 cm soil depth (p = 0.04) and the 10–15 cm depth (p = 0.07), but not in the top 5 cm (p = 0.11). Average bulk density increased 0.09 g cm^{-3} at 5–10 cm, and 0.11 g cm^{-3} at the 10–15 cm depth (Fig. 5). Cattle trampling on the highly organic surface layer caused water to be forced from the expansive organic soil, but this organic layer probably rehydrated within minutes given the extremely wet conditions of the sites. The highly organic top layer may also dissipate the force of cattle hooves on the soil surface that should result in less compaction of the soil underneath. However, even in this near pristine community, the soil under the organic layer showed evidence of compaction immediately after grazing (Fig. 5). Protection of lower soil depths by the organic surface layer may be significant, but further work should be done to determine the amount of organic matter needed to serve this purpose. No significant interactions in bulk density as affected by season of grazing (spring vs. summer) x grazing treatment (grazed vs. control) were detected for any of the soil depths sampled, which again showed that the effects of the grazing treatments were similar, regardless of season of grazing. Opposite trends were seen in soil porosity values as compared with bulk density data. Porosity decreased significantly at the 5–10 cm and 10–15 cm depths after grazing (p = 0.05 and 0.08, respectively) in grazed plots and increased slightly in control plots. The reduction in soil porosity within grazed paddocks was an effect of cattle trampling that reduced pore space.

Although porosity is a good measure of total pore space, a measure of changes in pore size distribution would have been more helpful to assess changes in the distribution of macropores. Macropores are considered the dominant force behind vertical flow in soil (Beven and Germann 1982). Studies have shown that trampling by livestock can destroy the large macropores that conduct large volumes of water into the soil profile (Dreccer and Lavado 1993). Methods used in this study to evaluate aggregate stability and thus indirectly pore size distribution were inconclusive because of the high interaction of soil properties with vegetation. The role of plant roots in binding soil aggregates could not be assessed by the wet sieve method, although the interaction of the riparian vegetation with soil stabilization
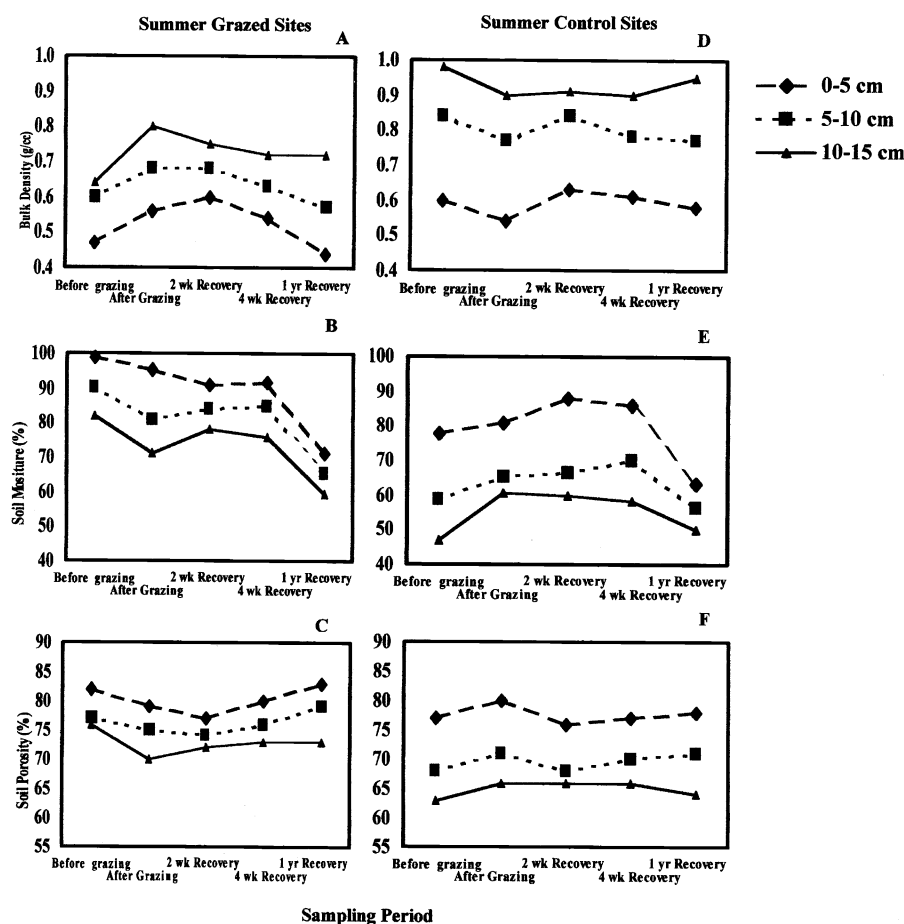
Fig. 4. Trends in soil bulk density (A,D), moisture (B,E), and porosity (C,F) for summer grazed and control paddocks at 5 sampling periods.

interspaces between vegetation tussocks, and how each of these are affected by grazing.

It may be possible to calculate grazing impacts and recovery rates of riparian areas with the use of quantitative assessment of initial characteristics of hydrology, soil characteristics and vegetation cover and production. If potential impacts and recovery rates are known, sustainable grazing regimes in riparian zones can be more accurately predicted.

Conclusions

This study showed the potential of a riparian zone to recover hydrologically from a heavy grazing event. The physical conditions present at the site, (namely abundant soil moisture, active vegetative growth, and abundant organic matter in the soil) facilitates recovery to pre-disturbance soil physical properties within 1 year after a heavy grazing event. However, the study area had not been grazed by livestock since 1956, so the conditions prior to grazing were near pristine in terms of vegetation composition and cover. This unique situation should be kept in mind when considering the time needed for other riparian zones to recover from grazing practices. Interactions of abiotic and biotic processes within a riparian zone are tightly linked, and separation of these processes is extremely complex. Hydrology and geomorphology greatly influence sediment movement, sediment deposition, soil development and plant community succession. These characteristics in turn influence soil physical characteristics that are important for a functional hydrologic regime. Initial hydrological, soil and vegetation conditions of the riparian zone should be considered when recommendations for length of rest periods after grazing are to be made. This should result in a better assessment of interactions among various processes that operate within the riparian zone and how they might be affected by grazing.

The thick organic layer present in the surface soil in this system may have provided a protective layer against compaction at the soil surface. Oades (1984) suggested management of organic matter to maintain soil structure for water infiltration, active root growth and soil stabilization for dryland agriculture. A similar approach could be taken for riparian zones. Organic matter played an important role in the maintenance of soil physical properties in this riparian zone. Further

is a primary mechanism for bank stability (Swanson 1989). New methods for the quantification of pore size distribution and the role of roots in binding riparian soils are needed.

Longer Term Effects and Recovery of Soil Properties

An ANOVA model for bulk density was used for all statistical comparisons for long term grazing effects and recovery of bulk density. Analysis of bulk density data for the last 4 time periods revealed no evidence for a significant grazing treatment effect. A significant season of grazing X time of sample collection interaction for the 0–5 cm and 5–10 cm soil depths (p = 0.03 and 0.04, respectively), was most likely caused by changes in soil moisture. Differences in soil moisture between spring and late summer were also a probable cause for the significant season of grazing effect for the 5–10 cm soil depth. The significant grazing treatment x time of sample collection effect observed for the 0–5 cm depth was largely caused by a decrease in bulk density after 1 year of recovery, possibly caused by freezing and thawing activity during this period. Bulk density values in grazed and ungrazed paddocks showed no significant differences caused by grazing treatment, season of grazing, or grazing treatment x season interaction for any of the depths sampled 1 year after the grazing event (Fig. 5).

The spatial and temporal variability of soil properties in these ecosystems is difficult to capture accurately because of interactions with vegetation and hydrology (Krueper 1992). Future studies should include simultaneous quantification of hydrological characteristics such as water table depth and stream flow patterns and infiltration rates in distinct plant communities. Since infiltration is often augmented by root channels (Manning et al. 1989), different rooting systems may influence infiltration rates. Cattle have been shown to step preferably in the interspace between vegetation tussocks (Balph and Malechek 1985), it would be helpful to quantify the respective infiltration rates over crowns of vegetation as opposed to
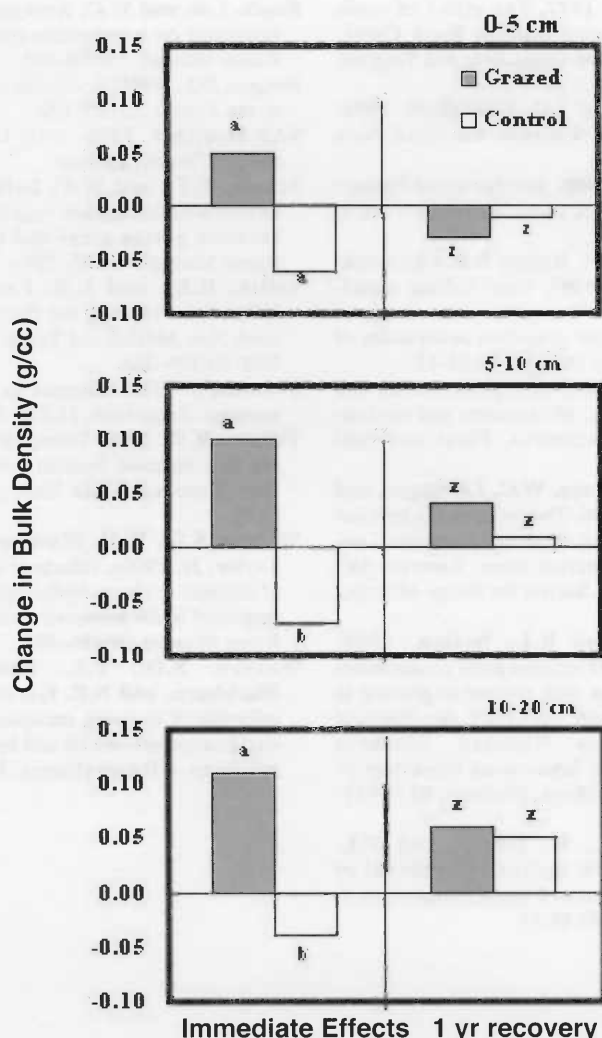
Fig. 5. Immediate effects and recovery of bulk density at 3 soil depths following a heavy grazing event in a montane riparian community. Different letters above and below bars at the beginning of the alphabet represent statistical differences (p < 0.10) in immediate effects. Different letters at the end of the alphabet represent statistical differences (p < 0.10) in recovery.

work should be conducted to determine the amount of organic matter needed in riparian soils to maintain desired soil physical properties, particularly for annually repeated grazing use.

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Intake and digestive kinetics of leaf and stem fractions

JAMES B. LAMB, DON C. ADAMS, TERRY J. KLOPFENSTEIN, RICK J. GRANT, PHILLIP L. SIMS, LARRY M. WHITE, AND STEVEN S. WALLER

Lamb is former Research Associate and Adams is Professor, Univ. of Nebraska-Lincoln, Institute of Agr. and Natural Resources, West Central Res. and Extension Center, 461 West University Drive, North Platte, Neb. 69101; Klopfenstein and Grant are Professor and Associate Professor, Dept. of Animal Science Univ. of Nebraska-Lincoln 68583; Sims and White are Research Leader and retired, USDA-ARS, Southern Plains Res. Station, Woodward, Okla. 73801; Waller is Professor Dept. of Agronomy Univ. of Nebraska-Lincoln 68583. Correspondence should be addressed: Don Adams, West Central Research and Extension Center, North Platte, Nebr. 69101.

Abstract

Ruminally fistulated steers were used in a 4 x 4 Latin square to test effects of immature (vegetative) and mature (post reproductive) leaf and stem fractions from subirrigated meadow hay on organic matter intake (OMI), organic matter digestibility (OMD), and digestive kinetics. Hay was harvested 1 June (immature) and 1 October (mature), chopped into 3- to 5-cm lengths, then separated into leaf and stem fractions using a modified Clipper Cleaner Model Super 69D. Steers were provided ad libitum access to fractions and supplemented with urea so that diets were iso-nitrogenous. Particulate passage was determined using Yb labeled large hay particles [$\geq$ 1.7-mm screen] and Er labeled small particles [< 1.7-mm and $\geq$ 0.212-mm screen]. Samples were collected from the rumen, omasum, feces, and un-masticated diets for particle size determination. Particle size was determined using wet sieving techniques. Voluntary OMI of immature fractions (15.4 g kg^{-1} BW) was greater (P < 0.05) than mature fractions (12.5 g kg^{-1} BW). Within maturity OMI and OMD of leaves and stems were similar. Immature fractions had greater (P < 0.05) OMD (63.2%) than mature fractions (55.7%). Large and small particle passage rates were faster (P < 0.05) for immature fractions [3.2% hour^{-1} (large) and 4.3% hour^{-1} (small)] than mature [(2.3% hour^{-1} (large) and 2.9% hour^{-1} (small)]. Critical particle size for ruminal escape was $\leq$ 1.18 mm for both leaves and stems regardless of maturity. Differences in OMI and OMD between immature and mature fractions were explained by changes in structural components of the cell wall that made particles more resistant to mechanical and microbial breakdown.

Key Words: digestibility, retention, particle size, rumen, feces, omasum

Forage maturity influences quality of forages (Streeter et al. 1968, Nichols 1989). A decline in forage quality can be attributed largely to changes in the leaf and stem ratios (Nelson and Moser 1994) and associated decline in stem quality. Forage intake is associated with the proportion of indigestible fiber and the length of time retained in the rumen (Ulyatt et al. 1986). Particle size and passage rate were inversely related (Ehle 1984). Poppi et al. (1985) and Hendricksen et al. (1981) found differences in voluntary intake of leaves and stems. They attributed changes in intake

Resumen

Se utilizaron novillos fistulados ruminalmente en un diseño de Cuadro Latino 4 x 4 para probar los efectos de las fracciones inmaduras (vegetativo) y maduras (post-reproductiva) de hoja y tallo de heno producido en praderas subirrigadas en el consumo de materia orgánica (CMO), digestibilidad de la materia orgánica (DMO) y cinética digestiva. El heno se cosechó el 1 de Junio (inmaduro) y el 1 de Octubre (maduro), se pico en trozos de 3 a 5 cm de longitud y luego se separo en hojas y tallos utilizando un Cortador Limpiador modelo Super 69D modificado. A los novillos se les permitió acceso ad libitum heno de las fracciones de hoja y tallo y se suplementaron con urea de tal forma que las dietas fueron iso-nitrogenadas. El paso de las partículas fue determinado utilizando partículas grandes de heno marcadas con Yb [malla $\geq$ 1.7-mm] y partículas chicas marcadas con Er [malla < 1.7-mm y $\geq$ 0.212-mm). Para determinar el tamaño de partícula se colectaron muestras del rumen, omaso, heces fecales y dietas sin masticar. El tamaño de partícula se determino usando la técnica de cribado húmedo. El consumo voluntario de materia orgánica de fracciones inmaduras (15.4 g kg^{-1} PV) fue mayor (P < 0.05) que el de las fracciones maduras (12.5 g kg^{-1} PV). Dentro de madurez, el consumo de materia orgánica y la digestibilidad de la materia orgánica de hojas y tallos fueron similares. Las fracciones inmaduras tuvieron una mayor (P < 0.05) DMO (63.2%) que las fracciones maduras (55.7%). Las tasas de paso fueron mas rápidas (P < 0.05) para las fracciones inmaduras [3.2% hora^{-1} (grandes) y 4.3% hora^{-1} (pequeñas)] que para las maduras [(2.3% hora^{-1} (grandes) y 2.9% hora^{-1} (pequeñas)]. El tamaño de partícula crítico para le escape ruminal fue de $\leq$ 1.18 mm, tanto para tallos como para hojas, sin importar la madurez. Las diferencias en el CMO y la DMO entre las fracciones maduras e inmaduras fueron explicadas por cambios en los componentes estructurales de la pared celular que hicieron a las partículas mas resistentes a el desdoblamiento mecánico y microbial

to differences in ruminal retention times. Longer retention times were associated with fractions that were more resistant to mechanical and microbial breakdown. Leaves within maturity were less resistant to particle size reduction than stems, thus passage rate of leaves was faster than stems.

Limited information is available on the effects of individual leaf or stem fractions on intake, digestibility, and rumen kinetics in beef cattle. Our objectives were to determine effect of plant maturity on voluntary intake, digestibility, digestive kinetics, and escape protein of leaf and stem fractions of meadow hay.

Materials and Methods

Treatments and Feeding

Four ruminally cannulated steers (avg body weight = 418 kg) fitted with 10.2-cm i.d. ruminal cannulae were used in a 4 x 4 Latin square to determine effects of immature and mature leaf and stem hay fractions on organic matter intake (OMI), organic matter digestibility (OMD), and ruminal retention time, passage rate, and particle size distribution. Steers were fistulated and housed at the University of Nebraska-Lincoln Animal Science building under conditions described in the animal use protocols approved by the Institutional Animal Care and Use Committee at the University of Nebraska. Leaf and stem hay fractions were harvested at the University of Nebraska Gudmundsen Sandhills Laboratory (elevation 1,073 m, 42°05'N Lat, 101° 26'W Long) located 11 km northeast of Whitman, Nebr. Hay was harvested and baled into 500-kg round bales from 2 rectangular (100 x 330 m), subirrigated meadow plots. Soils of the subirrigated meadow are classified as Gannett-Loup fine sandy loam (coarse-loamy, mixed, mesic Typic Haplaquoll). Plots were harvested to represent 2 stages of plant growth: immature hay (1 June 1994), characterized as being vegetative to elongation phase; and mature hay (1 October 1994), characterized as being post-reproductive (Moore and Moser 1995). Dominant species of the subirrigated meadow plots were Kentucky bluegrass (*Poa pratensis* L.), slender wheatgrass [*Elymus trachycaulum* (Link) Gould ex Shinn.], quackgrass [*Elytergia repens* (L.) Nevski], redtop (*Agrostis stolonifera* L.), timothy (*Phleum pratense* L.), several species of sedges (*Carex* spp.), smooth bromegrass (*Bromus inermis* Leyss.), and reed canarygrass (*Phalaris arundinacea* L.). Less abundant species were prairie cordgrass (*Spartina pectinata* Link), rushes (*Juncus* spp. and *Eleocharis* spp.), big bluestem (*Andropogon gerardii* Vitman), indiangrass [*Sorgastrum nutans* (L.) Nash], switchgrass (*Panicum virgatum* L.), and several species of clover (*Trifolium* spp). Mean percentage of total plant basal area for species of an adjacent meadow with similar soils and elevation was 26% Kentucky bluegrass, 25% wheatgrass (composite of slender wheatgrass and quackgrass), 14% sedge, 8% timothy, 8% red clover (*Trifolium pratense* L.), 5% rushes, 4% redtop, 3% smooth bromegrass, and 3% reed canarygrass. The remaining component was comprised of big bluestem, indiangrass, and other forbs (Nichols 1991, Reece et al. 1994).

Hay was separated into leaf and stem fractions at the USDA-ARS Southern Plains Range Research Station at Woodward, Okla. Bales were unrolled and hay was chopped with a forage chopper into 3- to 5-cm lengths. Chopped hay was separated into leaf and stem fractions using a Clipper Cleaner Model Super 69D[1] dual flow air separation system (A.T. Ferrel & Co., Saginaw, Mich.). The dual air system forces air into the separation chamber from opposing directions (e.g. top and bottom). Chopped hay enters at the center and moves across the opposing air flows. The opposition from the flows results in separation based on weight of the fractions. The heavier stem fraction separates and moves across the chamber at a lower angle than the lighter leaf fraction. Fractions are individually recovered. Air flows were continually monitored and adjusted to obtain leaf stem separation. Sub-samples of leaf and stem fractions were collected and manually separated and found to be 90% of their intended fraction.

Steers were housed under environmentally controlled conditions in metabolism stalls. Fourteen days before trial initiation, steers were allowed ad libitum access to long-stem subirrigated meadow hay that was harvested 1 August from an adjacent meadow of similar species composition. Steers were assigned randomly to 1 of 4 hay fraction diets: immature leaf, immature stem, mature leaf, or mature stem. Steers were fed every 2 hours with automatic feeders which allowed ad libitum (10% daily refusal) access to diets. To avoid associated effects of potential ruminal N deficiencies on intake, passage rates, and particle breakdown of the fiber component, solubilized urea was supplemented via the rumen cannula. Urea was added at 12-hour intervals to steers fed immature stem (77 g day^{-1}), mature leaf (91 g day^{-1}), and mature stem diets (108 g day^{-1}). Urea was supplemented as a percentage of the total dietary N and calculated to equal the percentage of total N in the immature leaf diet. Period lengths were 15 days, with 7 days for diet adaptation and 8 days for collection. Refusals were collected, weighed, and subsampled daily. Subsamples were stored for later analysis. Daily OMI was determined by difference. On day 8, steers were fitted with fecal collection bags and

total feces were collected until day 13. Fecal bags were weighed, emptied, and subsampled every 12 hours. Subsamples were frozen for later analysis of dry matter (DM), organic matter (OM), and particle size.

Particulate Passage Estimates

Particulate passage rates and retention times were determined on 2 different particle sizes. Large particles were classified as those that were retained on a 1.7-mm screen, whereas small particles were classified as those that cleared a 1.7-mm screen but were retained on a 0.212-mm screen. Hay fractions were soaked in water for 24 hours before being separated into large or small particles. Particles were sieved with a FRITSCH electromagnetic siever (Idar-Oberstein, West Germany), the lid of which was equipped with a shower and the pan with a vacuum system. Sieving was done with a vibration amplitude of 6 mm for 10 min (Shaver et al. 1988). Screen sizes were: 6.30, 4.75, 3.35, 1.70, and 0.212 mm. Particles on upper screens were combined into a large particle pool while those retained on the 0.212-mm screen constituted the small particles.

Large particles from the 4 hay fractions were labeled with Yb acetate and small particles were labeled with Er acetate using modified procedures described by Teeter et al. (1984). Large particles were soaked for 24 hours in a 15 mM aqueous Yb solution. After soaking, excess fluid was poured off and the remaining sample was soaked in 100 mM acetic acid solution for 12 hours with occasional stirring. After soaking in acetic acid, particles were rinsed with slow flowing water overnight into a plastic tub covered with several layers of cheese cloth. Particles were then squeezed dry and soaked again in 100 mM acetic acid solution for 5 to 6 hours with occasional stirring, squeezed dry, spread on trays, and dried in a forced-air oven at 50°C. Small particles were labeled with Er following the same procedures using 20 mM Er aqueous solution.

In each period on day 3 at 2000 hours, steers were pulse-dosed intraruminally with both Yb and Er labeled particles. The dose was placed in the mid-dorsal region of the rumen (Krysl et al. 1987). Each steer was dosed with 200 g air-dried Yb labeled large particles and 150 g air-dried Er labeled small particles. At 0800 hour the following 3 days, ruminal evacuations were made (Vanzant et al. 1993). Rumen contents were weighed and mixed thoroughly, sampled for pH and subsampled for DM and marker determinations.

Subsamples obtained during ruminal evacuations represented 12, 36, and 60 hours post-marker dosing. Following each rumen evacuation, the omasum orifice was palpated and approximately 30 g of contents were removed from between the omasal folds (Moir 1984). Omasal contents were combined across days, frozen and stored for subsequent particle size analysis.

Particulate Size and Distribution

Particle size was determined using wet sieving techniques on subsamples of individual hay fractions, ruminal and omasal contents, and feces. Individual hay fractions were collected and soaked in water for 24 hours, excess water was removed, and samples were stored at –18° C for later particle size determination. Ruminal digesta samples were collected from 4 sites within the reticulorumen on day 8 at 0800 hour, before interval feeding and stored at –18° C for later particle size analysis. Reticulorumen sampling sites were: 1) anterior dorsal sac; 2) caudo-dorsal sac; 3) caudo-ventral sac; and 4) reticulum. At 0800 hour on days 13 to 15, ruminal evacuations were made and subsamples collected to estimate DM content of the reticulorumen (Vanzant et al. 1993). Samples collected at the anterior dorsal sac or caudo-dorsal sac were a composite of 2 grab samples. Samples collected at the caudo-ventral sac or reticulorumen were obtained by passing a 300-ml cup, capped by placing the hand over the opening, into the sampling sites. Omasal samples were a composite collected during ruminal evacuations. Fecal samples were a composite of subsamples collected during total fecal collections.

Particle size was determined on duplicate samples of the hay fractions, ruminal, omasal, and fecal contents using wet sieving techniques described by Prigge et al. (1990). Particles were separated using a FRITSCH (Idar-Oberstein, West Germany) electromagnetic siever equipped with a lid shower and an evacuation system. Approximately 15 g of wet sample (3 to 4 g DM) were placed on the top screen and sieving was done with a vibration amplitude of 6 mm for 10 min (Moseley 1984, Shaver et al. 1988) with screen apertures of 6.30, 4.74, 3.35, 1.70, 1.18, 0.85, 0.60, and 0.212 mm. Particles retained on individual sieves were rinsed onto preweighed 15-cm filter paper and dried (50° C) in a forced-air oven for 48 hours to determine retained DM. Dry residue retained on individual screens was expressed as a percentage of the total DM

sieved (Shaver et al. 1988). The soluble fraction and particles less than the 0.212-mm screen size were calculated by difference. Geometric mean diameter was calculated according to procedures outlined by Waldo et al. (1971). Five particle pools were determined based on the cumulative DM retained on selected sieve screens (≥ 3.36, ≥ 1.18, ≥ 0.60, <0.60, or <0.212-mm screen).

In Situ Procedures

Rate and extent of in situ neutral detergent fiber (NDF) disappearance were determined on individual hay fractions during all periods. A 5-g subsample of each hay fraction was ground to pass through a 2-mm screen in a Wiley Mill and was placed into a pre-weighed, labeled Dacron bag (10 x 20 cm, avg pore size = 53 ± 10 μm; Ankom, Fairport, N.Y.). Individual bags were sealed by wrapping the open end around a #8 rubber stopper that was secured with a #18 rubber band. The bag was folded over the rubber band and a second rubber band was added. Sample bags were soaked in water (39° C) for 20 min before rumen incubation. Incubation times were: 4, 8, 12, 24, 48, 72, and 96 hours. Duplicate sample bags were incubated in a polyester mesh bag (36 x 42 cm). Bags were placed in the fluid phase of the ruminal ventral sac and incubated in descending order which facilitated removal of all bags at 1 time point. Bags were washed and rinsed according to procedures outlined by Wilkerson et al. (1995).

Neutral detergent fiber of in situ residue was determined using methods described by Van Soest et al. (1991). Approximately 0.5 g of in situ residue was analyzed for NDF in duplicate for the 0, 4, 8, 12, 24, 48, 72, and 96 hour incubations. Rate and extent of fiber degradation and apparent extent of ruminal digestion were calculated as described by Grant and Mertens (1992) and Grant and Weidner (1992).

Laboratory Analyses

Diets, refusals, ruminal contents, and fecal samples were dried in a forced-air oven (50° C) and ground to pass through a 1-mm screen in a Wiley Mill. Samples were analyzed for DM (AOAC 1984), NDF (Van Soest et al. 1991), acid detergent fiber (ADF, Van Soest 1963), and crude protein (AOAC 1984). In vivo OMD was calculated following procedures outlined by Schneider and Flatt (1975).

Rumen subsamples with labeled Yb or Er fractions were prepared for analysis

(Karimi et al. 1986) by adding 14.9 ml of 0.01 M Diethylenetriaminepentaacetic acid (DTPA) to 0.2 g of sample. Samples were shaken for 35 min, then filtered (Whatman #4 filter paper, Whatman, Maidstone, UK) into vials and analyzed by atomic absorption spectroscopy with a nitrous oxide/acetylene flame (McCollum and Galyean 1985). Passage of particles was assumed to follow first order kinetics. Rumen Yb and Er disappearance curves were used to calculate the rate of particle passage (k_p) out of the rumen. Fractional passage rate represented the natural logarithmic slope of the descending portion of the disappearance curve. Retention time was calculated as the reciprocal of the natural logarithmic slope.

Undegraded intake protein (UIP) of the individual hay fractions was determined by combining large particle passage rate (k_p) and rate of in situ N degradation (k_d). Undegraded intake protein values were determined using a dacron bag procedure with incubation times of 4, 8, 12, and 24 hours (Wilkerson et al. 1995) and by using the following equation: [b fraction x $((k_p/(k_p + k_d))$]. The b fraction represented the N pool that has the potential for escape. Undegraded intake protein values were corrected for microbial attachment using purine analysis as described by Zinn and Owens (1986) and Aharoni and Tagari (1991).

Undegraded intake protein values were also determined based on protein solubility classifications as described by Van Soest (1994). The b fraction and k_d were determined using in situ residues at 4, 8, 12, and 24 hours. Neutral detergent-insoluble protein was selected as the protein fraction that best represented the b fraction. This protein fraction was classified as being insoluble in neutral detergent but soluble in acid detergent and having a slow rate of enzymatic degradation.

Neutral detergent-insoluble protein was determined on the initial hay fractions and on in situ residue from bags incubated in the rumen for 4, 8, 12, and 24 hours. About 1 g of residue was allowed to reflux for 1 hour in NDF solution (Van Soest et al. 1991). After refluxing, the NDF residue and solution were filtered (Whatman #541 filter paper, Whatman, Maidstone, UK) and rinsed 3 times with boiling water to remove NDF solution. Percentage neutral detergent insoluble protein was calculated by determining the crude protein concentration of the filtered NDF residue (AOAC 1984) divided by the sample weight. A blank filter paper treated with hot NDF solution and rinsed 3 times with boiling

water was used to correct for any N contamination originating from the filter paper or NDF solution. Rate (k_d) was determined by taking the natural logarithm of the percentage NDF multiplied by the percentage neutral detergent-insoluble protein at each time point. Rate represented the natural logarithmic slope of the descending portion of the disappearance curve.

Statistical Analysis

Organic matter intake, (OMI), organic matter digestibility (OMD), rumen dry matter (DM) fill, rumen volume, particulate passage of large and small particles, pH (single time point), undergraded intake protein (UIP), and rate and extent of NDF disappearance were analyzed as a 4 x 4 Latin square. Factors included in the model were steer, period, maturity, and individual leaf or stem fraction. Steer was considered a random effect. Treatments were compared using predetermined contrasts. Due to the expense of fraction separation and an under-estimation of actual fraction intake at the time of separation, there were only enough mature stems for 2 complete collection periods compared to 4 periods for immature leaves, immature stems, and mature leaves. Results for mature stems were analyzed using 2 periods (Cochran and Cox 1992). Data were analyzed using Mixed Model Procedures of SAS (1992). All differences mentioned are significant at the P < 0.05 probability level unless otherwise noted.

Results

Diet Composition

The separation technique on a dry weight basis provided purity values greater than 90%. The stem fraction for both immature and mature hays contained stems plus some leaf sheaths and seed heads, while the leaf fractions contained leaf blades plus leaf sheaths, and some lighter seed heads.

Crude protein (CP) of immature hay fractions was greater than mature hay fractions. Immature leaves contained 26% more CP than immature stems and mature leaves contained 27% more CP than mature stems (Table 1). Neutral detergent fiber of immature and mature hay fractions were similar. Leaf and stem fractions within stage of maturity did not differ in NDF. Mature hay fractions had higher ADF than immature hay fractions. Immature leaves and stems did not differ in ADF content. However, mature leaves had higher ADF concentrations than

mature stems. Why ADF content of immature leaves and stems did not differ while mature leaves had a greater ADF concentration than mature stems is not apparent. A partial explanation for the lack of difference in ADF content between the immature hay fractions could be related to the concentration of leaf sheaths in the leaf fraction.

Intake, DM Fill, Digestibility and Passage

Organic matter intake (OMI) of steers fed immature hay fractions was greater than that of steers fed mature fractions (Table 2). Organic matter intake of leaves and stems within stage of maturity did not differ. Organic matter digestibility (OMD) was lower for steers fed mature hay fractions when compared with steers fed immature hay fractions (Table 2). Immature leaf and stem fractions did not differ in OMD. Likewise, OMD of mature leaves and stems was similar.

Particulate passage rates of large and small particles were faster for immature hay fractions than mature fractions (Table 2). Passage rate of immature leaves, regardless of particle size, was faster than rates for immature stems. Large particle passage rate was faster for mature leaves than for mature stems. However, passage rate of small particles for mature stems and leaves did not differ.

Dry matter (DM) fill and total rumen volume were not affected by stage of maturity and leaf and stem fractions within stage of maturity did not differ. Ruminal pH was similar for immature and mature hay fractions, and leaf and stem fractions within stage of maturity did not differ.

Particle Size Distribution

Geometric mean diameter of mature hay fractions was 42% larger than for immature fractions. Geometric mean diameter of mature leaves was 20% greater than mature stems (Table 3). About 89% of the total DM sieved for mature leaf and stem fractions was retained within the ≥ 1.18-mm pool. More DM was retained (4.5%) within the ≥ 1.18-mm pool for immature stems than for immature leaves).

Geometric mean diameter of particles or particle pools at the 4 rumen sites was not different. No 2-way interaction existed for maturity x site or fraction x site. Given that the 4 sites were not different, sites within maturity level and fraction were pooled (Table 3). The geometric mean diameter of rumen particles for mature stems was 38% larger than mature leaves. Immature stems had a geometric mean diameter 25% larger than immature leaves. No differences between immature leaves and stems were observed for coarse particles (≥ 3.36-mm) with approximately 18.1% of the total ruminal DM sieved retained in this pool. Retained ruminal DM for the coarse (≥ 3.36-mm) particle pool was similar for mature stems and leaves and approximately 13.5% of the total sieved DM was retained (Table 3). The fine particle pool (< 0.60-mm) comprised a large portion of the total retained DM. Immature leaves had approximately 17% more DM retained in this pool than did immature stems. Similarly, mature leaves had approximately 24% more DM retained within the fine particle pool than mature stems (Table 3).

Estimates of geometric mean diameter for both omasal and fecal contents were similar. Stage of maturity did not affect geometric mean diameter or particle distri-

Table 1. Chemical composition of subirrigated meadow immature and mature leaf and stem fractions fed to beef steers.

Item[2]	Immature		Mature		Contrasts[1]		
	Leaf	Stem	Leaf	Stem	(1)	(2)	(3)
Organic matter (% of DM)	87.6	91.3	85.0	90.5	NS[3]	NS	NS
Ash (% of DM)	12.4	8.7	15.0	9.5	*	*	*
Crude protein (% of OM)	12.9	9.6	9.2	6.7	*	*	*
NDIN (% of DM)	3.4	2.1	2.4	1.9	*	NS	*
BEP (% of DM)	2.1	2.0	2.3	2.2	NS	NS	NS
NDF (% of OM)	78.4	74.0	77.9	75.4	NS	NS	NS
ADF (% of OM)	46.6	44.7	53.0	45.7	NS	*	*
ADIN (% of N)	15.6	16.0	20.9	22.0	NS	NS	*

[1]Contrasts 1 = immature leaves vs immature stems; 2 = mature leaves vs mature stems; 3 = immature hay fractions vs mature hay fractions.
[2]NDIN = Escape protein calculated using neutral detergent insoluble N (% of DM); BEP = Escape protein calculated from in situ data corrected for microbial attachment; NDF = neutral detergent fiber; ADF = acid detergent fiber; ADIN = acid detergent insoluble nitrogen.
[3]NS contrast not significant P > 0.05.
*Contrast significant P < 0.05.

Table 2. Organic matter intake, digestibility, rumen DM fill, and passage rates in steers fed subirrigated meadow immature and mature leaf and stem hay fractions.

| Item[2] | Immature | | Mature | | Contrasts[1] | | | | | |
	Leaf	Stem	Leaf	Stem	(1)	SE	(2)	SE	(3)	SE
OMI, kg	7.0	7.0	5.5	5.7	NS[3]	0.2	NS	0.3	*	0.2
OMI, g/kg BW	15.4	15.4	12.1	12.8	NS	0.4	NS	0.5	*	0.3
OMD, %	62.9	63.5	54.5	56.9	NS	1.9	NS	2.4	*	1.5
RDMF, g/kg BW	17.6	19.3	18.3	21.5	NS	1.3	NS	1.8	NS	1.3
RV, g/kg BW	138.3	149.1	143.3	151.5	NS	7.4	NS	9.9	NS	6.3
pH	6.6	6.6	6.8	6.8	NS	0.2	NS	0.2	NS	0.1
LPP, %/h	3.8	2.5	2.5	2.1	*	0.1	*	0.1	*	0.1
LPR, time, h	26.3	40.0	40.0	47.6	*	0.8	*	1.1	*	0.7
SPP, %/h	5.1	3.5	3.0	2.8	*	0.1	NS	0.1	*	0.1
SPR time, h	19.6	28.6	33.3	35.7	*	1.2	NS	1.7	*	1.1
NDFD, %/h	5.3	3.8	3.9	3.7	*	0.0	NS	0.0	NS	0.0
ENDF, h	79.1	70.8	67.5	55.7	*	1.5	*	2.0	*	1.3
AEDL	43.8	41.3	37.7	35.7	NS	1.7	NS	2.3	*	1.5
AEDS	37.8	35.0	35.3	31.8	NS	1.8	NS	2.4	NS	1.5

[1]Contrasts 1 = immature leaves vs immature stems; 2 = mature leaves vs mature stems; 3 = immature hay fractions vs mature hay fractions.
[2]OMI = organic matter intake; OMD = organic matter digestibility; RDMF = rumen dry matter fill; RV = rumen volume; LPP = passage rate of Yb-labeled large particles > 1.7 mm screen; LPR = mean retention time of Yb-labeled large particles; SPP = passage rate of Er-labeled small particles < 1.7 mm and > .212 mm screen; SPR = mean retention time of Er-labeled particles; NDFD = in situ neutral detergent fiber disappearance; ENDF = in situ neutral detergent fiber extent of disappearance; AEDL = apparent extent of digestion of Yb-labeled large particles; AEDS = apparent extent of digestion of Er-labeled small particles.
[3]NS contrast not significant P > 0.05.
*Contrast significant P < 0.05.

bution (Table 3). A large portion of retained fecal and omasal DM sieved was retained within the fine particle pool (<0.60-mm). More immature leaf DM was retained compared with immature stem. Similarly, more mature leaf DM was retained within the fine particle pool than mature stems (Table 3).

In Situ Disappearance

Rate of NDF disappearance was faster for immature leaves than immature stems. Mature leaves and stems had similar rates of NDF disappearance. Extent of NDF disappearance was affected by maturity and immature fractions required longer rumen incubation times to reach extent of NDF disappearance than mature hay fractions (Table 2). Immature stems reached extent of NDF disappearance more quickly than immature leaves and mature stems also required longer rumen incubation to reach extent of NDF disappearance than mature leaves (Table 2).

Apparent extent of ruminal digestion was similar for small particles regardless of maturity level or fraction type. Apparent extent of digestion of large particles was greater for immature hay fractions than mature fractions. Apparent extent of ruminal digestion of leaf and stem large particles within maturity were similar (Table 2).

Discussion

Organic matter intake (OMI) of the leaf or stem hay fractions within stage of maturity was similar. Previous work (Poppi et al. 1980, Laredo and Minson 1975, and Cherney et al. 1990) found marked differences in voluntary intake of leaves or stems within stage of maturity by steers and sheep when diets were supplemented with rumen degradable N. They attributed the reduction in voluntary intake of stems to differences in retention time, apparent digestion, and passage rates between the 2 fractions. In contrast, differences observed for passage rate and ruminal retention time between leaf and stem fractions within maturity were not associated with differences in OMI in this study. The similarity in OMI between leaves and stems is best explained by similarities in fraction quality. Immature leaves and stems and mature leaves and stems contained similar NDF levels. Acid detergent fiber concentrations were similar for immature leaves and stems; however, mature leaves contained more ADF than mature stems. Dry matter (DM) fill of steers fed either immature stems or immature leaves was similar which indicated that rumen kinetics were similar for leaves and stems. Differences in DM fill and voluntary intake observed in previous work might be related to the resistance of forage fractions to mechanical and microbial breakdown. Generally as forages mature, secondary cell wall devel-

opment increases. This, coupled with lignification, makes mechanical and microbial breakdown more difficult (Van Soest 1994). Differences between leaf and stem cell structures and epidermal attachment can make stems more resistant to both microbial and mechanical breakdown (Minson and Wilson 1994). Previous work has demonstrated that the slower passage of stem material from the rumen apparently reduced voluntary intake and as forage matured, passage rates were reduced for both leaves and stems. In the current study, passage rates and rates of ruminal NDF disappearance of mature hay fractions were slower than immature hay fractions, thus resulting in a reduction in OMI and organic matter digestibility (OMD).

Similarity of leaf and stem fraction OMD within respective stage of maturity can be attributed to slower passage and longer ruminal retention time of the stem fraction when compared with the leaf fraction. These findings are similar to those reported by Poppi et al. (1985) and Hendricksen et al. (1981). Haferkamp et al. (1995) observed that the leaf fraction of RS-2 (quackgrass x bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh.) Love]) hybrid had consistently higher in vitro OM digestibility than stem throughout the growing season. Ruminal retention time is important to digestion and particle size reduction. In vitro data do not reflect differences in retention times and resistance to mechanical breakdown. Therefore, differences in in vitro OM digestibility are

not surprising because in vitro digestion does not account for passage rate and retention time, whereas in vivo procedures do. Differences in the 2 methods would likely occur if passage rate and retention were different. The longer forage is retained within the rumen the greater the opportunity for digestion and particle breakdown. Stems were retained longer, thus they had a greater opportunity for digestion.

For particles to exit the rumen via passage, Poppi et al. (1985) reported that particles must be reduced to a size small enough to pass through a 1.18-mm screen. Changes in the chemical composition of forage due to maturation can alter the relative resistance of a forage particle to digestibility and particle size reduction.

Bailey et al. (1990) reported that particle size of ruminal contents had a direct effect on the rate at which diets are passed from the rumen. They suggested that ruminal particle size was a function of the initial particle size of masticated feed and the rate of particle size reduction due to rumination and microbial breakdown. The geometric mean diameter of pre-ingested hay fractions in this study was larger for leaves than stems, and larger for immature fractions than mature fractions. Following ingestion of the hay fractions, geometric mean diameter of ruminal digesta was larger for stems than leaves which suggested that leaves were less resistant to particle breakdown than are stems.

Poppi et al. (1981) observed that cattle and sheep consumed more leaf than stem, apparently due to shorter retention of the leaf fraction within the rumen. They concluded that the controlling factor of particle retention and hence voluntary intake, was retention time of the small particle pool (particles $\leq$ 1.18 mm). They observed that the small particle pool contained about 72% of the total ruminal dry matter (DM). In this study, the small particle pool of the hay fractions accounted for 48 to 60% of the total rumen DM. If small particle retention was the rate limiting factor for organic matter intake (OMI), then the longer retention time of small particles for mature fractions compared with immature fractions could have depressed OMI of the mature fractions. However, if the small particle pool was the rate limiting factor, there should have been OMI differences between immature stem and leaf fractions. In contrast, Prigge et al. (1990) did not find a relationship between digesta passage and ruminal particle size, and concluded that other factors regulate passage from the rumen besides just particle size. Lechner-Doll et al. (1991) observed that

Table 3. Particle size of leaves and stems, ruminal digesta, omasal, and fecal content of subirrigated meadow immature and mature leaf and stem hay fractions fed to beef steers.

Site[2]	Immature		Mature		Contrasts[1]		
	Leaf	Stem	Leaf	Stem	(1)	(2)	(3)
Diet							
Screen size, mm							
$\geq$ 3.36	57.5	48.7	76.8	70.2	*	*	*
$\geq$ 1.18	74.5	82.6	89.6	87.5	*	NS[2]	*
$\geq$ 0.60	86.9	91.3	93.2	90.7	*	NS	*
< 0.60	13.1	8.7	6.8	9.2	*	NS	*
< 0.212	8.3	6.0	6.0	8.8	*	*	NS
GMD[3], mm	3.1	2.9	5.7	4.5	NS	*	*
Rumen							
Screen size, mm							
$\geq$ 3.36	15.3	20.8	9.7	17.3	NS	NS	NS
$\geq$ 1.18	33.0	41.5	27.7	39.8	*	*	NS
$\geq$ 0.60	42.0	51.7	38.6	53.0	*	*	NS
< 0.60	58.0	48.3	61.4	47.0	*	*	NS
< 0.212	33.8	27.0	35.3	23.3	NS	*	NS
GMD, mm	0.6	0.8	0.5	0.8	*	*	NS
Omasum							
Screen size, mm							
$\geq$ 3.36	0.9	1.1	0.3	1.4	NS	*	NS
$\geq$ 1.18	8.3	6.9	6.7	7.2	NS	NS	NS
$\geq$ 0.60	13.9	14.4	12.7	15.3	NS	NS	NS
< 0.60	86.1	85.6	87.3	84.7	NS	NS	NS
< 0.212	55.3	45.6	56.1	43.0	NS	NS	NS
GMD, mm	0.2	0.3	0.2	0.3	NS	NS	NS
Feces							
Screen size, mm							
$\geq$ 3.36	0.5	0.7	0.6	0.7	NS	NS	NS
$\geq$ 1.18	3.4	5.6	4.2	5.3	*	NS	NS
$\geq$ 0.60	7.9	13.4	8.4	14.0	*	*	NS
< 0.60	92.1	86.6	91.7	86.0	*	*	NS
< 0.212	69.4	52.9	62.7	47.4	*	NS	NS
GMD, mm	0.2	0.2	0.2	0.2	NS	NS	NS

[1]Contrasts 1 = immature leaves vs immature stems; 2 = mature leaves vs mature stem; 3 = immature hay fractions vs mature hay fractions.
[2]NS Contrast not significant (P > 0.05).
[3]GMD = geometric mean diameter (Waldo et al. 1971).
*Contrast significant (P < 0.05).

the breakdown of large particles is faster than passage of small particles, suggesting that small particles are selectively retained in the rumen. They concluded that particle density and size are the primary determinants of passage. Minson and Wilson (1994) suggested that as plants mature vascular cells and sclerenchyma strands thicken and lignify in both stems and leaves, making these particles stronger and more resistant to size reduction.

Poppi et al. (1980) reported that fecal particle size can provide an indication of the critical size for digesta to pass from the rumen. Poppi et al. (1981) observed that the critical size for ruminal passage was 1.18 mm for both cattle and sheep. Similarly, no differences were observed between the critical passage size of leaves and stems. Shaver et al. (1988) suggested that the critical particle size for rumen escape in dairy cattle was greater than 1.18 mm since 20 to 36% of fecal DM was retained on screens $\geq$ 1.18 mm compared

with the 1 to 2% retention reported by Poppi et al. (1981). Findings of this study are in agreement with those observed by Poppi et al. (1981) in that the critical particle size for rumen escape for both leaves and stems was $\leq$ 1.18 mm.

Although differences were observed in particle passage rates, retention times, resistance to particle breakdown, and digestion rates of leaf and stem fractions, these differences had no effect on OMI. Previous studies have demonstrated marked differences in voluntary intake of leaves and stems. Previous studies differ from this study in that leaf and stem differences were evaluated using a single monoculture forage species (i.e. ryegrass *Lolium perenne* L., crabgrass *Digitaria decumbens* Stent., windmill grass *Chloris gayana* Kunth, sorghum *Sorghum bicolor* (L.) Moench., pearl millet *Pennisetum glaucum* L., barley *Hordeum vulgar* L., or oats *Avena sativa* L.). Hay fractions evaluated in the present study were harvested

from a complex population consisting of 69% cool-season grasses, 23% sedges and rushes, and 8% forbs. Temperature, competition for water and nutrients, shading, and other environmental factors can cause deviations in forage quality, even when harvested at the same maturity (Buxton and Fales 1994). Hay was harvested in this study under conditions such that the quality of leaf and stem fractions within stage of maturity were similar, thus no differences in OMI or organic matter digestibility (OMD) occurred. Differences in quality between immature and mature forages resulted in lower OMI and OMD in steers fed mature leaf or stem hay fractions compared with steers fed immature fractions.

Conclusions

As forage grasses mature, particulate passage rates decrease, ruminal retention times increase, and forage particles become more resistant to mechanical and microbial breakdown. We conclude that these changes reduced voluntary intake of steers fed mature leaf and stem fractions compared with steers fed immature fractions, even when diets were similar in rumen degradable N. The reduction in OMI was a function of the physical and chemical properties of the hay fractions. Quality of immature leaves and stems was similar, thus resulting in similar OMI and OMD of steers fed these fractions. Likewise, quality of mature leaves and stems was similar, which resulted in similar OMI and OMD of steers fed those fractions. In this study, time of harvest had a greater impact on animal OMI than did the individual leaf or stem fractions when rumen degradable N was similar.

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Does ruminal retention time affect leafy spurge seed of varying maturity?

BRET E. OLSON AND ROSEANN T. WALLANDER

Authors are Professor and Research Associate, Department of Animal and Range Sciences, Montana State University, Bozeman, Mont. 59717-2900.

Abstract

Grazers ingest seeds of invasive forbs and may contribute to their spread by depositing viable seeds in uninfested areas. Some mature seed pass through the gastrointestinal (GI) tract of ruminants, but grazers consume flowerheads of invasive species from anthesis to dehiscence. We collected seed from the Eurasian leafy spurge (*Euphorbia esula* L.) at 3 stages of maturity (soft dough, hard dough, mature). With seed collected from these different stages, our objectives were to determine effects of 1) rate of passage through the GI tract of sheep on leafy spurge seed recovery, germinabilty and viability, 2) residence time in sheep rumen on seed germinability and viability, and 3) acid pepsin digestion, simulating the lower GI tract, on seed germinability and viability after different residence times in the rumen. More seed from the later stages of maturity were recovered in the manure. The greatest number of seed recovered only represented 3.9% of the number of ingested seed. Few seeds were recovered after day 4. Soft dough seed in manure would not germinate and was not viable, whereas hard dough and mature seed collected from manure during the first 4 day were viable. Pepsin had a slight effect on the number of mature seed recovered, but eliminated viability of recovered seed. Viability of non-pepsin treated seed from the hard dough and mature stages declined with greater residence time in the rumen. Thus, managers should be aware that livestock ingesting hard dough as well as mature seed may be dispersing viable weed seed.

Key Words: weed, *Euphorbia esula*, rumen, sheep

Resumen

Los herbivoros ingieren semillas de hierbas invasoras y pueden contribuir a su diseminación depositando semillas viables en áreas no infestadas. Algunas semillas maduras pasan a través del tracto gastrointestinal (TGI) de los rumiantes, pero los herbívoros consumen inflorecencias de especies invasivas desde la antesis hasta la dehiscencia. Colectamos semilla de "Eurasian leafy spurge" (Euphorbia esula L.) en tres estados de madurez (masa blanda, masa dura y madura). Utilizamos la semilla colectada en estas diferentes etapas de madurez para realizar un estudio con el objetivo de determinar los efectos de: 1) la tasa de paso a través del TGI de los borregos en la recuperación, germinabilidad y viabilidad de la semilla de "Leafy spruge" 2) el tiempo de residencia en el rumen del borrego en la germinabilidad y viabilidad y 3) la digestión de ácido pepsina, simulando el TGI bajo, en la germinabilidad y viabilidad de la semilla después de diferentes tiempos de residencia en el rumen En las heces se recuperó más semilla de los estados de madurez mas avanzados. El mayor número de semillas recuperadas solo represento el 3.9% del total de semillas ingeridas. Pocas semillas se recuperaron después del cuarto día. La semilla del estado de masa blanda presente en las heces no germinarían y no fueron viables, mientras que la semilla madura y en estado de masa dura colectadas de las heces durante los primeros 4 días fueron viables. La pepsina tuvo un efecto ligero en el número de semillas maduras recuperadas, pero elimino la viabilidad de la semilla recuperada. La viabilidad de la semilla madura o de masa dura no tratada con pepsina declinó al aumentar el tiempo de residencia en el rumen. Así los manejadores deben estar concientes de que el ganado que ingiere semilla en las etapas de masa dura y madura puede estar dispersando semilla viable de malezas.

Leafy spurge (*Euphorbia esula* L.), a deep-rooted perennial, was introduced to North America from Russia in the early 1800s and has become a noxious weed in the north central United States and southern Canada (Best et al. 1980). Herbicides will not eradicate extensive infestations of leafy spurge, although they can be used to control this noxious weed (Fay 1992). Sheep readily graze leafy spurge (Johnston and Peake 1960, Landgraf et al. 1984, Olson et al. 1996). Sheep will not eradicate leafy spurge, but they may be a cost-effective method to control leafy spurge (Fay 1991, Williams et al. 1996). However, sheep ingest leafy

spurge seed and deposit viable seed in their manure (Olson et al. 1997), thus they should be managed accordingly (Olson 1999).

Mature seed of some invasive species will pass through the gastrointestinal (GI) tract of ruminants. Most mature leafy spurge seed are digested completely in the GI tract, and viability of mature seed that pass through the GI tract is usually reduced (Lacey et al. 1992, Olson et al. 1997). However, grazers consume flowerheads from anthesis to dehiscence. Ripening of leafy spurge seed can extend from early July until fall (Hanson and Rudd 1933, Best et al. 1980). Seed in earlier stages of development may also pass through the animal and some may remain viable. For example, we collected fecal pellets of sheep grazing leafy spurge-infested rangeland from late June until early August

(Olson et al. 1997); the sheep passed viable seed over a 4 week period. However, we could not measure when or how many leafy spurge seed were ingested by sheep during that field study. Thus, we could not determine residence time, or the impact of digestion on seed viability.

For this study, we collected leafy spurge capsules (seed) at 3 stages of maturity (soft dough, hard dough, mature), and pulse-dosed sheep with a known amount of seed from these different stages. Our objectives were to determine 1) effects of rate of passage on seed recovery, germinabilty, and viability, 2) effects of residence time in the rumen on seed germinability and viability, and 3) effects of acid pepsin digestion, simulating the lower GI tract, on seed germinability and viability after different residence times in the rumen.

Materials and Methods

The leafy spurge fruit develops from a superior three-celled ovary (Messersmith et al. 1985). This capsule dehisces when ripe to distribute the seeds. Color differences in seedcoats have been used to determine seed maturity. Seed color changes from yellow, to yellow with brown tips, to brown, to grey brown, to mottled as seeds mature (Selleck et al. 1962, Wicks and Derscheid 1964). In contrast, Bakke (1936) suggested that immature seeds were grey and mature seeds were brown. Differences between age of maturity and seedcoat color may reflect that environments or biotypes differed at their collection sites. We distinguished immature from mature seeds using Selleck et al.'s (1962) and Wicks and Derscheid's (1964) approach. Yellow or partially yellow seeds were considered immature.

We collected capsules (seeds) of leafy spurge 3 times during the summer of 1994 (Lat 110°33'W, Long 45°46'). The first collection (24 June 1994) coincided with the "soft dough" stage when seed is immature and most capsules were easily cut with a fingernail (Stage 1). The second collection (19 July 1994) coincided with the "hard dough" stage when most capsules are indurate and difficult to cut with a fingernail (Stage 2). For the third collection (10 August 1994), we harvested fully developed capsules and opened these capsules to remove mature seed (Stage 3). In the field, all leafy spurge seed does not mature at the same time (Olson et al. 1997). Some mature seed were present in collections of all 3 stages (Stage 1, 25%;

Stage 2, 80%; Stage 3, 100%). We did not remove mature seeds from these first 2 stages because they would be available to grazing animals.

Rate of Passage and Viability

Capsules from Stages 1 and 2, and mature seeds from Stage 3 were fed to 5 rumen-cannulated ewes in separate trials. Each trial was separated by at least 14 days To ensure mastication of seed for each trial, 960 capsules (2,880 seed in Stage 3) were mixed with a small amount of barley and molasses in a feed bucket. Sheep had been exposed to the barley-molasses mix earlier. Most of the sheep consumed this mixture within a few hours, and all capsules were consumed within 24 hours. Before and during each trial ewes were fed grass hay ad libitum, and had access to water and a mineral block.

Sheep were in individual pens with plywood floors. All manure from each sheep was collected every 24 hours for 6 days after feeding the capsules (seeds). Each sheep averaged 95 g manure day^{-1} (dry weight). For each sheep, the 24 hour collection of manure was mixed, weighed while fresh, and divided into 9 subsamples. Three subsamples were selected randomly, and air-dried to determine moisture content. Three subsamples were selected randomly to recover seed. They were washed over sieves to remove excess organic material, and stored in a cool (2°C), dark location to prevent seed maturation until samples from all 6 days had been collected. Then, leafy spurge seed and capsules were identified and removed from this material, categorized (immature, mature, capsule), counted, and stored under cool, dark conditions. The remaining 3 subsamples of each 24 hour collection were dried at 37° C and used in a different study (unpublished).

We determined our ability to recover leafy spurge seed from manure by adding 30 leafy spurge seeds to each of 5 manure samples from penned sheep with no access to leafy spurge. These spiked manure samples were washed according to procedures described above. All 30 seeds were recovered in each of the 5 manure samples.

To determine germinability, seeds were soaked in 10% (v/v) chlorine bleach solution for 10 minutes to remove mold and bacteria, rinsed 3 times with distilled water, and then placed on moistened blotter paper. The number of recovered seed varied considerably. When more than 5 seeds were recovered, they were placed on moistened blotter paper in 5 petri plates. When more than 100 seeds were recov-

ered, 20 seeds were tested on each of the 5 petri plates. Petri plates were placed in a shaded box in a greenhouse with day and night temperatures of 22° C and 16° C, respectively. By allowing diffuse short-wave radiation but preventing direct short-wave radiation from reaching the seeds, the shaded box mimicked a plant canopy. Although alternating 30° C/20° C maximizes germination of leafy spurge seed (Hanson and Rudd 1933), most leaf spurge seed germinates in early spring in the field (Selleck et al. 1962). In their study, most seeds germinated after 10 days of maximum air temperatures of 21° or higher in late April, which is why we used the 22° C/16° C regimen. Photoperiod was approximately 16 hours day/ 8 hours night during this 28 June–20 July period. Distilled water was added as needed. Germinated seeds (radicles > 10 mm) were counted every other day and removed.

After 3 weeks, seeds in these petri dishes were stratified in cold (4°C), moist storage for 4 weeks. Germination of leafy spurge seed increases greatly when stratified for 4 weeks at 2–5° C, preceding a constant 20°C treatment (Best et al. 1980). Petri dishes were returned to the greenhouse for 18 days, and germinability was tested as above. Photo period was approximately 14 hour day/10 hour night during this 21 August–8 September period. Germinability included seeds that germinated during the first test and those that germinated after stratification. Control seed which had not been fed and had been stored under cool, dark conditions were tested alongside recovered seed. We used 20 unfed seeds on each of 5 petri plates from each of the 3 stages.

Seeds that did not germinate could be viable, i.e. will germinate later, or be nonviable. After the second germinability test, seeds that did not germinate were tested for viability using a 0.1% unbuffered tetrazolium solution (Grabe 1970). Viability included seeds that tested positive with tetrazolium. Total viability included seeds that germinated and seeds that tested positive with tetrazolium.

Residence Time, Acid Pepsin Digestion

Effect of residence time in the rumen was tested by nylon bag technique with 5 rumen cannulated sheep. Sixteen nylon mesh bags (5 cm x 10 cm, 50 mm mesh) per stage, each containing 100 capsules (300 seed - Stage 3), were placed in the rumen of each sheep. Four of the 16 bags were removed at each of 4 retention times

from each sheep: 12, 24, 48 and 72 hours. The bags were rinsed immediately with cold water to remove as much rumen fluid as possible, and then placed on paper towels until the bags were dry, but the capsules were still moist. Two bags of each set of 4 bags were air-dried for 48 hours. The other 2 were placed in a fresh, acid pepsin solution for 24 hours (Simao Neto and Jones 1987) to simulate conditions in the abomasum, then rinsed and dried as above. All seeds were tested for germinability and viability as described previously. Control seeds that were not placed in the rumen or treated with acid pepsin (controls) were tested for germinability and viability at the same time. For these tests, 3 subsamples of 30 seeds each were randomly selected from each nylon bag, including control seeds, and placed on 3 separate petri dishes. Mature and immature seeds were distinguished by seed color, and added together to determine total seed.

Statistical Analyses

We used the same sheep in the "rate of passage" and "residence time" studies. Each sheep was considered an experimental unit. The number of recovered leafy spurge seeds was estimated by determining the mean recovery from 3 of 9 subsamples, and then multiplying this mean by 9, which was an estimate of each sheep each 24 hour period. Number of mature seed recovered, germinability (%), viability (%), and total viability (%) were analyzed with repeated measures analysis of variance (n = 5; SAS 1988). Seed stage

was the between treatment effect; day (manure collection) within stage was the within treatment effect.

For the residence time-acid pepsin digestion trial, number of intact seed and total seed viability (%) were analyzed with repeated measures analysis of variance. Again, each sheep was an experimental unit. Seed stage was the between treatment effect; when the nylon bags were removed (0, 12, 24, 48, 72 hours) from the rumens of the sheep was the within treatment effect. Because there were only 5 experimental units (sheep), P-values less than 0.10 are presented (Gill 1981).

Results

Rate of Passage and Viability

The number of mature seed recovered over the 5 day period varied by stage (day by stage, P = 0.02; Table 1), but consistently declined with time (day, P = 0.02). Number of mature seed recovered was greatest for seed from Stage 3, intermediate for seed from Stage 2, and least for seed from Stage 1 (stage; P = 0.002). However, for any 1 day, the greatest number of mature seed recovered (Stage 3, day 2) only represented 2.4% of the number of seed consumed. Summed across the 5 day collection period, recovery of mature seed was 0.2% for Stage 1, 1.5% for Stage 2, and 3.8% for Stage 3. Few seeds were recovered after day 4.

Immature seed did not germinate because it did not contain a viable embryo. Germinability of mature seed collected

over the 5 day varied by stage (day by stage, P = 0.01; Table 1). The relatively high germinability of Stage 2 seed from day 4 reflected germinability of seed from only 1 of the 5 sheep (data not shown). Overall, germinability was greatest for seed from Stage 3, intermediate for seed from Stage 2, and 0 for seed from Stage 1 (stage; P = 0.07).

Viability was greatest for seed from Stage 3, intermediate for seed from Stage 2, and 0 for seed from Stage 1 (stage, P = 0.09; Table 1). No viable seed were passed after day 2. Overall, total viability (germinability + viability) was greatest for seed from Stage 3, intermediate for seed from Stage 2, and 0 for seed from Stage 1 (stage; P = 0.006).

Residence Time, Acid Pepsin Digestion

We could not control residence time of seed in the GI tract in the rate of passage trial. In this trial, we controlled residence time of seed in the rumen, with and without acid pepsin digestion. The number of total seed recovered, which included mature seed, immature seed, and seed within capsules, was lowest from Stage 1 (166 ± 3), intermediate from Stage 2 (226 ± 2), and greatest from Stage 3 (300 ± 0; stage, P < 0.0001). Overall, the total number of seed was not affected by residence time in the rumen (hour by stage; P = 0.36).

Viability of control seed, seed that was not placed into the rumen, was 65, 75, and 84% for Stages 1–3, respectively.

Table 1. The number of immature and mature seed recovered (No), and germinability (%), viability (%), and total viability (%, total viability = germinability + viability) of mature seed from Stages 1–3 recovered over a 5 day collection period. Each sheep received approximately 960 capsules (or 2,880 seed) of soft dough (Stage 1), hard dough (Stage 2), and mature seed (Stage 3). Some mature seed were present in seed fed for all 3 stages (Stage 1, 25%; Stage 2, 80%, Stage 3, 100%). Immature seed (yellow seed coat) never germinated and was never viable. Means plus or minus 1 SE (n = 5 sheep).

| Stage | Day | Seed recovered | | | | |
		Immature seed	Mature seed	Germinability	Viability	Total Viability
		---------(No)---------	---------(No)---------	----------------------------(%)----------------------------		
1	1	7.2 ± 3.2	2.4 ± 10.6	0.0	0.0	0.0
	2	1.2 ± 1.0	1.2 ± 6.0	0.0	0.0	0.0
	3	1.8 ± 1.8	0.6 ± 1.8	0.0	0.0	0.0
	4	0	0	0.0	0.0	0.0
	5	0	0.6 ± 0.6	0.0	0.0	0.0
2	1	3.6 ± 8.7	15.5 ± 10.7	19.4 ± 8.9	21.9 ± 15. 1	41.4 ± 12.0
	2	1.2 ± 3.1	6.9 ± 6.0	0.0	0.0	0.0
	3	0	3.0 ± 1.8	0.0	0.0	0.0
	4	0.6 ± 1.4	2.4 ± 1.2	10.0 ± 6.1	0.0	10.0 ± 6.1
	5	0	0	0.0	0.0	0.0
3	1	0	24.3 ± 12.5	31.7 ± 10.4	49.4 ± 17.8	81.3 ± 14.0
	2	0	71.1 ± 7.0	24.4 ± 4.1	11.6 ± 1.2	36.0 ± 5.0
	3	0	9.8 ± 2.0	0.0	0.0	0.0
	4	0	2.8 ± 1.5	0.0	0.0	0.0
	5	0	0.7 ± 0.7	0.0	0.0	0.0
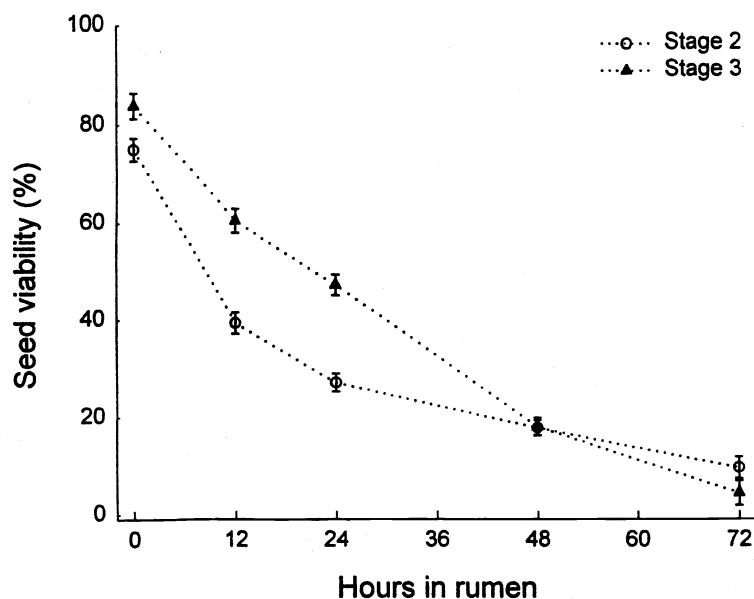
Fig. 1. Effect of residence time (h) in sheep rumen on total viability (%) of mature leafy spurge seed from Stages 2 and 3. Seed from Stage 1 were not viable after exposure to the rumen. Some mature seed were present in collections of all 3 stages (Stage 1, 25%; Stage 2, 80%, Stage 3, 100%). Total viability of seed which had not been placed in the rumen (0 h) was 65, 75, and 84% for Stages 1–3, respectively. Means plus or minus 1 SE (n = 5 sheep).

Viability of pepsin treated seed from all 3 stages was 0, thus this treatment was removed from the statistical model. Viability of non-pepsin treated seed varied with stage and time in the rumen (Fig. 1; hour by stage; P = 0.0001). Other than control seed (0 hour), viability of seed from Stage 1 was 0, whereas viability of seed from Stages 2 and 3 declined with time spent in the rumen.

Discussion

Rate of Passage and Viability

Some mature seed were present in collections of all 3 stages (Stage 1, 25%; Stage 2, 80%, Stage 3, 100%). On most days, immature and mature seed were recovered in the same proportions that they were fed, indicating immature seeds were resistant to digestion, at least structurally. For legumes, soft seed is destroyed by digestion whereas hard seed is relatively resistant to digestion (Simao Neto and Jones 1987, Gardener et al. 1993).

The greatest number of seed recovered (Stage 3) only represented about 4% of the number of seed consumed. In another study with leafy spurge, 18% of seed fed to sheep and goats was recovered in the manure of both animal species (Lacey et al. 1992). With a different invasive weed Centaurea

maculosa, 4% of the seed dosed was recovered in 1 trial with ewes, whereas 17% of the seed dosed was recovered in a second trial with rams (Wallander et al. 1995). Experimental protocol differed slightly between those trials; presumably these differences were not related to gender.

Few seeds were recovered after day 4. In related studies, most weed seeds pass within 4–5 days (Piggin 1978, Lacey et al. 1992, Wallander et al. 1995). Thus, animals grazing weed infested areas with mature seed should not be moved to uninfested areas for at least 4–5 days to prevent dispersal of viable seed.

Seed recovered from Stage 1 did not germinate and was not viable, even though about 25% of the seed was mature. Apparently, seed of leafy spurge at this early stage of development will not survive the GI tract of sheep. Some seed in the hard dough and mature stages (Stages 2, 3) germinated and remained viable, especially when passed within 2 days of ingestion.

Only seed recovered within 1 (Stage 2) to 2 days (Stage 3) would germinate or was viable, except for some Stage 2 seed recovered 4 days after ingestion. However, these seeds were recovered from the manure of only 1 of the 5 sheep. Possibly, seed had been entrapped within the GI tract, and were released all at once.

No viable seed were recovered after day

4, which may reflect the effect of the GI tract on seed passage and seed viability. Leafy spurge seed imbibes water quickly, beginning within 6 hours of exposure and continuing for an additional 42 hours (Selleck et al. 1962). Germinability was equal to (Stage 2) or less than (Stage 3) viability in seed recovered from the first day, whereas germinability was greater than viability on seed recovered on day 2 from Stage 3. This may reflect that germinability was enhanced by short-term residence time in the rumen. Lacey et al. (1992) found that leafy spurge seed did not germinate after 1 day in the rumen of sheep; seed recovered after 4 days were not viable. In a related study, viability of Centaurea maculosa seed was minimal after 5 days in the GI tract of sheep, but retained viability up to 10 days (end of trial) in mule deer (Wallander et al. 1995). Blackshaw and Rode (1991) also found that weed seeds survive for short periods of time in the rumen but viability drops off rapidly. The effect of different exposure periods in the rumen vary among different weed species (Harmon and Keim 1934), diets (Blackshaw and Rode 1991), and ruminants (Harmon and Keim 1934, Simao Neto et al. 1987).

Residence Time, Acid Pepsin Digestion

Control seed not placed in the rumen from Stages 1–3 were 65, 75, and 84% viable, respectively. Others have found viability of leafy spurge seed ranging from 51% to 90% (Hanson and Rudd 1933, Bakke 1936, Bowes and Thomas 1978, Lacey et al. 1992).

The survival of seed passing through the GI tract is influenced by residence time in the GI tract and exposure to digestive enzymes. Nylon bags placed in the rumen, such as in this study, can be used to simulate different residence times in the rumen but do not expose seeds to digestive secretions in the lower GI tract, which is why we included the pepsin treatment. In addition, using seed in nylon bags does not include the effects of mastication during prehension or rumination on the seed coat, which may be a key factor that influences digestion, disintegration, and viability of seed. This would explain why more seed were recovered in this trial compared with the "rate of passage" trial where seed were ingested by the sheep and passed through their entire GI tract.

Our pepsin treatment may have been excessive; none of the pepsin-treated seed were viable. In another nylon bag trial, a 24 hour pepsin treatment greatly reduced

viability of seed from signal grass *Bracharia decumbens*, but had much less of an effect on carpet grass *Axonopus affinis* (Simao Neto and Jones 1987). Our 24 hour pepsin treatment exceeded the 10–12 hours where seed is normally exposed to acid pepsin in the GI tract (Ocumpaugh and Swakon 1993), which may explain why our seed were no longer viable following this treatment. In the seed recovery-seed viability part of our study and in related studies, viability of seed passing through the GI tract is greatly reduced but not completely eliminated (Heady 1954, Lacey et al. 1992, Wallander et al. 1995, Olson et al. 1997). In the lower GI tract, some seed apparently escape gastric secretions in the abomasum (pepsin, hydrochloric acid) and small intestine (trypsin, chymotrypsin), possibly by passing through the system quickly.

Even without the pepsin treatment, soft dough seed were not viable, presumably because the seed was too soft and could not resist disintegration or microbial digestion in the rumen. Most soft seeds disintegrate after 2 days in the GI tract (Gardener et al. 1993). Viability of seed from the hard dough and mature stages which was not exposed to pepsin declined with time spent in the rumen, indicating that the seed coat softens with time and becomes susceptible to microbial digestion. Germinability (viability) of ingested seed typically declines with greater digestion times (Ocumpaugh and Swakon 1993, Ocumpaugh et al. 1995).

Conclusion

Many mature seed from the hard dough and mature stages were digested in the GI tract, but some of the recovered seed were viable. Thus, managers should be aware that livestock ingesting hard dough leafy spurge seed in late June and early July may be dispersing viable seed. With one exception, all viable seed passed within 2 days of ingestion. Because of this exception and results from another study (Lacey et al. 1992), livestock grazing leafy spurge should not be moved until all possible viable leafy spurge seed has passed, conservatively 4–5 days. Sheep will graze leafy spurge (Olson 1999); however, they need to be managed in a manner that will help control the problem, not contribute to it.

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Cheatgrass competition and establishment of desert needlegrass seedlings

DAWN L. RAFFERTY AND JAMES A. YOUNG

Authors are formerly research assistant and range scientist, USDA/ARS, Exotic and Invasive Weed Management Research Unit, 920 Valley Rd., Reno, Nev. 89512. Current address of first author, Nevada Department of Agriculture, 350 Capital Hill, Reno, Nev. 89502.

Abstract

Desert needlegrass (*Achnatherum speciosum* [Trin. & Rupr.] Barkworth) is potentially a valuable native species for use in restoration seedings in the more arid portions of the Great Basin. Seedlings of desert needlegrass were grown in a greenhouse with 5 different densities of cheatgrass (*Bromus tectorum* L.). The densities of cheatgrass used in the greenhouse experiments were derived from sampling populations in the field where desert needlegrass is adapted and seedling recruitment is desired. Cheatgrass is known to close sites to the establishment of seedlings of perennial grasses through competition for moisture. The response variable was height of desert needlegrass shoots. Height measurements were taken weekly for 12 weeks following seedling emergence. During the first 5 weeks following emergence there were no significant ($P \leq 0.05$) differences in the height of desert needlegrass seedlings among treatments. From week 5 through week 12, there was a highly significant ($P \leq 0.001$) difference in the height of desert needlegrass shoots between the control and all levels of cheatgrass density. Reducing the density of cheatgrass seedlings in the greenhouse to the equivalent of 25% of the density present in the field still did not allow the establishment of the perennial grass seedlings. Even though desert needlegrass is adapted for natural establishment in the drier portions of the central Great Basin, some form of cheatgrass control is required for the perennial grass seedling establishment if cheatgrass is present. Cheatgrass control has to be more than a reduction in density, it has to be near complete control of the annual grass.

Key Words: *Achnatherum speciosum, Bromus tectorum*, restoration, temperate deserts.

Resumen

El "Desert needlegrass" (*Achnatherum speciosum* [Trin. & Rupr.] Barkworth) es una especie nativa potencialmente valiosa para uso con fines de siembras para restaurar las porciones mas áridas de la Gran Cuenca. En un invernadero se cultivaron plántulas de "Desert needlegrass" con 5 diferentes densidades de "Cheatgrass" (*Bromus tectorum* L.). Las densidades de "Cheatgrass"utilizadas en los experimentos de invernadero se derivaron de muestreos de poblaciones en el campo donde el "Desert needlegrass" es adaptado y se desea el establecimiento de plántulas. El "Cheatgrass"es conocido por cerrar los sitios para el establecimiento de plántulas de zacates perennes mediante la competencia por humedad. La variable respuesta fue la altura de los tallos del "Desert needlegrass". La altura se midió semanalmente por 12 semanas después de la emergencia de las plántulas. Durante las primeras 5 semanas después de la emergencia la diferencia de altura de las plántulas de "Desert needlegrass" no fue significativa ($P \leq 0.05$) entre tratamientos. De la semana 5 a la 12 la diferencia de altura de los tallos de "Desert needlegrass" entre el tratamiento control y todos los niveles de densidad de "Cheatgrass" fue altamente significativa ($P \leq 0.001$). Ni aun reduciendo en el invernadero la densidad de plántulas de "Cheatgrass" a un equivalente del 25% de la densidad presente en el campo permitió el establecimiento de plántulas de zacates perennes. Aunque el "Desert needlegrass" esta adaptado para el establecimiento natural en la porciones más secas de la Gran Cuenca central, si el "Cheatgrass"esta presente se requiere algún grado de control de esta especie para que ocurra el establecimiento de plántulas de zacates perennes. El control del "Cheatgrass" tiene que ser mas que una reducción en la densidad. Tiene que ser casi un control completo del zacate anual.

Revegetation attempts in semi-arid environments of the Great Basin often fail due to competition from the exotic annual cheatgrass (*Bromus tectorum* L.) (Robertson and Pearce 1945, Evans 1961, Harris 1967, Nelson et al. 1970, Aguirre and Johnson 1991, Monsen 1992, Nasri and Doescher 1995). The nature of this competition between cheatgrass and seedlings of perennial species has been investigated in numerous studies (Hull 1963, Melgoza et al. 1990, Francis and Pyke 1996).

In the drier portions of Great Basin rangeland, areas with 100 to 200 mm of annual precipitation, revegetation attempts have seldom been attempted because of the lack of suitable plant mate-

rial. If the site is too dry for crested wheatgrass (*Agropyron desertorum* [Fischer] Schultes) revegetation has seldom been attempted except on sand where Indian ricegrass (*Achnatherum hymenoides* [Roemer & Schultes] Barkworth) has been successfully established from seeding (Young et al. 1995). Disturbance does occur in these near arid environments in the form of utility and highway construction. The contractors for such projects are required to attempt to revegetate the disturbed areas. Obviously, an adapted source of a native plant material is required for these attempts.

Desert needlegrass (*Achnatherum speciosum* [Trin. & Rupr.) Barkworth) is a perennial bunchgrass native to some of the driest portions of the temperate deserts of the Great Basin that have non-salt affected soils (Young and Evans 1980). Among the *Achnatherum* species, desert needlegrass is fairly unique in hav-

ing seeds that readily germinate without the constraints of dormancy.

Field work associated with this study was conducted on the right-of-way of a large natural gas transmission line that crosses the base of the Dog Skin Mountains some 35 km north of Reno, Nev. (39° 51' N, 119° 48' W).

Pipeline rights-of-way, like mining exploration roads, create a unique revegetation problem on semi-arid rangelands. They create linear disturbances that cross many plant communities and pastures. It is seldom feasible to fence these linearly disturbed areas to prevent grazing during the seedling establishment stage. Because of the relatively short distance across such linearly disturbed areas and the obvious large edge effect, it is often possible to encourage spontaneous seedling recruitment from the adjacent, undisturbed plant communities (Young et al. 1995). Unfortunately, if the adjacent vegetation happens to include a highly invasive species such as cheatgrass, succession on the disturbed right-of-way is going to be truncated by the exotic weed. In the construction of large diameter pipelines, the excavation and burial process creates a raw, undeveloped soil in at least the center of the right-of-way. Such levels of soil disturbance create ideal conditions for invasive weeds. If the right-of-way is not returned to dominance by desirable perennial species, it will serve as a corridor for the movement of new invasive species. The passage of construction equipment and mulching with straw almost insures inoculation of the sites with new weeds.

Our purpose in this portion of the study of pipeline revegetation was to determine the effect of varying densities of cheatgrass on the growth and establishment of seedlings of desert needlegrass.

Materials

The study was conducted in a greenhouse located at Reno, Nev. Plants were grown in cylinders 95 cm deep by 30 cm in diameter. They were filled with soil collected from the pipeline right-of-way. The soils adjacent to the collection site are a coarse-loamy, mixed, mesic Xerollic Haplargid (Melgozoa et al. 1990). Seed of both cheatgrass and desert needlegrass were collected at the Dog Skin Mountains, adjacent to the field study site.

The density of cheatgrass seeds used in the experiment was arrived at by randomly locating plots along the utility corridor and counting the number of cheatgrass

plants per unit of area. From the average density the following seeding densities were established: 1) 100% of field conditions, 283 seeds per cylinder; 2) 75% of field density, 212 seeds per cylinder; 3) 25% of field density, 71 seeds per cylinder; and 4) the control with no cheatgrass. A preliminary germination trial indicated the cheatgrass seeds collected had about 90% germination. Each cylinder was over planted by 10% and thinned after 7 days to insure the final densities were as designed. Desert needlegrass seeds were planted at the rate of 3 per cylinder and thinned after 7 days to 1 per cylinder. Both species were planted on the same day. Cheatgrass seeds were distributed equally over the soil surface and the desert needlegrass seeds planted in the center of the cylinder.

The soil in each cylinder was saturated and allowed to drain to field capacity prior to seeding. The surface soil was kept moist until emergence occurred. No further water was added until the 7th week when seedlings of both species exhibited signs of severe moisture stress. After the 7th week, 2 liter of water were added to each cylinder weekly.

The experimental design was completely randomized with 4 replications (cylinder) per treatment. The treatment design was 5 densities x 12 weeks in a factorial on the random factor of weeks. The cheatgrass density was treated as a fixed effect. The data was analyzed with a one way analysis of variance with cylinders nested within density by week.

Results and Discussion

During the first 4 weeks there were no significant differences ($P < 0.05$) in the shoot height of desert needlegrass seedlings among treatments. Beginning

Table 1. Significant differences among densities as measured by desert needlegrass shoot height beginning in the 5th week. Weeks on through 4 (data not shown) had no significant differences at the 0.05 level of probability.

Weeks from planting	df	f-value	p-value
5	4	3.82	0.025
6	4	7.00	0.002
7	4	5.76	0.005
8	4	6.36	0.003
9	4	5.85	0.005
10	4	7.33	0.002
11	4	7.30	0.001
12	4	7.73	0.001

with the 5th week of growth, there was a significant($P < 0.001$) main effect of cheatgrass density (Table 1). Both the control with no cheatgrass and the 100% of the field density of cheatgrass were significantly ($P < 0.05$) different from the other 3 densities at week 5. From week 6 through week 12, the control was significantly different from all other densities (Table 2).

Starting with the soil in the cylinders at field capacity and keeping the surface soil damp until emergence occurred allowed desert needlegrass to compete with cheatgrass for the first 4 weeks after planting. Apparently, as the root systems of cheatgrass plants occupied sufficient area of the soil within the cylinders, the competition for moisture became severe. Not even the addition of supplemental moisture would prolong the life of the desert needlegrass seedlings.

Research by Evans (1961) with a similar greenhouse experiments with cheatgrass and crested wheatgrass that was followed by extensive monitoring of micro-environmental conditions in the field (Evans et al. 1970), clearly determined that virtually total control of cheatgrass was necessary

Table 2. Mean desert needlegrass shoot height in cm in relation to cheatgrass density by week. Percentage density was calculated based on 3,875 cheatgrass plants per m^2 as 100%. Weeks 1 through 4 showed no significant differences and were not included in table .[1]

Weeks after planting	Cheatgrass density				
	0	25	50	75	100
	(cm)				
5	9.9a	7.5ab	6.9ab	6.4ab	5.9b
6	12.4a	7.5b	6.9b	6.6b	5.9b
7	13.1a	7.5b	6.8b	5.6b	5.0b
8	13.2a	6.3b	6.0b	4.4b	3.9b
9	13.2a	5.5b	4.6b	4.4b	4.0b
10	13.3a	5.9b	4.3b	3.8b	3.6b
11	13.5a	6.0b	4.8b	3.0b	3.0b
12	13.9a	6.3b	4.8b	3.3b	3.1b

[1]Means within rows followed by the same letter are not significantly different at the 0.055 level of probability as determined by Duncan's Multiple Range Test.

to insure the establishment of crested wheatgrass. Despite the natural adaptation of desert needlegrass to extremely arid conditions, cheatgrass can still out compete seedlings of the perennial for moisture. Cheatgrass only became abundant in the most arid portions of the Great Basin during the last 2 decades of the 20th century (Young and Tipton 1990).

The need for weed control before seeding perennial grasses in right-of-way revegetation projects such as the one along the Dog Skin Mountains is obvious. However, in such industrial revegetation projects on rangelands the contracts for revegetation often ignore biological reality. The pipeline contractor often has to post a bond to insure restoration of the disturbed site. In such arid situations, fall seeding of perennial grasses gives the best results, but weed control has to wait until after cheatgrass germinates in the spring. In such arid situations cheatgrass rarely germinates in the fall. This requires a year delay in the revegetation process and prolongs the bonding period. Contractors for large transmission pipelines in non-petroleum producing areas are not always aware of local concerns and are not interested in prolonging the revegetation process once the construction is completed. Their request is for research agencies to provide them with an adapted perennial grass that will fit the environmental requirements of the site. The results of this study clearly illustrate this is impossible with out an adequate weed control program for cheatgrass. Industrial weed control and revegetation on utility rights-of-way on rangelands should be coordinated with grazing management systems for the pastures through which the construction passes. If the grazing management system accommodates a year of rest, make it the seedling year for the revegetation. This will create a patch work of weed control and revegetation activities instead of a continuous flow of revegetation along the rights-of-way, but it has a chance for successful revegetation of the disturbed sites.

Yes, such an approach would be more expensive, but if you can not afford to restore the rangeland environment, do not destroy the vegetation fabric in linear disturbance.

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Drought and grazing: IV. blue grama and western wheatgrass

E.J. ENEBOE, B.F. SOWELL, R.K. HEITSCHMIDT, M.G. KARL AND M.R. HAFERKAMP[1]

Authors are former graduate student and Associate Professor, Dept. of Animal and Range Sci. Mont. State Univ., Bozeman, Mont. 59715; Supervisory Rangeland Scientist, former Postdoctoral Rangeland Scientist, and Rangeland Scientist USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Rt. 1 Box 2021, Miles City, Mont. 59301.

Abstract

An understanding of the impacts of grazing during and following drought on rangeland ecosystems is critical for developing effective drought management strategies. This study was designed to examine the effects of drought and grazing on blue grama [*Bouteloua gracilis* (H.B.K) Lag. ex Griffiths] and western wheatgrass [*Pascopyrum smithii* Rydb. (Love)] tiller growth dynamics. Research was conducted from 1993 to 1996 at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Mont. An automated rainout shelter was used during 1994 to impose a severe late spring to early fall (May to October) drought on 6 of twelve, 5- x 10-m non-weighing lysimeters. Twice replicated grazing treatments were: 1) grazed both the year of (1994) and the year after (1995) drought; 2) grazed the year of and rested the year after drought; and 3) no grazing either year. Drought had minimal impact on tiller relative growth rates of plants grazed twice, although it reduced (P ≤ 0.01) rates of axillary tiller emergence for blue grama (79%) and western wheatgrass (91%), respectively. Defoliation periodically increased relative growth rates (P ≤ 0.05) and tiller emergence (P ≤ 0.01) of both species. Neither drought nor grazing affected tiller densities or tiller replacement rates of either species nor did they affect productivity of blue grama. Drought, however, reduced (P ≤ 0.01) productivity of western wheatgrass 50% in 1994 whereas grazing reduced productivity (P ≤ 0.01) by 46% in 1994 and 69% in 1995. Moderate stocking levels (40–50% utilization) during and after drought did not adversely affect the sustainability of these dominant native grasses.

Key Words: *Bouteloua gracilis, Pascopyrum smithii*, production, rainout shelter, rest, water potential

Resumen

Un entendimiento de los impactos del apacentamiento durante y después de la sequía en los ecosistemas de pastizal es critico para desarrollar estrategias efectivas de manejo de la sequía. Este estudio se diseño para examinar los efectos de la sequía y el apacentamiento en al dinámica de crecimiento de los hijuelos de "Blue grama" [*Bouteloua gracilis* (H.B.K) Lag. ex Griffiths] y "Western wheatgrass" [*Pascopyrum smithii* Rydb. (Love)]. La investigación se condujo de 1993 a 1996 en el Laboratorio de Investigación de Ganado y Pastizales Fort Keogh cerca de Miles City, Mont. Durante 1994 se utilizo un protector de lluvia automatizado para aplicar una sequía severa de fines de primavera e inicios de otoño (Mayo a Octubre) en 6 de los 12 lisímetros de 5 x 10 m. Los tratamiento de apacentamiento se repitieron 2 veces y fueron:1) apacentado en el año de la sequía (1994) y el año siguiente (1995), 2) apacentado el año de la sequía y descansado el año siguiente y 3) sin apacentamiento en ambos años. La sequía tuvo un impacto mínimo en las tasas relativas de crecimiento de los hijuelos de plantas apacentadas doble, aunque redujo (P ≤ 0.01) las tasas de emergencia de hijuelos auxiliares del "Blue grama" (79%) y "Western wheatgrass" (91%). La defoliación periódica incremento las tasas relativas de crecimiento (P ≤ 0.05) y la emergencia de hijuelos (P < 0.01) de ambas especies. Ni la sequía ni el apacentamiento afectaron las densidades de hijuelos o las tasas de remplazo de estos en ninguna de las especies, tampoco afectaron la productividad del "Blue grama". Sin embargo, la sequía redujo la productividad (P ≤ 0.01) de "Western wheatgrass", en 50% en 1994, mientras que el apacentamiento redujo la productividad (P ≤ 0.01) en 46% en 1994 y 69% en 1995. Niveles moderados de carga (40–50% de utilización) durante y después de la sequía no afectan adversamente la sustentabilidad de estos zacates nativos dominantes.

The Northern Great Plains support 7 million animal units (AUs) in the U.S. and Canada (USDA 1993, Willms and Jefferson 1993). Campbell (1936) stated that 2 or 3 years out of 10 would be drought years in the Northern Great Plains. Drought and grazing can affect plant productivity and decrease plant longevity (Ludlow 1986). Large portions of plant communities within the Northern Great Plains are dominated by blue grama (*Bouteloua gracilis*, [H.B.K] Lag. ex Griffiths) and western wheatgrass (*Pascopyrum smithii*, Rydb.). It is apparent that these 2 plant species have evolved with the combined effects of drought and herbivory. Therefore, it is important when managing rangelands to know how individual plants persist in the face of these stressors.

Many researchers have examined the role of tillers in plant survival (Richards et al. 1987, Olson and Richards 1988, Bullock et al. 1994, Zhang and Romo 1995), but quantitative studies on the

impacts of grazing during and after drought on tiller population dynamics are lacking. It has been hypothesized that grazing during and following drought can suppress recovery rates of individual plants as well as plant communities (Pieper and Heitschmidt 1988, Burkhardt 1996). To test this hypothesis, we examined the effects of grazing during and after a growing season drought on xylem water potentials, tiller relative growth rates (RGR), seasonal axillary tiller emergence, annual tiller replacement, tiller densities, and aboveground net primary production (ANPP) of blue grama and western wheatgrass. Heitschmidt et al. (1999) have published effects of drought on soil water, vegetative productivity and plant species composition.

Fig. 1. Monthly precipitation (cm) from January 1993 through December 1996 and long-term (115 yr) average at Miles City, Mont. including the drought treatment in 1994 (NOAA 1996; Heitschmidt et al. 1999).

Materials and Methods

Study Area

This study was part of a large rainout shelter project conducted on the USDA, ARS Fort Keogh Livestock and Range Research Laboratory near Miles City, Mont. (46°19'45'N 105°49'45'W). This area is representative of the semi-arid mixed grass prairie of the Northern Great Plains. Native vegetation on the 22,500-ha research station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mix (Kuchler 1964). Long-term annual precipitation averages 34-cm (NOAA 1996) with about 60-70% received during the mid-April through mid-September growing season (Fig 1). Temperatures may exceed 38°C during summer and decrease to –40°C during winter. The average frost-free period is 150 days.

Lysimeters and Treatments

Twelve, 5- X 10-m non-weighing lysimeters were arranged perpendicularly to the slope along a 65-m transect in 2 groups of 6 lysimeters with a 5-m area between groups within a grazing exclosure. An automated rainout shelter was constructed to control the amount of precipitation received on 1 of the 2 sets of 6 lysimeters. The 12- X 35-m metal framed "roof" was mounted on 15-cm diameter plastic wheels atop seven, 5-cm wide rails stationed about 75-cm above the soil surface. Rails extended from the top edge (i.e., upslope) to 15-m below the bottom edge of the lysimeters. Rails were located directly over lysimeter borders. The shelter was equipped with a moisture sensitive conductance plate that when wetted, activated a small electric motor and its associ-

ated drive system, which moved the shelter across the lysimeters.

Following the 1993 pre-treatment baseline year, twice replicated treatments were: 1) grazed during the year of drought and rested the year after, hereafter referred to as G94; 2) grazed both the year of the simulated drought and the year after, hereafter referred to as the G94-95; and 3) rested in all years, hereafter referred to as the ungrazed treatment (UG). The same 3 treatments were repeated in the non-drought set of lysimeters. Lysimeters were grazed intensively with 6 ewes and their twin lambs for a few hours in early June and early July of both 1994 and 1995 to achieve 40–50% utilization. The simulated drought was imposed (1 growing season) from mid-May to early October 1994.

Precipitation, Soil Water, and Xylem Water Potentials

Precipitation was monitored on site using standard rain gauges (Heitschmidt et al. 1999). Soil water was estimated a minimum of once a month from April through October at depths of 15-, 30-, 60-, 90- and 120-cm using a dielectric soil water probe (Heitschmidt et al. 1999).

Xylem water potentials of blue grama and western wheatgrass plans growing in the ungrazed drought and non-drought treatments were estimated on 7 dates between 18 May and 28 July, 1994 and 6 dates between 15 May and 2 August, 1995. Measurements were made at 0430 and 1230 hours on the youngest fully expanded leaves of individual plants using standard pressure chamber technqiues (Scholander et al. 1965). Sample plants were randomly selected along a transect

within each lysimeter. Sample size per species/sample date/sample time/lysimeter was 1 in 1994 and 2 in 1995.

Tiller and Production Measurements

Six permanent 14- x 18-cm quadrats per lysimeter were randomly established within mixed blue grama and western wheatgrass communities. Quadrat locations were restricted to areas not previously sampled, and at least 50-cm inside the plot edge. Colored wire rings were used to permanently identify 10 study tillers per quadrat, 5 each of blue grama and western wheatgrass. The same quadrats were used for the duration of the research. If a marked tiller produced axillary tillers at anytime during the growing season, the axillary tillers were marked with a different color to distinguish them from primary tillers. Different tillers were marked in the same manner in 1995.

From an initial population of 360 tillers per species, repeated, season-long measurements (n = 17 in 1994; n = 14 in 1995) were taken on 270 blue grama and 329 western wheatgrass tillers in 1994 and 320 blue grama and 341 western wheatgrass tillers in 1995. Differences between marked and measured tillers were due to lost markers or excluding data from tillers which were not grazed twice. Tiller measurements began in mid-May and continued weekly through August with additional measurements for quantification of any autumn growth. Information gathered on an individual tiller during each visit included: plant height, phenology, number of leaves, axillary tillering and tiller senescence.

Measuring tillers nondestructively prevented direct estimates of cumulative biomass through time. Height measurements were converted to biomass by developing hiehgt-weight relationships of tillers located on the same clayey range site in the near vincinity of the lysimeters. For each species, tillers were measured, clipped at the soil surface and bundled together with other tillers of the same height (+/– 1 cm). Five bundles per species representing the range of heights for those tillers found in the lysimeters were collected before each grazing event. Individual bundles containing 5 western wheatgrass and 10 blue grama tillers were placed in plastic bags, transported to the laboratory and immediately cut into segments. Tiller bundles were cut from the base upward in segments of 1-cm for blue grama and 3-cm for western wheatgrass in a manner similar to Tusler (1993), so all height ranges of plants found in the lysimeters were represented. All segments were oven dried at 60°C for 48 hours before weighing.

Tiller relative growth rates (g g^{-1} day^{-1}) were calculated according to Radford (1967) as:

Tiller relative growth rates = $(\log_e W_{t+1} - I^{-1}$

(1)

Density of western wheatgrass was determined by counting total number of live tillers within each quadrat. Because of the "mat-like" growth form of blue grama, density was determined by counting the number of tillers within a 5.75-cm^2 circular plot, or 2% of the quadrat area, randomly located within each permanent quadrat. Densities were measured on 24 May 1994, 1995, and 1996.

Standing crop inside 20 randomly located 250-cm^2 quadrats per lysimeter was harvested monthly by species from 1993 to 1996 (Heitschmidt et al. 1999). Samples were oven dried at 60°C, separated into live and dead components and then weighed. Aboveground net primary production was calculated for blue grama and western wheatgrass by summing all positive increases in standing crop from April to November.

Data Summarization and Analyses

Soil water measurements were analyzed using repeated measures analysis of variance (AOV) with year, depth, treatments and dates in the model. Years and/or dates and all associated 2- and 3-way interactions were analyzed as within plot repeated measures and tested using full model residuals (Heitschmidt et al. 1999).

Pre-dawn and mid-day water potential data were analyzed separately using repeated measures AOV with drought treatment, plant species, and date as main effects. The error terms for testing the main effects of drought treatments were the replication by treatment interaction. The error terms for testing the main effects of species and the interaction effects of species and drought treatments were replication by treatment by species. The full model residuals were used to test the repeated measures effects of dates and all associate 2- and 3-way interaction effects.

Growth records were summarized using average tiller relative growth rate within 3 time periods. Time periods were: 1) the last 2 weeks of May before the first grazing event; and 3) July to October of 1994 and July to early September 1995. The number of 1994 post-grazing sampling dates was 8, but this was reduced to 4 in 1995, as both species were essentialy dormant throughout both summer periods.

A univariate, repeated measures analysis of variance model was used to analyz data. A 2-way AOV was used to determine the effects of drought and grazing on percent tiller recruitment. Tiller relative growth rates and tiller recruitment are reported for tillers that were grazed twice, since the majority (≥ 85%) of the tillers in the lysimeters were grazed during both grazing events. This was done to reduce confounding effects of combining once grazed and twice grazed tillers.

Tiller densities from May 1994 (i.e., pre-treatment) were included as a covariate in the 2 following years' data. Means were considered to be significantly different when P ≤ 0.05, unless noted otherwise. Individual lysimeters were considered experimental units for all analyses.

Heitschmidt et al. (1999) reported plant functional group and species compositional differences among treatment plots in 1993. We initially used the pre-treatment year (1993) blue grama and western wheatgrass productivity estimates as covariates in subsequent year analyses. Since the covariates were never significant (P ≥ 0.22), they were subsequently excluded from the final analyses.

Drought treatments might be considered pseudo-replicated, according to Hurlbert (1984), since the rainout shelter size and cost precluded classical treatment replication. The use of a single rainout shelter to test the effects of drought is common in the literature (Busso 1988, Busso et al. 1989, 1990, Frank and Ries 1990, NeSmith and Ritchie 1992, Busso and Richards 1993, 1995). Statistical tests used in our study were conservative, since the experimental units were not quadrats, individual plants or individual tillers. In addition, analyses were conducted in a manner similar to the first paper in this series (Heitschmidt et al. 1999).

Results

Precipitation, Soil Water, and Water Stress

In 1993, the pre-treatment year, total annual precipitation was 38% above the long-term average of 34-cm (Fig. 1). Annual precipitation in 1994 was 24.7-cm, 24% below average. Precipitation from 1 May to 31 October 1994 was 16.3 cm compared to the 27.1-cm average. Total annual precipitation for 1995 and 1996 was similar to the long-term average (Heitschmidt et al. 1999).

Heitschmidt et al. (1999) previously reported no differences in soil water dynamics between imposed 1994 drought and natural precipitation and grazing treatment lysimeters. The only significant main effects were year and date .

The drought treatment did not affect either pre-dawn or mid-day leaf water potential of either blue grama (P = 0.93) or western wheatgrass (P = 0.40; Table 1). Water potentials were affected by plant species (midday; P ≥ 0.01), date (P ≥ 0.01) and their interaction (P ≥ 0.01). Date was the most important factor accounting for 85% of the total sum of squares for predawn and 58% for midday water potentials. Species accounted for less than 5% of the total sum of squares. The date effect followed anticipated seasonal trends of increasing water potentials with decreasing soil water content. The absence of significant drought treatment-by-date (P ≥ 0.18) and drought treatment-by-date-by-species (P ≥ 0.86) interactions showed that the magnitude of water stress was similar in both the drought and non-drought treatment plots during 1994 (i.e., the year of the imposed drought) as well as 1995.

Utilization

Ninety-eight percent of marked blue grama tillers (265 of 270) in 1994, and 97% (309 of 320) in 1995 remained in a vegetative phenological stage. On average, utilization was 39% and 47% on blue grama tillers for the first and second grazing events in 1994, and 23% and 45% for the first and second grazing events in 1995. Over 85% of the marked blue grama tillers in the grazed lysimeters were grazed twice in both years.

Ninety-eight percent (323 of 329) in

Table 1. Predawn and midday leaf water potentials (MPa) for western wheatgrass (Pasm) and blue grama (Bogr) plants growing in drought and nondrought[1] lysimeters at Fort Keogh in 1994 and 1995.

Year	Date	Pre-dawn[2] Pasm	Pre-dawn[2] Bogr	Mid-day[2] Pasm	Mid-day[2] Bogr
			(MPa)		
1994	18 May	−0.32d	−0.42d	−2.36cde	−0.62e
	31 May[3]	−0.24d	−0.31d	−2.81bcd	−2.12cd
	14 Jun[3]	−0.44cd	−0.20d	−3.62ab	−2.69bc
	23 Jun[3]	−0.75cd	−1.39c	−3.16abc	−2.11e
	30 Jun	−4.18a	−4.04b	−2.90bcd	−2.29cd
	13 Jul[4]	−1.04bc	−4.92a	−4.00a	−4.28a
	28 Jul[3]	−4.46a	−5.00a	−3.15abc	−4.48a
1995	15 May	−0.43cd	−0.26d	−1.58e	−0.71e
	2 Jun	−0.99bc	−0.59d	−2.22de	−2.08cd
	16 Jun	−0.51cd	−0.31d	−2.48cd	−1.75d
	30 Jun[3]	−0.46cd	−0.50d	−2.02de	−0.70e
	17 Jul	−1.42b	−1.42c	−2.84bcd	−2.62bcd
	2 Aug	−3.88a	−4.25b	−3.18abc	−3.30b

[1]There were no significant (P ≥ 0.10) differences in drought versus nondrought treatments.
[2]Means within columns with different letters are significantly different at P ≤ 0.05.
[3]Significant (P ≤ 0.05) mid–day species effects.
[4]Significant (P ≤ 0.05) predawn species effects.

1994 and 94% (322 of 341) in 1995 of marked western wheatgrass tillers remained in a vegetative phenological stage during the growing seasons. On average, utilization was 49% and 51% for the first and second grazing events in 1994 and 53% and 46% for the first and second grazing events in 1995. Over 90% of marked western wheatgrass tillers were grazed twice in 1994 and 1995.

Tiller Relative Growth Rates

Analyses of relative growth rates of twice-grazed blue grama tillers revealed significant (P ≤ 0.01) treatment-by-time interactions (Fig. 2). Relative growth rates were reduced (P = 0.01) 29% by drought before grazing treatments were imposed (i.e., May) but not different (P ≥ 0.30) from June through October in 1994 (Fig. 2). Growth rates of defoliated tillers were 107% greater (P ≥ 0.01) than undefoliated tillers after the first grazing event (i.e., June), but similar (P = 0.08) thereafter and not different (P ≥ 0.10) from zero from July through October (Fig. 2).

The year following the imposed drought (i.e., 1995), the blue grama time-by-drought (P = 0.02) and time-by-grazing treatment interactions were significant (P ≤ 0.01). In May, relative regrowth rates were 18% greater (P = 0.01) for plants exposed to the imposed 1994 drought than for non-drought plants, but rates were similar (P ≥ 0.30) thereafter (Fig. 2). Relative growth rates in the ungrazed treatment during May 1995 were 19% greater (P = 0.02) than in either grazing treatment. However, following the first grazing event

of 1995 (i.e., June), relative growth rates were greater (P = 0.02) in the G94-95 treatment than the ungrazed control and greater (P = 0.003) than the G94 treatment. Relative growth rates from July through August were not different (P ≥ 0.10) from zero (Fig. 2).

Relative growth rates of marked western wheatgrass tillers grazed twice, were unaffected by drought in 1994 (P = 0.61). Relative growth rates were greater (P ≤ 0.01) in the 2 grazed treatments (G94 and G94-95) compared to the ungrazed treatment (0.007 vs. 0.002 g⁻¹ day⁻¹) in June, and declined from July to October (Fig. 3). Tiller relative growth rates were not different (P ≥ 0.15) from zero from July through October (Fig. 3).

Results were similar for western wheatgrass in 1995 in that relative growth rates were unaffected by drought treatment (P = 0.69), were greater (P ≤ 0.01) in the

grazed (G94-95) than the 2 ungrazed (G94 and ungrazed) treatments in June, and declined through the season (Fig. 3).

Tiller Recruitment

The percent of primary blue grama tillers which produced an axillary tiller, varied during the 1994 growing season in response to drought and grazing (Table 2). Drought reduced (P ≤ 0.01) total recruitment 80%, whereas grazing increased (P ≤ 0.01) recruitment 315% compared to ungrazed treatments. Sixty percent of daughter tillers were produced after the first grazing event. Of those producing axillary tillers, none in the drought treatment produced more than 1 axillary tiller. Eighteen percent in the non-drought treatment produced 2 secondary tillers.

In 1995, the magnitude of recruitment by blue grama was similar (P = 0.16) between drought and non-drought treatments (Table 2). Tiller recruitment for combined grazing treatments was 78% greater (P ≤ 0.01) than without grazing. Ninety-eight percent of the tiller recruitment occurred after the first grazing event. On average, 30% of the blue grama tillers producing axillary tillers produced 2 secondary tillers. It appeared that the seasonal pattern of axillary tillering by blue grama was similar in 1994 and 1995.

Recruitment by western wheatgrass tillers grazed twice also varied in magnitude between the 1994 drought and grazing treatments (Table 2). Drought reduced (P ≤ 0.01) recruitment 91% (Table 2). Grazed tillers exhibited greater (P = 0.04) recruitment compared to ungrazed tillers (Table 2). More than 95% of the recruitment occurred in the fall (September and October) of 1994. No tillers in drought plots recruited more than 1 tiller. In contrast, of the primary western wheatgrass

Table 2. Least square means (%), SE and P-values proportions of marked primary tillers that produced at least 1 axillary tiller during the growing season for blue grama and western wheatgrass subjected to drought and grazing treatments.

Year	Drought Treatments[1] D	ND	SE	P	Grazing Treatments[2] G94	G94-95	UG	SE	P	D*G[3]
Blue Grama[4]										
		(%)				(%)				
1994	8a	40b	3	≤ 0.01	31a	32a	10b	3	≤ 0.01	0.08
1995	39	49	4	0.16	47a	60a	30b	5	0.01	0.50
Western Wheatgrass[4]										
1994	7a	79b	3	≤ 0.01	47a	46a	35b	3	0.04	0.07
1995	6	11	3	0.18	5	15	6	3	0.12	0.84

[1]D = Drought, ND = Non Drought.
[2]G94 = Grazed in 1994, G94-95 = Grazed in 1994 and 1995, UG = Ungrazed.
[3]D*G = Drought by grazing interaction P-value.
[4]Drought or grazing treatment means in the same year (row), with different letters are significantly different at P ≤ 0.05.
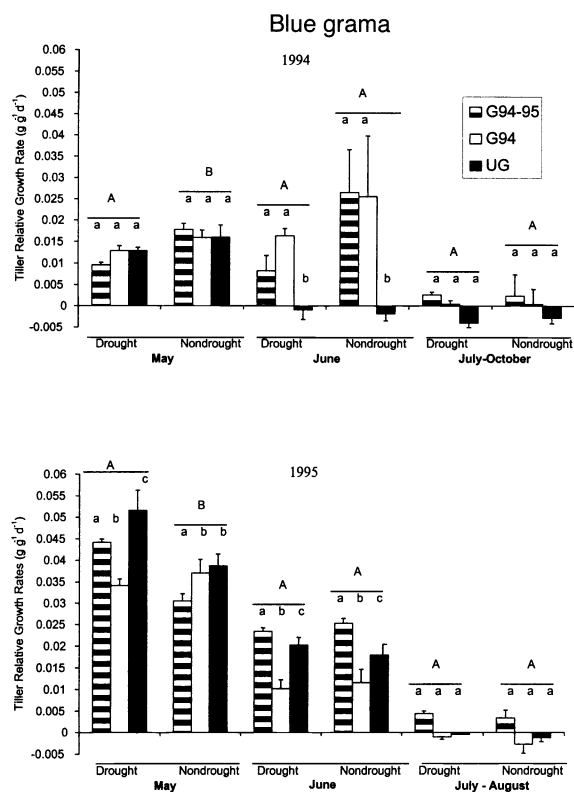
Blue grama

Western wheatgrass

Fig. 2. Mean tiller relative growth rates (g g⁻¹ day⁻¹) for blue grama in response to drought and grazing. Grazing treatments were grazed during and after drought (G94-95), grazed during drought and ungrazed after drought (G94), and ungrazed during and after drought (UG). Different capital letters (A and B) denote significant (P ≤ 0.05) differences between drought and nondrought within the same monthly period. Small letters (a, b and c) denote significant (P ≤ 0.05) differences between grazing treatments within the same monthly period.

Fig. 3. Mean tiller relative growth rates (g g⁻¹ day⁻¹) for western wheatgrass in response to drought and grazing. Grazing treatments were grazed during and after drought (G94-95), grazed during drought and ungrazed after drought (G94), and ungrazed during and after drought (UG). Different capital letters (A and B) denote significant (P ≤ 0.05) differences between drought and nondrought within the same monthly period. Small letters (a, b and c) denote significant (P ≤ 0.05) differences between grazing treatments within the same monthly period.

tillers producing axillary tillers in non-drought plants, 11% produced 2 daughter tillers. Eighty percent of the axillary tillers were produced in September through October in 1994.

Tiller recruitment by western wheatgrass during the growing season was similar between drought (P = 0.18) and among grazing (P = 0.12) treatments in 1995 (Table 2). Only 26% of the western wheatgrass tillers were recruited in the fall (September-October) of 1995. No western wheatgrass tillers produced more than 1 daughter tiller in 1995.

Tiller Density

Estimated pre-treatment tiller densities of blue grama were greater (P = 0.06) in 1994 in drought compared to non-drought lysimeters (8,646 vs. 9,854 tillers/m²) but not (P ≥ 0.60) among grazing treatment lysimeters in 1994. Initial tiller densities were included as covariates for the 1995 and 1996 analyses. Tiller densities of blue

grama were not (P = 0.10) affected by drought in 1995 (8,068 vs. 9,420 tillers m⁻²), but in 1996, 2 years after the drought was imposed, tiller densities of blue grama stands subjected to drought were 59% greater (P = 0.02) than not subject to drought (9,967 vs. 6,263 tillers m⁻²). Grazing did not (P = 0.49) affect densities in 1995 or 1996. No significant (P ≥ 0.20) drought-by-tiller interactions occurred either year.

Initial (1994) tiller densities of western wheatgrass were different (P ≥ 0.01) and their covariates were significant (P ≥ 0.04) in 1995 but not (P ≥ 0.12) in 1996. Tiller densities were not (P = 0.71) affected by drought in 1995 but were reduced 42% (P = 0.007) in 1996 (476 vs. 814 tillers m⁻²) when compared to non-drought treatments. Tiller densities were not affected (P = 0.49) by grazing treatment or drought by grazing treatment (P ≥ 0.52) interactions in 1995 or 1996.

Aboveground Net Primary Production (ANPP)

Blue grama production averaged 551 kg ha⁻¹ across years and grazing treatments (Table 3). Pre-treatment ANPP for blue grama (i.e., 1993) did not differ (P = 0.11) between drought treatments, but it was greater (P = 0.03) in the 2 grazed treatment plots than the ungrazed (Table 3). Analyses for years 1994 through 1996 showed all drought and grazing treatment effects were non-significant (P ≥ 0.10). Drought-by-grazing treatment interactions were not significant (P ≥ 0.10) in any year.

Estimated 1993 ANPP for western wheatgrass did not differ (P = 0.10) between drought treatment plots, but was greater (P = 0.05) in the G94-95 and ungrazed treatment plots than the G94 treatment plots (Table 3). Pre-treatment ANPP were not significant (P ≥ 0.22) covariates in any initial analyses, therefore, they were not included in the final analysis. Aboveground net primary pro-

Table 3. Least square means (kg ha^{-1}), SE, and P-values for aboveground net primary production estimates for blue grama and western wheatgrass subjected to drought and grazing treatments.

Year	Drought Treatments[1]				Grazing Treatments[2]					
	D	ND	SE	P	G94	G94-95	UG	SE	P	D*G[3]
Blue Grama[4]	------ (kg ha^{-1}) ------				------ (kg ha^{-1}) ------					
1993	1,473	1,276	78	0.11	1,421a	1,588a	1,101b	96	0.03	0.14
1994	712	639	90	0.58	680	566	781	110	0.43	0.10
1995	564	476	81	0.47	562	334	663	99	0.13	0.48
1996	516	398	64	0.24	395	357	619	78	0.10	0.90
Western Wheatgrass[4]										
1993	1,117	1,687	211	0.10	1,138a	1,595b	1,472b	259	0.05	0.49
1994	649a	1,277b	90	≤ 0.01	757a	756a	1,378b	110	0.01	0.98
1995	978	1,376	129	0.07	1,608a	481b	1,442a	158	≤0.01	0.17
1996	961	1,347	166	0.15	1,275	1,029	1,157	204	0.70	0.40

[1]D = Drought, ND = Non Drought.
[2]G94 = Grazed in 1994, G94-95 = Grazed in 1994 and 1995, UG = Ungrazed.
[3]D*G = Drought by grazing interaction P-value.
[4]Drought or grazing treatment means in the same year (rows), with different letters are significantly different at P ≤ 0.05.

duction was less (P = 0.01) in the drought than non-drought treatment in 1994 and greater (P = 0.01) in the ungrazed than grazed treatments (G94-95) in 1994. The only difference found thereafter, was that ANPP in G94-95 (which was grazed in 1995) was less (P ≤ 0.01) in 1995 than in the 2 non-grazed treatments in 1995 (NG and G94). There were no drought by grazing treatment interactions (P ≥ 0.17) in any year.

Discussion

Based on the results of this study, we conclude that: 1) relative growth rates of tillers which were grazed twice, were largely unaffected by drought and seasonally enhanced by grazing (Fig. 2 and 3); 2) axillary tillering was impeded by drought during the growing season and enhanced by grazing (Table 2); 3) tiller densities were unaffected by drought or grazing; and 4) neither drought nor grazing affected blue grama ANPP whereas drought reduced western wheatgrass ANPP with mixed grazing treatment effects (Table 3).

The major effects of drought were expressed by a slight (19%) reduction in tiller relative growth rates of blue grama in May 1994, a large reduction in tillering for western wheatgrass (91%) and blue grama (80%) during the growing season in 1994, and a large reduction of ANPP for western wheatgrass. Growth and tillering are often reduced by water stress (Brown 1995). Zhang and Romo (1995) reported the number of emerging northern wheatgrass (*Agropyron dasystachyum* (Hook.) Scriton.) tillers was positively correlated with soil water. Haferkamp et al. (1997 and 1998), Haferkamp and Heitschmidt

(1999) and Rummell (1946) reported western wheatgrass tiller density increased with the removal of competition of Japanese brome (*Bromus japonicus* Thunb.).

The responses to the initiation of the drought began to appear early in 1994 as shown by the change in blue grama tiller relative growth rates and the lack of a significant date-by-treatment interaction for western wheatgrass tiller relative growth rates. However, the response to the imposed drought and control lysimeters were similar due to the natural drought-like conditions which existed during 1994. Precipitation was 24% below average, and this drought caused plants to be equally water stressed by May 1994 regardless of drought treatment (Table 1). This conclusion is also supported by the precipitation (Fig. 1), xylem water potentials, and soil water data reported previously by Heitschmidt et al. (1999).

Our results also suggest the effects of a 1-year drought on growth rates did not carry over to the next year. Carry over effects may have been limited by the initial drought as well as above average precipitation that fell in March, April, and May 1995. Busso and Richards (1995) and Busso et al. (1989) did not find the effects of a 1-year drought on numbers of active axillary buds carried over to the next year. Only after 3 consecutive years of drought did Busso et al. (1989) find reduced numbers of metabolically active axillary buds.

Fewer axillary tillers were produced by western wheatgrass in 1995 than in 1994. Increased western wheatgrass tillering is associated with increased fall precipitation the previous year (Haferkamp et al. 1997). However, in this instance, the fall of 1994 was wetter than fall of 1993 (Fig. 1). Thus, the reduction of tillering in 1995 was more

likely due to the dry summer of 1994.

Grazing had little long-term effect on blue grama or western wheatgrass. The increase in tiller recruitment with grazing during the growing season agrees with findings of Sims et al. (1973). They reported mowing blue grama plants in late June and early July stimulated additional tillering, mostly from reproductive shoots that had elevated above the mowed height. Mowing earlier in the growing season depressed tillering, whereas mowing in late July and early August stimulated tillering, but insufficient growing season remained for complete development of these late tillers. They also reported increased tillering with mowing for sand bluestem (*Andropogon hallii* Hack.) a rhizomatous warm-season grass.

Our findings that grazing did not reduce ANPP of blue grama, but did decrease ANPP of western wheatgrass can best be explained by the different morphologies of the 2 species. Grass species like blue grama are characterized by short growing shoots and when grazed, these species can maintain much higher proportions of photosynthetic tissue than can species with long shoots like western wheatgrass (Dahl and Hyder 1977). Klipple and Costello (1960) noted that herbage production of western wheatgrass remained the same when utilization of that species increased from about 10% to about 20% but declined sharply when utilization increased to 40%. Launchbaugh (1967) found that forage production of western wheatgrass declined as utilization increased from 44 to 80%. Reed and Peterson (1961), Everson (1966), and Branson (1953) concluded that forage production of western wheatgrass declined with increased utilization.

Many studies have shown the importance of environmental factors on production of mixed-grass rangelands (Coupland 1958, Reed and Peterson 1961, Hyder et al. 1975). Extended drought usually shifts species composition toward short grasses (Smoliak et al. 1972), but species composition shifts toward mid grasses when precipitation is above average (White et al. 1978). Shifts in plant species composition in this study were not observed (Heitschmidt et al. 1999). This lack of change in species composition may have been due to the timing and severity of the imposed drought. We failed to detect an increase in warm-season herbage production as reported by Heitschmidt et al. (1999), but our findings were probably due to slightly different methodologies.

Management Implications

Our results demonstrate a 1-year growing season drought combined with grazing (both during and after drought) did not appear to adversely affect tiller processes. Elimination of livestock grazing during or after a 1-year growing season drought may not be necessary to maintain plant populations on the tiller level for blue grama and western wheatgrass. Moderate stocking levels (40–50% utilization) during and after drought did not adversely affect sustainability of dominant native grasses on these Northern Great Plains rangelands within the conditions of this study.

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Salinity affects development, growth, and photosynthesis in cheatgrass

KAYLIE E. RASMUSON AND JAY E. ANDERSON

Authors are Plant Ecologist, Bechtel SAIC Comapny, LLC, Las Vegas, Nev. 89144, and Professor, Department of Biological Sciences, Idaho State University, Pocatello, Ida. 83209-8007. At the time of the research, the senior author was a Ph.D. student, Department of Biological Sciences, Idaho State University, Pocatello, Ida.

Abstract

The effects of salt stress on growth and development of cheatgrass (*Bromus tectorum* L.) were investigated in 2 greenhouse studies. The first study assessed developmental and physiological responses of this grass to 4 salinity levels. Salinity stunted growth through reduced leaf initiation and expansion, and reduced photosynthetic rates. Reduction of photosynthetic rates appeared to be primarily due to stomatal limitation. Salinity also reduced carbon isotope discrimination, indicating long-term effects on conductance and carbon gain. Root growth was severely inhibited by high salinity, resulting in a shift in the root to shoot allocation pattern. The second study investigated growth patterns of cheatgrass in relation to intraspecific variation in salt tolerance using plants grown from seeds collected at non-saline and saline sites. Salinity reduced growth of plants from both environments. However, plants from the saline site accumulated leaf and root area at nearly twice the rate as those from the non-saline site, even in the control group. Because plants were grown in a common environment, growth differences between populations were genetically based. Thus, the potential for rapid growth may enable plants from the saline site to rely on shallow, less saline moisture reserves available early in the growing season.

Key Words: biomass partitioning, *Bromus tectorum*, intraspecific variation, developmental response, root growth, photosynthetic rates, population differences, salt stress, stomatal conductance

Resumen

Mediante 2 estudios en invernadero se investigaron los efectos del estrés por salinidad en el desarrollo y crecimiento del "Cheatgrass" (*Bromus tectorum* L.). El primer estudio evaluó el desarrollo y la respuesta fisiológica de este zacate a 4 niveles de salinidad. La salinidad suprimió el crecimiento a reducir la iniciación y expansión de las hojas y tasas fotosintéticas. La reducción de las tasas fotosintéticas parece ser principalmente debido a una limitación estomática. La salinidad también redujo la discriminación del isótopo de carbón, indicando efectos a largo plazo en la conducción y ganancia de carbón. El crecimiento de la raíz fue severamente inhibido por la alta salinidad, resultando en un patrón de asignación desviado de la raíz a los tallos. En el segundo estudio se investigaron los patrones de crecimiento del "Cheatgrass" en relación a la variación intrespecífica a la tolerancia a sales, utilizando para ello plantas desarrolladas a partir de semillas colectadas en sitios salinos y no salinos. La salinidad redujo el crecimiento de las plantas de ambos ambientes. Sin embargo, las plantas del sitio salino acumularon el área foliar y radical a una tasa casi del doble que las plantas provenientes del sitio no salino, aun en el grupo control. Porque las plantas se cultivaron en un ambiente común, las diferencias de crecimiento entre poblaciones estuvieron basadas en su genética. Así, el potencial para un rápido crecimiento puede permitir a las plantas de sitios salinos depender de reservas superficiales menos salinas disponibles a inicios de la estación de crecimiento.

Cheatgrass (*Bromus tectorum* L.), a cleistogamous annual grass, was introduced to the western United States from Eurasia in the 1800's (Novak et al. 1993). Since its introduction cheatgrass rapidly occupied overgrazed rangelands and other disturbed areas reaching its current geographic range by 1930 (Mack 1981). Its success in cold deserts and many other habitats of western North America is attributed to several developmental and morphological characteristics including rapid growth of an extensive root system, tremendous phenotypic plasticity, and the ability to germinate and establish over a wide range of temperature and moisture conditions (Smith et al. 1997). Its presence has been recorded in pristine as well as disturbed sagebrush steppe communities. The ubiquitous nature of this weedy annual and its tenacity once established suggest that few factors have a negative influence on its distribution. Nevertheless, cold desert habitats exist where it does not occur, indicating certain soil and climatic factors influence its ability to successfully establish and persist (see Smith et al. 1997 or Upadhyaya et al. 1986 for reviews). It has been suggested that soil salinity is 1 of those factors (Stewart and Hull 1949, Upadhyaya et al. 1986).

Salinity can cause osmotic stress, suppress nutrient absorption, and affect biomass allocation patterns, physiological processes, and biochemical reactions (Greenway and Munns 1980, Levitt 1980, Munns and Termaat 1986). Disruption of these processes may reduce growth or alter developmental patterns in nonhalophytic plants (Levitt 1980, Munns and Termaat 1986). Salt tolerance varies widely in both halophytic and nonhalophytic plants (Levitt 1980). In addition, intraspecific variation in salt tolerance

has been demonstrated in grass species growing in habitats of varying salinity (Hester et al. 1996).

In this study we examined growth and physiological responses of cheatgrass to varying levels of salinity, and explored the possibility of intraspecific variation in salt tolerance in cheatgrass from habitats differing in soil salinity. Specific objectives were 1) to assess the effects of salinity on growth parameters and biomass partitioning of cheatgrass, 2) to assess the importance of developmental stage on salinity-induced differences in growth, 3) to assess the effects of salt stress on stomatal behavior and photosynthesis, and 4) to compare responses of cheatgrass plants from non-saline and saline sites to determine whether growth characteristics account for a higher degree of salt tolerance in the population from the saline site.

Materials and Methods

Cheatgrass seeds were collected from the U.S. Department of Energy (DOE) Idaho National Engineering and Environmental Laboratory (INEEL) (42°52'00"N, 111°54'14.74"W) on the upper Snake River Plain in southeast Idaho, and from the Arid Lands Ecology Reserve (ALE) at the DOE Hanford Reservation (46°30'15"N, 119°42'03"W) in eastern Washington. These areas were chosen because previous studies suggested that soils at the INEEL (referred to hereafter as the non-saline site) were less saline than those at the ALE (referred to hereafter as the saline site). Rasmuson (1996) showed that soil salinity potentially restricts emergence and growth of cheatgrass populations at the non-saline site and that salinity reduced percent germination of cheatgrass seeds collected from this site. In contrast, Rickard (1965) reported a population of cheatgrass growing at the saline site where soil salinity at 1-m depth was 10.0 dS/m. Salinity was low in surface soils and increased with depth. The bulk of cheatgrass roots were shallower than 1 m and it was unclear whether roots were actually exploring the high salinity soil.

Two greenhouse studies were conducted to address the experimental objectives. The first assessed growth, developmental and physiological responses of cheatgrass to increasing salinity using plants grown from seeds collected from the non-saline site. The second study compared growth responses of cheatgrass plants grown from seeds collected from the non-saline site

and from seeds collected from the saline study sites described by Rickard (1965). The population comparison study was initiated upon completion of the growth and development study, following the determination that salinity caused reductions in growth and photosynthetic rates in populations from the non-saline sites. The population of cheatgrass from the saline site was chosen because previous research indicated that it might be more tolerant of salinity than populations found at the non-saline site.

Salinity Treatments

Salinity treatments in both studies were designated control, low, medium and high. Low- and medium-salinity treatments were based on soil salinity values that had been determined previously for the non-saline and saline field sites, respectively. The high-salinity treatment was below tolerance levels of common *Artemisia* species (West 1983) which are dominant shrubs in cold desert shrub-steppe habitats. Sodium chloride was added to watering solutions in concentrations of 0.0, 0.025 M, 0.070 M and 0.10 M resulting in electrical conductivities of 1.8 (control), 4.5 (low), 9.0 (medium) and 13.7 (high) dS/m, respectively. The stock watering solution was half strength Raukura nutrient solution (Smith et al. 1983). Studies were conducted in 2 greenhouses located in Pocatello, Ida..

Growth and Development

Cheatgrass seeds collected from non-saline soils were grown in 3.5-liter PVC pots filled with washed sand. Mean day/night temperatures were 27/20°C and mean daily maximum photosynthetic photon flux density (PPFD) was ca. 900 μmol m^{-2} sec^{-1} (ambient light). Six seeds were planted per pot. After 3 weeks each pot was thinned to 1 plant. Care was taken to leave plants of similar size and developmental stage to ensure that results of the first harvest would not be confounded by initial differences among plants. Treatments were randomly assigned and began after plants were thinned. Each plant was watered with 300-ml of saline/nutrient solution every third day. After 26 days of treatment, 4 plants per treatment were harvested at approximately 8-day intervals (6 harvests).

Population Comparisons

Plant culture and salinity treatments were the same as described above using the 2 seed collections. Treatment and seed

sources were replicated 3 times. This study was conducted in a different greenhouse, consequently environmental conditions differed from above. Mean day/night temperatures were 24/18° C; mean PPFD was 525 μmols m^{-2} sec^{-1} (ambient light). Because of the depth to saline soil reported by Rickard (1965) it was reasoned that plants would be somewhat older when their root systems encountered the saline soil than those were in the growth and development study when treatments were initiated. Therefore, plants were allowed an additional week of growth before treatments were applied. Also, treatment period was reduced in the population study to determine whether effects of salinity appeared earlier than 26 days (treatment period of the first harvest in the growth and development study). Treatments were initiated when plants were 28 days old. Plants were harvested 17 days later.

Growth Measurements

Growth measurements were the same for both studies except where otherwise noted. Leaf length was measured from the base of the sheath to the tip with a ruler to the nearest mm, and the number of emergent leaves and tillers were counted. Mean leaf elongation rates were determined for plants in the growth and development study by dividing leaf length for plants in each treatment by the number of growing days. Leaves and stems were separated and area was determined with a model CI-201 area meter (CID, Inc., Vancouver, Wash., USA). Roots were extracted from the sand by removing the sand/root column from the PVC container, placing the whole column on a screen above a catchment basin, and rinsing the bulk of the sand away. Any root material was retrieved from the basin. Roots were then floated in clean water and remaining sand particles were removed. Leaf, stem and root biomass were dried at 70° C until weight loss ceased and weighed on a Mettler H31AR analytical balance (Denver Instruments, Arvada, Colo., USA). Root area and length were measured with a Pseudo-color Agvision image analyzer (Decagon Devices, Inc., Pullman, Wash., USA).

Development Indices

Two indices were used to evaluate effects of salt stress on development. The plastochron index is a commonly used developmental scale based on the time between initiation of successive leaves (Erickson and Michelini 1957). As an approximation of the plastochron index,

mean leaf initiation rates were calculated by dividing the number of leaves produced per plant by the number of growing days. This was used to determine if salt treatments directly affected plant development. Plants of the same chronological age may differ in their stages of development, thus obscuring mechanisms of reduced growth caused by treatment. Because the natural log (ln) of whole plant dry mass was linearly related to time for plants in the 4 salinity treatments, we used this parameter as a second developmental index. Leaf area was related to this index for each plant in the study to determine if salt induced effects on growth were the same for plants compared at similar developmental stages as those observed at equivalent chronological ages. Second order polynomials with 95% confidence intervals were fitted to leaf area versus ln total dry mass for each treatment. Polynomials from the low, medium and high treatments were compared to the control treatment.

Gas Exchange Measurements, Leaf Water Potentials and Carbon Isotope Discrimination

Leaf water potentials were measured in both studies. Leaf gas exchange and leaf carbon isotope concentrations were measured only in the growth and development study. Mid-day water potential of leaves was measured with a pressure chamber (PMS Instruments Co., Corvallis, Ore., USA) at the time of gas exchange measurements. For population comparisons, leaf water potential was measured just prior to harvest. Gas exchange characteristics were measured on 3 plants per treatment at the first, third and fifth harvests. Measurements were made with an open gas exchange system described by Toft et al. (1989). Young, fully expanded leaves on one or more tillers were sealed in a nickel plated cuvette and photosynthetic rate at ambient CO_2 concentration and stomatal conductance were measured under typical atmospheric conditions. Incident photon flux density supplied by a 300-watt projector lamp was maintained at about 1800 μmol m^{-2} sec^{-1}. Leaf temperature was 20° C. Ambient CO_2 concentration was 350 ± 5 μl liter^{-1}, and the vapor pressure deficit was 1.8 kPa. Measurements were taken after steady state rates were reached. Intercellular CO_2 concentration, photosynthetic rates, and stomatal conductance were calculated according to von Caemmerer and Farquhar (1981).

Plant material from 3 plants per treatment at the first and third harvests was collected for determination of carbon iso-

tope values. Young, fully expanded leaves were dried, ground and sent to the Stable Isotope Research Facility for Environmental Research at the University of Utah for analysis. Carbon isotope discrimination (Δ) was calculated from carbon isotope ratios according to Farquhar and Richards (1984). Carbon isotope discrimination is linearly related to intercellular CO_2 concentration:

$$\Delta = a + (b - a)(c_i/c_a) \quad (1)$$

where a is discrimination against $^{13}CO_2$ relative to $^{12}CO_2$ by diffusion in air (4.4 ‰), b is discrimination against $^{13}CO_2$ by carboxylation (27 ‰), c_i is the intercellular CO_2 concentration of the leaf, and c_a is the concentration of CO_2 in the atmosphere (350 μl liter^{-1}). Because a, b and ca are constant, variation in Δ reflects changes in intercellular CO_2 concentration which occur due to changes in stomatal conductance and mesophyll capacity to fix CO_2 (Farquhar et al. 1982). An integrated mean intercellular CO_2 concentration was estimated from Δ using the above equation and constants. Changes in Δ and intercellular CO_2 concentration, relative to the control group, were evaluated for plants in the low-, medium- and high-salinity treatments.

Statistical Analysis

Two-way analyses of variance (ANOVA) with time and salinity, or seed source and salinity, as independent variables were used to analyze growth and physiological parameters. Tests for differences were considered significant for P ≤ 0.05. Growth parameters were ln transformed for analysis. Differences in relative growth rates (RGR, the rate of increase in plant weight per unit of plant weight) among treatments were assessed by examining the interaction between time and salinity treatment for transformed total dry mass (Poorter 1991). Post-hoc com-

parisons were made among treatments for specific leaf area, leaf elongation rates, and leaf initiation rates. Bonferroni pairwise comparisons were used to examine differences in specific leaf area among the 4 salinity treatments. Leaf elongation and initiation rates were examined at the last harvest by comparing individual treatment means within that harvest (i.e., analysis of simple effects, Keppel 1991).

Physiological variables were normally distributed, met the assumption of equal variance, and consequently were not transformed for analysis. The time effect was not significant for gas exchange variables, Δ, or leaf water potential, and was therefore dropped from the analysis, resulting in a 1-way ANOVA with salinity as the independent variable. Post-hoc pairwise multiple comparisons were made between treatments using the Tukey HSD test (Keppel 1991). The relationships between photosynthetic rates, stomatal conductance, intercellular CO_2 concentration, leaf water potential, Δ, and electrical conductivity of the salinity treatments were evaluated with Pearson correlation. Relationships between photosynthetic rates, stomatal conductance and intercellular CO_2 concentration were also explored with Pearson correlation.

Results

Growth and Development Analysis

Biomass accumulation was significantly depressed by salinity (Fig. 1, Table 1). The significant interaction between time and salinity for transformed whole plant dry mass indicated differences occurred in relative growth rates (RGR) among treatments (Fig. 1 ln total dry mass, Table 1). The RGR of plants in the high-salinity treatment was lower than that of the other

Table 1. Results of analyses of variance (ANOVA) of growth variables for cheatgrass plants grown in 4 salinity treatments. F = F-ratio of the ANOVA, P = probability of Type I error. Error term df = 68 (all tests).

| Source of variation:	Time (df = 5)		Salinity (df = 3)		Time x salinity (df =15)	
	F	P	F	P	F	P
Total dry mass	128.8	<0.001	149.9	<0.001	5.11	<0.001
Root dry mass	47.3	<0.001	166.1	<0.001	5.12	<0.001
Leaf dry mass	123.2	<0.001	155.1	<0.001	4.43	<0.001
Leaf area	99.1	<0.001	175.4	<0.001	4.33	<0.001
Leaf number	55.0	<0.001	42.5	<0.001	1.32	0.217
Leaf initiation rates	12.6	<0.001	42.5	<0.001	1.36	0.217
Leaf elongation rates	38.3	<0.001	102.7	<0.001	3.72	<0.001
Specific leaf area	14.3	<0.001	14.9	<0.001	0.66	0.810
Shoot:root ratio	12.7	<0.001	35.1	<0.001	2.53	0.005
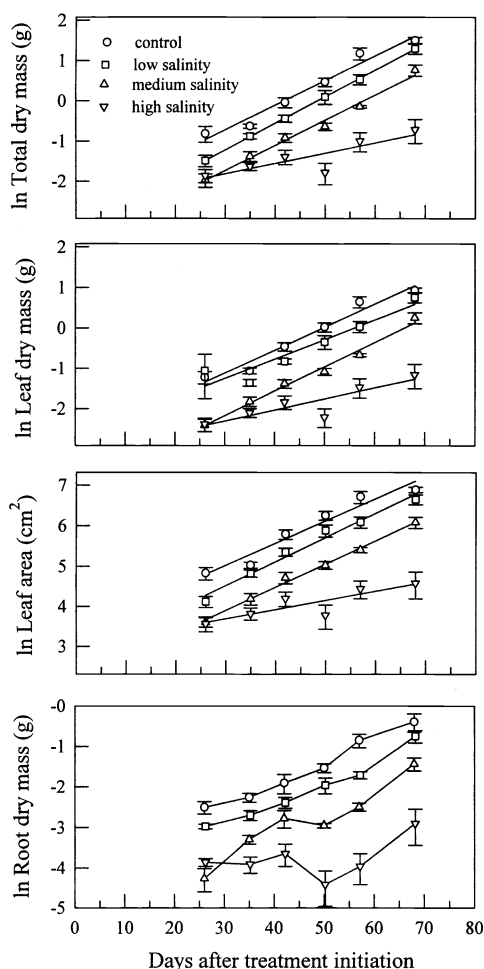
Fig. 1. Growth parameters for cheatgrass plants grown in 4 salinity treatments. Symbols are means for 4 plants at 6 harvests. Bars are SE. Note differences in scale for each variable.

3 treatments. Slopes of transformed total dry mass vs time for plants in the control, low- and medium-salinity treatments were roughly parallel indicating RGRs were similar (Fig. 1).

The interaction between time and salinity was significant for root dry mass (Table 1). Root dry mass of plants in the medium-salinity treatment was lower than that of plants in the high-salinity treatment at the first harvest (Fig. 1). At subsequent harvests, root dry mass for plants in the high-salinity treatment was reduced below that of plants in the medium-salinity treatment. The relative rankings of salinity treatments did not change for root dry mass after the second harvest (Fig. 1). With the exception just noted, salinity caused significant reductions in root dry mass at all harvests (Table 1, Fig. 1). Root area and length showed similar responses to salt stress as root dry mass (data not shown).

Interactions between time and salinity for leaf dry mass and leaf area were also significant (Table 1). The interactions were caused by changes in the magnitude of difference among treatments over time, relative rankings of salinity treatments were not affected (Fig. 1). Leaf area and dry mass were significantly reduced by increasing salinity (Table 1, Fig. 1). Both leaf area and dry mass were negatively correlated with salinity at the final harvest (Fig. 2). The same patterns were observed for stem area and dry mass (data not shown).

Leaf initiation rates were slowed by medium and high salinity (Table 2) resulting in fewer leaves per plant (Table 1, Fig. 2). Plants in the high-salinity treatments at the final harvest exhibited a reduction in mean leaf initiation rates of nearly 70% compared to plants in the control treatment (Tables 1 and 2). Leaf elongation rates were also significantly reduced by salinity (Table 1). Mean leaf elongation rates for plants from the final harvest were reduced by an average of 10% in low-, 22% in medium-, and 58% in high-salinity plants compared to control plants (Table 2).

Mean specific leaf area (leaf area:leaf dry mass) was higher for control plants than for medium- and high-salinity plants (P = 0.043 and P < 0.001, respectively, from Bonferroni pairwise comparisons). Mean specific leaf area decreased from the fourth to the sixth harvest for plants in all treatments (Fig. 3).

Shoot:root ratios were higher for plants in the high-salinity treatment than for plants in the remaining treatments, but the magnitude of this difference changed over time (Fig. 3). Shoot:root ratios for plants in the medium-, low- and control-salinity treatments were similar, with a slight trend
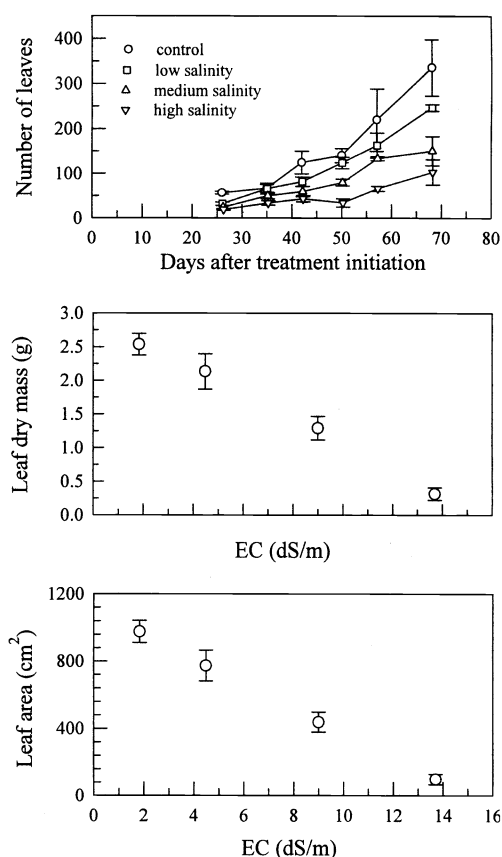
Fig. 2. Leaf accumulation over time and leaf parameters at the final harvest for cheatgrass plants grown in 4 salinity treatments. Symbols are means for 4 plants. Bars are SE. EC = electrical conductivity of the watering solution.

for higher ratios for plants in the medium-salinity treatment (Table 1, Fig. 3).

No differences were observed in leaf area between plants in the control and low-salinity treatments when compared at similar developmental stages (95% confidence intervals for second order polynomials overlap, Fig. 4) indicating that differences observed at equal chronological ages were due to differences in developmental stages. Polynomial coefficients of the medium and high treatments were reduced from control; there was no overlap in the 95% confidence intervals (Fig. 4) indicating that both the rate and pattern of development were affected.

Table 2. Mean rates (± SE) of leaf initiation (leaves day⁻¹) and leaf elongation (cm day⁻¹) for cheatgrass plants grown in 4 salinity treatments. Means are based on 4 plants per treatment.

Treatment	Leaf initiation rate	Leaf elongation rate
	(leaves day^{-1})	(cm day^{-1})
Control	4.9 (0.92)[a,1]	0.31 (0.03)[a]
Low salinity	3.6 (0.11)[a]	0.28 (0.01)[ab]
Medium salinity	2.1 (0.48)[b]	0.24 (0.02)[b]
High salinity	1.5 (0.42)[b]	0.13 (0.01)[c]

[1]Means within columns with the same superscript are not significantly different at P = 0.05.
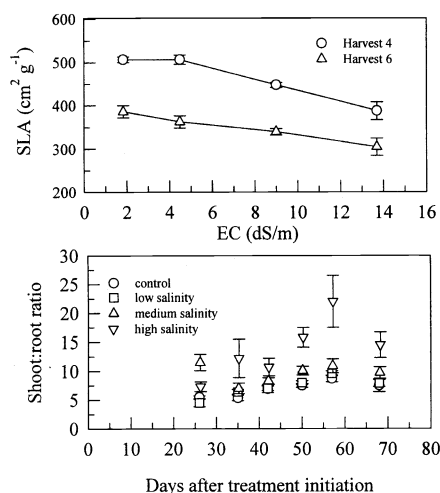
Fig. 3. Specific leaf area (SLA) and shoot:root ratios for cheatgrass plants grown in 4 salinity treatments. Specific leaf area's are the means of 4 plants at 2 harvest periods. EC = electrical conductivity of the watering solution. Shoot:root ratios are means of 4 plants at 6 harvests. Bars are SE.
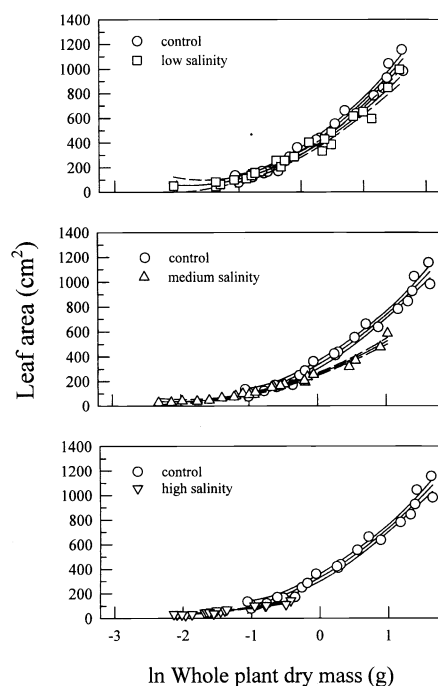

Fig. 4. Relationship between leaf area and natural log transformed (ln) whole plant dry mass for cheatgrass plants grown in four salinity treatments. Comparisons are between control and salinity treated plants. Symbols represent individuals. Lines are second degree polynomials with 95% confidence intervals fitted to the data. The following coefficients describe the curves: control, $b_0=332$, $b_1=317$, $b_2=84$, $r^2=0.98$, $P<0.001$; low, $b_0=304$, $b_1=273$, $b_2=75$, $r^2=0.97$, $P<0.001$; medium, $b_0=257$, $b_1=212$, $b_2=51$, $r^2=0.98$, $P<0.001$; high, $b_0=176$, $b_1=105$, $b_2=16$, $r^2=0.96$, $P<0.001$.

Table 3. Results of 2-way analyses of variance (ANOVA) for growth parameters of cheatgrass plants from the 2 seed sources grown in 4 salinity treatments. Interaction terms were not significant (P > 0.05). F = F ratio of the ANOVA, P = probability of a Type I error.

Source of variation:	Salinity (df = 3)		Seed source (df = 1)	
	F	P	F	P
Leaf area	9.29	0.001	9.22	0.008
Stem area	6.89	0.003	5.14	0.038
Root length	5.12	0.011	4.09	0.060
Root area	6.01	0.006	4.31	0.050
Specific leaf area	2.84	0.070	9.72	0.007

Population Comparisons

Growth parameters were significantly reduced by increasing salinity for plants from both seed sources (Fig. 5) with the exception of shoot:root ratios, which increased with salt stress. Because growth responses were similar to those presented above, only differences that occurred between populations will be presented here. Leaf and stem area, root area, and specific leaf area were all greater for plants from the saline site than for plants from the non-saline site (Table 3, Fig. 5). Root length was not significantly different at the designated significance level of P = 0.05. However, there was a trend towards greater root length for plants from the saline site (P = 0.06). Stem area and root length showed similar patterns to leaf area and root area, respectively, and so were not included in Fig. 5.

Gas Exchange Characteristics

Photosynthetic rates, stomatal conductance, intercellular CO_2 concentration and leaf water potential were significantly different among salinity treatments (P < 0.001, df = 3, for all cases). Mean photosynthetic rate was maintained by plants growing under low-salinity conditions but was reduced by 18 and 41% for plants in the medium- and high-salinity treatments, respectively (Table 4). Stomatal conductance was negatively correlated with salinity (r = 0.88, P < 0.001, n = 35) and was reduced by as much as 67% for plants in the high-salinity treatment (Table 4). Intercellular CO_2 concentration and leaf

water potential were also negatively correlated with salinity (r = 0.89, P < 0.001, and r = 0.62, P < 0.001 respectively, n = 35). Photosynthesis and stomatal conductance were linearly related to intercellular CO_2 concentration (r = 0.63, P < 0.001 and r = 0.87, P < 0.001 respectively, Fig. 6). Photosynthesis was positively correlated with stomatal conductance (r = 0.89, P < 0.001, Fig. 7). Leaf water potentials did not differ between populations (P = 0.96, data not shown).

Carbon Isotope Discrimination

Carbon isotope discrimination differed significantly among treatments (P < 0.001, data not shown), and was negatively correlated with increasing salinity (r = 0.85, P < 0.001, n = 24, Fig. 8). Carbon isotope discrimination and intercellular CO_2 concentration calculated from Δ decreased relative to control in all treatments (Table 5). Time averaged intercellular CO_2 concentration calculated from Δ decreased by as much as 65 μl liter^{-1} for plants in the high-salinity treatment compared to control (Table 5).

Discussion

Growth, Development and Biomass Partitioning

Large reductions in leaf area at the first harvest (26 days of treatment) indicated that leaf production and/or expansion were stunted in response to salinity early in

Table 4. Means for net assimilation rate (A), stomatal conductance (g), intercellular CO_2 concentration (c_i) and leaf water potential (ψ) for cheatgrass plants grown in 4 salinity treatments. Means are for 9 plants per treatment. SE are in parentheses.

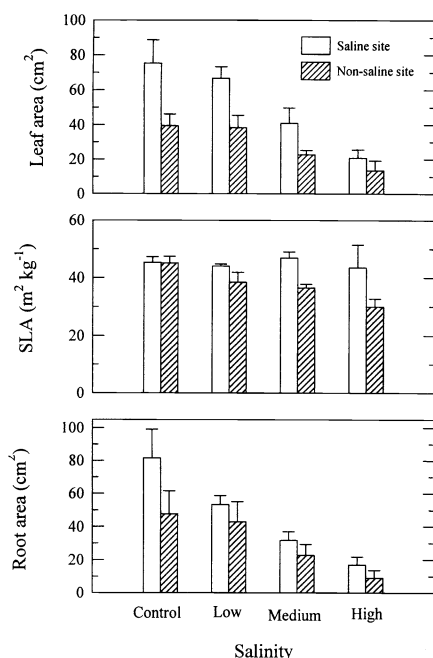| Treatment	A	g	ci	ψ
	(μmol m^{-2} sec^{-1})	(mol m^{-2} sec^{-1})	(μL liter^{-1})	(MPa)
Control	14.8 (0.81)[a,1]	0.208 (0.014)[a]	228 (5.5)[a]	-1.36 (0.074)[a]
Low Salinity	14.9 (0.63)[a]	0.165 (0.010)[b]	199 (3.1)[b]	-1.55 (0.110)[a]
Medium Salinity	12.1 (0.72)[b]	0.116 (0.007)[c]	175 (6.4)[c]	-1.73 (0.085)[a]
High Salinity	8.8 (0.79)[c]	0.069 (0.007)[d]	140 (7.4)[d]	-1.99 (0.143)[b]

Fig. 5. Growth parameters for cheatgrass plants from saline and nonsaline environments grown in 4 salinity treatments. Means are for 3 plants per treatment. Bars are SE. SLA = specific leaf area.

development for treated cheatgrass. Bernstein et al. (1993) found that growth velocity in sorghum leaves was most sensitive to salinity when leaves were elongating linearly at a rapid rate, and they were especially sensitive to salinity when the leaf was still enclosed in the encircling sheaths. Toward the end of the elongation period the sensitivity to salinity was reduced. Cheatgrass plants in the low- and medium-salt treatments experienced reduction in leaf elongation and production shortly after salinity treatments began, resulting in differences in plant size at the first harvest. At later harvests, with a greater number of leaves and therefore progressively more leaf tissue

Table 5. Salinity induced reductions in carbon isotope discrimination (Δ) and time averaged intercellular CO_2 concentrations (c_i) calculated from Δ for cheatgrass plants. Values are mean reductions in each treatment compared to control values. Means are based on 6 plants per treatment. All means were significantly different from control (P < 0.05, Tukey HSD test).

Salinity Treatment	Reductions From Control	
	Δ	c_i
	(°/oo)	(μl liter^{-1})
Low salinity	2.2	34.1
Medium salinity	3.3	51.1
High salinity	4.2	65.1

expanding, more tissue would have been past the most sensitive developmental stages than at the first harvest. This could have resulted in new steady state relative growth rathe (RGR's) that were similar to control plants in the low- and medium-salinity plants. However, because RGR is a compound rate of change, even small initial differences in rates can result in large differences in final biomass (Cramer et al. 1994). The number of leaves in the high-salinity treatment remained low throughout the study. Thus, plants subjected to the high-salinity treatment were unable to recover.

Specific leaf area varied for plants in the different treatments over time, increasing initially then decreasing. Lower specific leaf area indicates more biomass was allocated to leaf structure as the plants aged, which probably also influenced RGR's. The comparatively higher specific leaf area in control and low-salinity plants indicates a lower investment in biomass per unit area and increased photosynthetic surface of leaves, both of which would enhance whole-plant carbon gain. Thus, in a field setting, plants growing on non-saline soils could have the potential to increase leaf area at a greater rate which could increase competitive ability and flower production compared to plants growing in saline soils.

Mechanisms behind the strong reduction in leaf area and dry mass in response to salt treatments were both developmental and physiological in nature. Specifically, inhibition of leaf expansion observed in the salt-treated plants was partly related to low photosynthetic rates. Also, lower water potentials of plants in the high-salt treatment might have affected cellular expansion through effects on cell turgor, resulting in reduced leaf expansion (Cosgrove 1986). Reductions in the number and size of leaves induced by increasing salinity indicate development was affected at both the meristematic level and at subsequent leaf expansion stages, resulting in reduced leaf area and dry mass. Investigation of the leaf area vs. total dry mass relationships shows the primary effect of the low-salinity treatment was to slow the rate of development in cheatgrass. Similar developmental responses to salinity have been observed in salt-sensitive dicots such as lettuce (*Lactuca sativa* L., Lazof et al. 1991). The medium and high treatments had profound effects on cheatgrass which retarded the pattern of whole-plant development and severely delayed timing of growth. Cheatgrass often functions as a drought
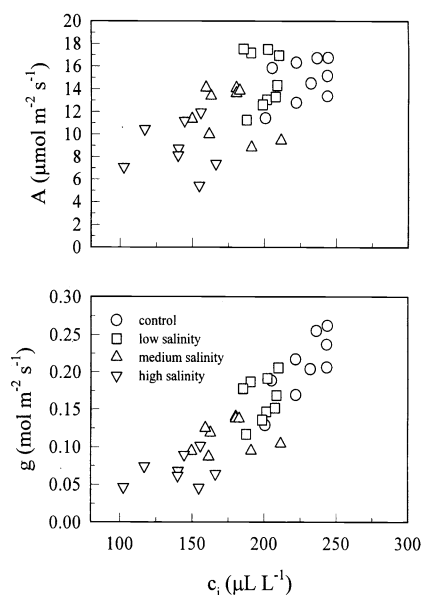

Fig. 6. Relationship of photosynthesis (A) and stomatal conductance (g) to intercellular CO_2 concentration (c_i) for cheatgrass plants grown in 4 salinity treatments. Symbols represent individual plants.

avoider in arid steppe environments with growth and seed set occurring early in the season before water becomes severely limiting (Rice et al. 1992). The delay in timing of growth caused by salinity may be great enough in saline environments to prevent or reduce seed production, thus inhibiting population maintenance and/or expansion in such environments.

It is noteworthy that salinity caused a shift in biomass allocation from roots to shoots in cheatgrass since the opposite response is commonly reported for other species (e.g., Seemann and Critchley 1985). Salinity caused a 50% increase in root to shoot ratios in bean plants (*Phaseolus vulgaris* L.) due to a smaller effect on root than shoot dry weight (Seemann and Critchley 1985). Cheatgrass root area and biomass were severely reduced by salinity. As a result, root growth may have been insufficient to sustain healthy shoot growth, particularly in the medium and high salinity treatments. The remarkable success of cheatgrass in the sagebrush steppe, where competition for water and nutrients can be intense, is in part a consequence of its ability to rapidly develop an extensive root system (Harris 1967, Smith et al. 1997). Harris (1967) suggested rapid, early root growth was responsible for cheatgrass' competitive displacement of bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn. & Smith). Mack and Pyke (1983) showed that reduced biomass production was
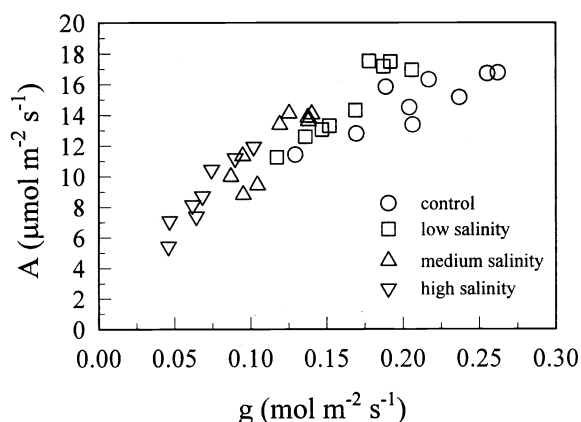
Fig. 7. Relationship between photosynthesis (A) and stomatal conductance (g) for cheatgrass plants grown in 4 salinity treatments. Symbols represent individual plants.
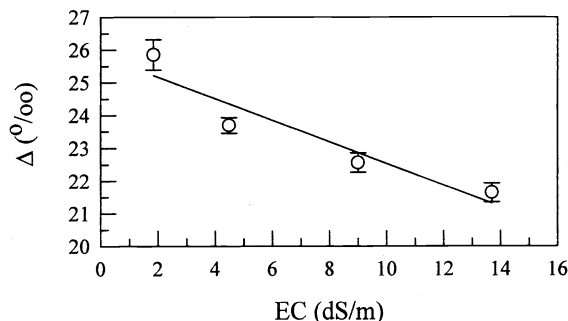
Fig. 8. Relationship between carbon isotope discrimination (Δ) and electrical conductivity(EC) for cheatgrass plants grown in 4 salinity treatments. Symbols represent means for 6 plants. Bars are SE.

strongly correlated with reduced seed production in cheatgrass. Therefore, restricted root development caused by salinity would be expected to affect both its fitness and competitive ability.

Photosynthetic Rates, Stomatal Conductance and Carbon Isotope Discrimination

Reduction in plant growth caused by salinity is often accompanied by decreased rates of photosynthesis in a variety of species (e.g., Meinzer et al. 1994, Seemann and Critchley 1985). This decline in photosynthesis has been attributed to decreased stomatal conductance in some studies (i.e., cotton [*Gossypium hirstutum* L.] and bean [*P. vulgaris*, cv Strike], Brugnoli and Lauteri 1991) and to decreased mesophyll capacity to fix CO_2 in others (i.e., bean [*P. vulgaris*, cv Hawkesbury Wonder, Seemann and Sharkey 1986). In this study, salinity reduced photosynthetic rates in cheatgrass by 18% in the medium- and 41% in the high-salt treatments compared to control. Photosynthesis and conductance decreased concomitantly in response to salt stress (Fig. 7). However, salinity caused greater reductions in conductance than in photosynthetic rate (67% and 41%, respectively). This difference caused the photosynthesis/conductance ratio to increase and therefore intercellular CO_2 concentration to decrease with salt stress. Thus, stomatal conductance was at least partially responsible for salinity induced reductions in photosynthesis. Additionally, both photosynthetic rate and stomatal conductance were positively correlated with intercellular CO_2 concentration across salt treatments (Fig. 6). The increase in photosyn-

thetic rate with intercellular CO_2 concentration also provides evidence that reductions in photosynthesis were primarily due to stomatal limitation rather than reduced mesophyll photosynthetic capacity (Meinzer et al. 1994). Had intercellular CO_2 concentration remained constant, or increased, with concomitant reductions in photosynthesis and stomatal conductance (g), this would have indicated that salinity affected the photosynthetic capacity of the mesophyll (Brugnoli and Lauteri 1991). Therefore, reductions in photosynthetic rate caused by salinity in cheatgrass seemed to be primarily due to reduced g. However, this hypothesis was not explicitly tested.

Carbon isotope discrimination reflects diffusional and assimilation components of leaf physiology averaged over the life of a leaf and can be used to investigate long term effects of environmental stresses (Farquhar et al. 1982). The 4.2‰ reduction in Δ caused by the high-salinity treatment was indicative of a 65 μl liter^{-1} decrease in the average intercellular CO_2 concentration. Similar salt induced shifts in Δ have been reported for other species (spinach [*Spinacia oleracea* L.] Downton et al. 1985; bean [*P. vulgaris*] Seemann and Critchley 1985; plantain [*Plantago maritima* L.] Flanagan and Jefferies 1989). The reductions in Δ and time averaged intercellular CO_2 concentration calculated from Δ caused by salt treatments indicate that long term effects of salinity on leaf physiology includes reduced g, even at low salinity levels. Decreased carbon gain would be one long-term result of reduced g.

Population Comparisons

Leaf area of cheatgrass plants from the saline site was nearly twice that of plants

from the non-saline site in the control, low- and medium-salinity treatments. In addition, root area and length were greater across treatments for plants from the saline site. However, it is important to note that the percent reduction in leaf and root area caused by salinity in plants from the saline site was similar to that in plants from the non-saline site and no differences were found in leaf water potential between populations. Thus, primary physiological responses to salinity appear to have been similar in these populations. Because plants were grown in a common environment, the accelerated growth of plants from the saline site suggests differences in response to environmental conditions were genetically based. If these differences were due to phenotypic plasticity, one would expect the same rates of area accumulation in the control plants from the 2 populations when grown under identical conditions. Cheatgrass is self pollinating and studies have indicated that outcrossing is rare, and that gene flow among populations occurs primarily through seed dispersal (e.g., Pyke and Novak 1994). This might constrain the evolution of locally adapted ecotypes. Studies suggest that genetic variation found among cheatgrass populations is probably due to multiple introductions (Novak et al. 1993) and that little ecotypic differentiation has occurred (Pyke and Novak 1994). Thus, it seems likely that plants from the saline site were pre-adapted for survival under saline conditions due to genetic potential for rapid growth.

Plants from the saline site maintained higher specific leaf area than those from the non-saline site, with the exception of plants in the control treatment. This indicates a lower investment in biomass per

unit area in leaves of the plants from the saline site, perhaps resulting in lower carbon requirements for maintenance respiration for those plants when subjected to salinity. Also, specific leaf area is positively correlated with relative growth rate (RGR) in many species (Poorter 1991). The faster growth of plants from the saline site could increase competitive ability and shorten time to flowering. Accelerated growth of these plants in a natural setting may enable use of shallow, less saline moisture reserves early in the growing season, prior to depletion by neighboring species that either do not become active as early as cheatgrass, or are not as competitive for water resources. Thus, low soil water potential that occurs later in the season could be avoided, as suggested by Rice and Mack (1991).

Conclusions

Increasing soil salinity had profound effects on photosynthesis and growth of cheatgrass. Responses to salt stress included 1) reduced whole-plant carbon gain as a consequence of low photosynthetic rates and reduced leaf area, 2) severely stunted root growth and 3) alteration of biomass allocation patterns from roots to shoots. The combined effects on growth and physiology could impair cheatgrass's competitive ability and/or lead to reduced seed production in environments where soil salinity is greater than approximately 4 dS/m in the rooting zone. Thus, success of cheatgrass in saline environments is probably limited by physiological and developmental mechanisms which stunt or delay growth and likely reduce fecundity.

Cheatgrass plants from the saline site accumulated leaf and root area faster than those from non-saline site and tended to invest less biomass per unit area in leaves. While plants from the saline site experienced salt induced reductions in area and biomass, accelerated growth may convey advantage to plants from this population in saline habitats.

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Effects of top-soil drying on saltceder photosynthesis and stomatal conductance

MOHAMED MOUNSIF, CHANGGUI WAN, AND RONALD E. SOSEBEE

Authors are Professor, Department of Ecology and Range Science, National School of Agriculture, Meknes, Morocco Research Associate and Professor, Department of Range, Wildlife, and Fisheries Management, Texas Tech University, Lubbock, Texas 79409. At the time c_f the research, the senior author was a Research Assistant, Department of Range, Wildlife, and Fisheries Management, Texas Tech University.

Abstract

Phreatophytes are trees and shrubs with deep roots tapping the water tables. As such they are presumed to be able to tolerate a water deficit in the top soil. Growth of some phreatophytes is decoupled from environmental factors such as incident precipitation. This study examined the effects of surface soil drying on gas exchange and stomatal conductance of a riparian phreatophyte *Tamarix gallica* L. (saltcedar) during 2 consecutive growing seasons in which summer precipitation varied substantially. Daily average gas exchange (A) was 13.5 μmol m^{-2} sec^{-1} in June and 13.4 μmol m^{-2} sec^{-1} in September, 1991 when surface soil was wet as compared to the same periods of 1990 in which very little rain occurred (6.44 and 8.08 μmol m^{-2} sec^{-1}, respectively, P < 0.0001). Stomatal conductance (g) or maximal conductance showed a similar trend of photosynthesis. Both average gas exchange and stomatal conductance were correlated with water content in the upper portion of the soil (r = 0.83 to 0.88 for A, P < 0 .05 and r = 0.65 to 0.70 for g, P < 0.05) in 1990 (a dry year). The variations in gas exchange or stomatac conductance of saltcedar were mainly caused by water availability in the upper soil layers, not by depth to the water table (0.65 vs 2.74 m). The responses of gas exchange and stomatal conductance to surface soil drying in the phreatophyte saltcedar were similar to that of several crop species [lupin (*Lupinus cosentinii* Guss. cv. Eregulla), wheat (*Triticum aestivum* L. cv. Cadensa) and sunflower (*Helianthus annuus* L.)]. Our data suggest that upon soil re-wetting, when water availability to shallow lateral roots increased, the entire root system of saltcedar was actively involved in water uptake, leading to higher stomatal conductance and photosynthesis.

Key Words: phreatophyte, water relations, gas exchange, drought tolerance, *Tamarix gallica* L.

Phreatophytes are woody or herbaceous plants that have roots that extend to the ground water table. There is much variability within this group in term of response to drought and relative use of water from deep vs. shallow soil horizons. According to Anderson (1982), the phreatophyte saltcedar (*Tamarix* spp.) typically derives its water supply from the water table and is able to tolerate drought. Busch et al. (1992), however, reported that facultative *Tamarix ramosissima* Ledeb. is capable of extracting

Resumen

Las freófitas son árboles y arbustos con raíces profundas que utilizan los mantos freáticos, se asume que ellas son capaces de tolerar el déficit de agua en al superficie del suelo. El crecimiento de algunas freófitas esta desacoplado de algunos factores ambientales, como la lluvia incidental. Este estudio examino los efectos del secado de la superficie del suelo en el intercambio gaseoso y la conductancia estomatal de la freófita ribereña Tamarix gallica L. (saltcedar). El estudio se condujo durante 2 estaciones de crecimiento consecutivas en las cuales la precipitación en verano varió substancialmente. El intercambio gaseoso diario promedio (A) fue de 13.5 Fmol m^{-2} sec^{-1} en Junio y de 13.4 Fmol m-2 sec-1 en Septiembre de 1991, cuando la superficie del suelo estaba húmeda comparada con los mismos periodos de 1990 en los cuales ocurrió muy poca lluvia (6.44 y 8.08 Fmol m^{-2} sec^{-1}, respectivamente, P < 0.0001). La conductancia estomatal (g) o conductancia máxima mostro una tendencia similar a la fotosíntesis. En 1990 (año seco), el intercambio gaseosos promedio y la conductancia estomatal estuvieron correlacionados con el contenido de agua de la porción superior del suelo (r = 0.83 to 0.88 for A, P < 0.05 and r = 0.65 to 0.70 for g, P < 0.05). Las variaciones en el intercambio gaseosos o la conductancia estomatal del "Saltcedar" fueron causadas principalmente por la disponibilidad de agua en las capas superiores del suelo, no por la profundidad del agua freática (0.65 vs 2.74 m). Las respuestas del intercambio gaseosos y la conductancia estomatal del "Saltcedar" al secado de la superficie del suelo fueron similares a las de varias especies cultivadas [lupin (*Lupinus cosentinii* Guss. cv. Eregulla), trigo (*Triticum aestivum* L. cv. Cadensa) y girasol (Helianthus annuus L.)]. Nuestros datos sugieren que en base al rehumedecimiento del suelo, cuando la disponibilidad de agua para las raíces laterales superficiales incrementa, el sistema radical completo del "Saltcedar" estuvo activamente involucrado en la absorción de agua, conduciendo a una mayor conductancia estomatal y fotosíntesis.

water from the unsaturated soil layers as well, which confer a significant competitive advantage over the native obligate phreatophytes *Populus* spp. and *Salix* spp. that derive water solely from the water table.

Despite their ability to extract water from the unsaturated shallow soil, water relations of phreatophytes are mainly affected by the depth to water tables (Van Hylckama 1963, Stromberg et al. 1992). Phreatophytes can reach a high level of productivity because growth is decoupled from the normal limiting factor of precipitation (Wilkinson 1966, Nilsen et al. 1981). More recently, Donovan and Ehleringer (1994) showed that some desert shrubs

do not respond to rainfall during the growing season. Devitt et al. (1997a) also concluded that it is doubtful that Tamarix would effectively utilize water from most summer rainfall events under hot, dry conditions. Because Tamarix can extract water from the unsaturated zone, plant water relations and photosynthesis of Tamarix may be affected by water deficit in the top soil. There is relatively little information, however, on the impact of surface soil drying on physiological responses of Tamarix. We evaluated the effects of surface soil drying on water relations and photosynthesis of the phreatophyte *T. gallica* L. growing in a riparian ecosystem in west Texas.

Materials and Methods

This study was conducted in Terry County, Texas (102°16' W and 33°11' N) in the southern portion of the Great Plains. The site about 12 km east of Brownfield was selected adjacent to a saline pond where saltcedar exists in a dense stand. Climate of the area is semiarid with an average annual precipitation of 450 mm. Monthly and annual precipitation vary considerably with May and June being the wettest months. Maximum potential evapotranspiration during May and June is about 16 mm day^{-1} (Texas Agricultural Experiment Station). The soil is an Amarillo fine sandy loam (fine-loamy, mixed, superactive, thermic aridic Paleustalf). The area supports a moderate stand of blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.], perennial three awns (*Aristida* spp.), and sideoats grama

[B. curtipendula (Michx.) Torr.]. Most of the area has been invaded by honey mesquite (*Prosopis glandulosa* Torr.) and saltcedar (*T. gallica*).

Saltcedar trees of approximately equal size were selected at 3 locations within the stand (within interior, on the periphery and at the exterior). Measurements of photosynthesis (A) and stomatal conductance (g) were conducted 4 days a week biweekly June through September during 1990 and 1991, which represented a dry and a wet year, respectively (Fig 1). A Li-Cor 6200 portable photosynthetic system (Li-Cor Inc., Lincoln, Nebr.) was used to measure photosynthesis and stomatac conductance. Xylem water potential (XWP) was measured 3 times daily (predawn, midday and at 1600 hours) with a Scholander pressure bomb. Soil water content was measured gravimetrically for 4 soil depths (0–15, 15–30, 30–45, 45–60 cm) on the first day of each sampling week (n = 4). Measurements of photosynthesis and stomatac conductance were also conducted on trees that grew adjacent to the pond and 60 m away from the pond in 1991 to study the impact of depth to water table (0.65 m vs 2.74 m) on the ecophysiology of *T. gallica*.

Since the environmental conditions varied from day to day, measurements made on 1 day represent a block. Each block contained 3 trees, e.g. 1 tree from each location within the stand. Since the measurements were made on the same individual trees at each location over the sampling period, the data were analyzed by Analysis of Variance (ANOVA) using a Randomized Block Design (RBD) with a repeated measures analysis. The means
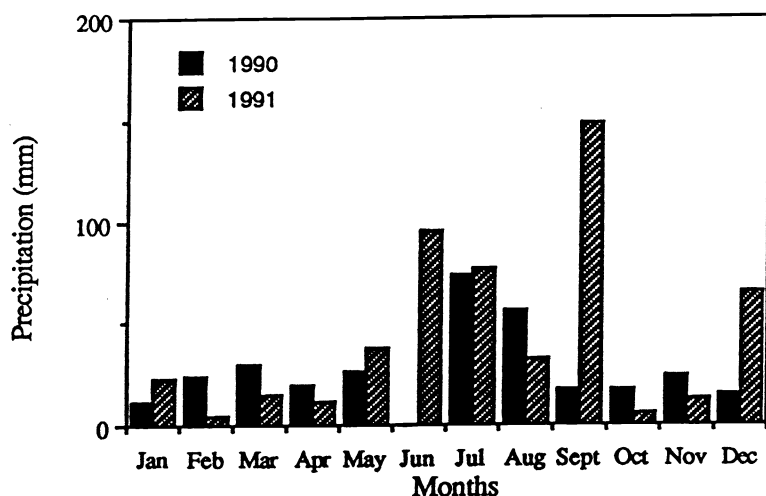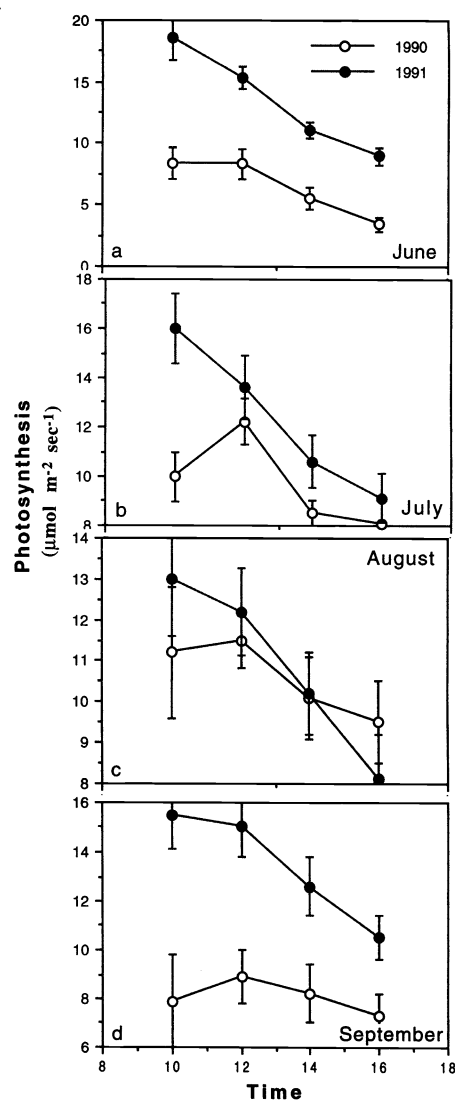

Fig. 2. Diurnal patterns of photosynthesis (μmol m^{-2} sec^{-1}) of saltcedar trees growing in Terry County, Texas in 1990 and 1991 (n = 24). Vertical bars are standard error of mean. Photosynthesis was higher in 2a and 2d in 1991 than in 1990 (P < 0.0001).

were separated using the protected Fisher's least significant difference (LSD) test.

Results and Discussion

The annual total precipitation was 316 mm for 1990 and 551mm for 1991; the monthly precipitation is presented in Fig. 1. The diurnal patterns of photosynthesis and stomatal conductance from June through September are summarized in Fig. 2-3. There were no differences in the July precipitation between the 2 years, nor were there differences in photosynthesis
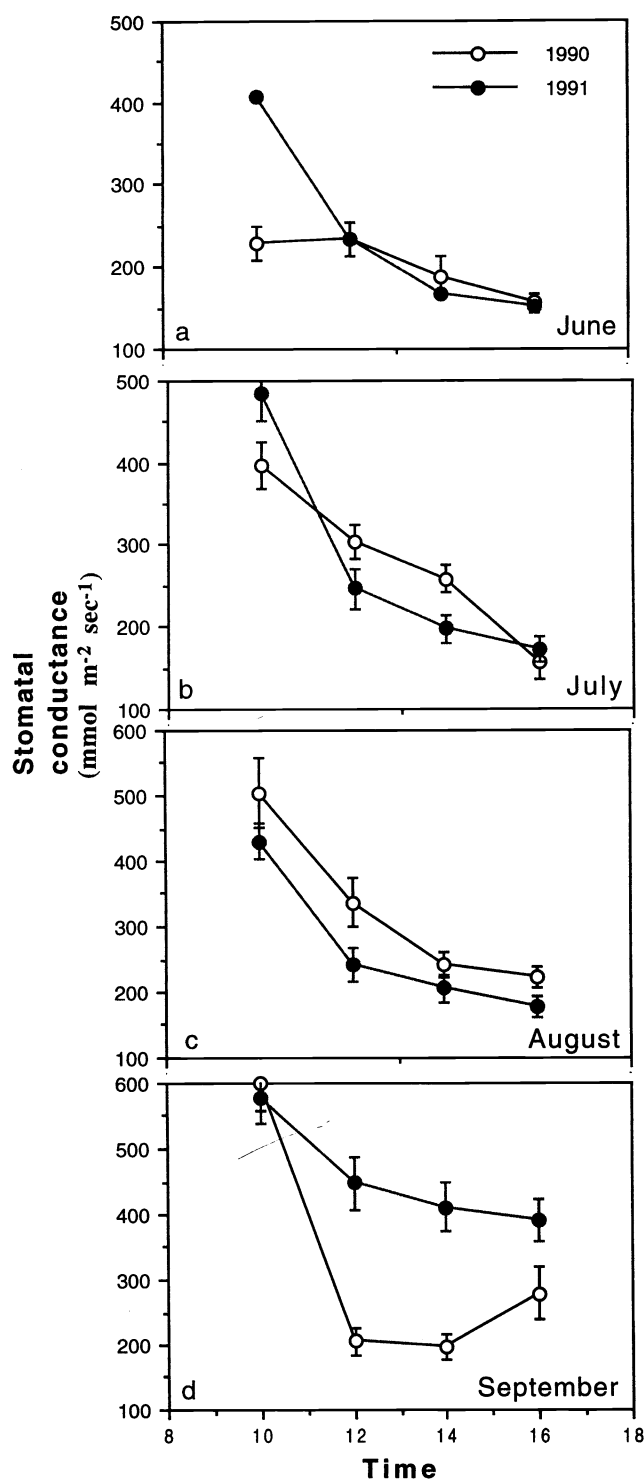

Fig. 1. Precipitation for Terry County, Texas in 1990 and 1991. The total precipitation was 316 mm for 1990 and 551mm for 1991.

Fig. 3. Diurnal patterns of stomatal conductance (mmol m^{-2} sec^{-1}) of saltcedar trees growing in
Terry County, Texas in 1990 and 1991 (n=24). Vertical bars are standard error of mean. The
maximum g in 3a and the average g in 3d in 1991 was higher than in 1990 (P < 0.01). The aver-
age g in 3c was higher in 1990 than in 1991 (P < 0.05), probably due to more precipitation in
August, 1990 (Fig. 1).

Stomatal conductance (or maximum g)
exhibited patterns similar to that of photo-
synthesis (Fig. 3a, 3d). August precipita-
tion in 1990 was higher than that in 1991,
as was stomatal conductance in August,
1990 (P < 0.05, Fig. 3c). The average leaf
temperatures during the sampling periods
ranged from 21.1° C (±0.60, n = 24) in
September to 40.3° C (±0.17, n = 24) in
June, and were not significantly different
between years (data not shown).

In the dry year (1990), the average A
was correlated (P < 0.05) with water con-
tent of soil depths at 15–30 cm (r = 0.88, n
= 8), 30–45 cm (r = 0.83,n = 8) and 45–60
cm (r = 0.87, n = 8), and the average stom-
atal conductance was correlated (P < 0.05)
with water content at 0–15 cm (r = 0.65, n
= 8) and 15–30 cm (r = 0.70, n = 8) soil
depths. Correlations, however, were not
significant in 1991. These results were
consistent with Devitt et al. (1997b) who
reported that in *T. ramosissima* growing at
a groundwater depth of 3 m, relative sap
flow and stomatal conductance were a
function of relative soil water in storage.
Devitt et al. (1997b) also reported that leaf
water potential of *Tamarix* declined to a
minimum of -3.5 MPa during the drydown
phase of their experiment, but plants
responded within 24 hours to surface irri-
gation.

Water relations of phreatophytes are
mostly affected by the depth to water table
(Van Hylckama 1963, Stromberg et al.
1992). In wet years, the water table could
rise due to high infiltration, which in turn
affects water relations of saltcedar. In the
riparian ecosystem where *T. gallica* grew,
however, the deepest water table was only
2.74 m below soil surface which was well
within the rooting depth of saltcedar (most
trees were > 4 m tall). In 1991, the trees
grown in proximity of the pond where
depth to water table ranged from 0.60 to
0.65 m had similar photosynthesis and
stomatal conductance when compared to
trees 60 m away from the pond where
depth to the water table was in the range
of 1.64 to 2.74 m (data not shown). It
appeared when saltcedar grew in soil with
a relatively shallow groundwater source,
variations in photosynthesis and stomatal
conductance were mainly caused by water
availability in the upper soil layers. This
was different from the results of Van
Hylckama (1963) who showed that
saltcedar (*T. pentandra* Pall.) trees grown
in evapotranspirometers at a water table
depth of 1.5 m, transpired 29 and 56%
more water than when the water table was
2.1 and 2.7 m deep. Our results agreed
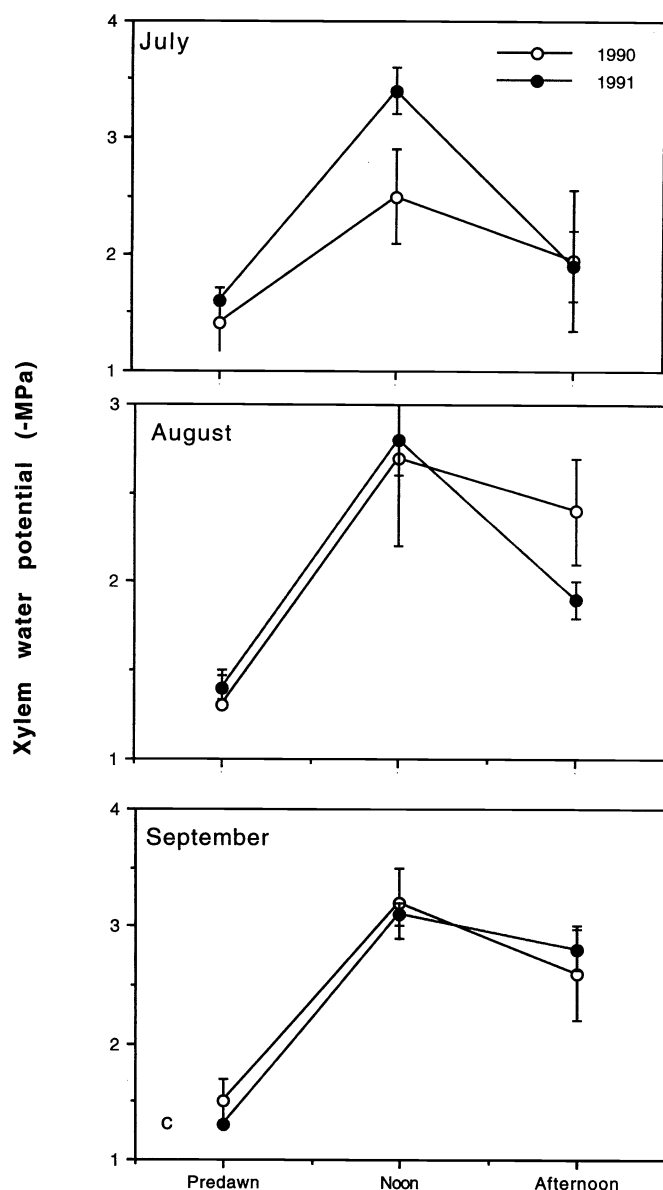with Dugas et al. (1992) who reported that

and stomatal conductance (Fig. 1, 2b, 3b).
Precipitation in June and September, 1991
was significantly higher than that in 1990
(Fig. 1). Likewise photosynthesis was 13.5

μmol m^{-2} sec^{-1} in June and 13.4 μmol m^{-2}
sec^{-1} in September 1991, 109% and 66%
higher, respectively, than during the same
periods in 1990 (P < 0.0001, Fig. 2a, 2d).

Fig. 4. Diurnal patterns of xylem water potential (XWP, -MPa) of saltcedar trees growing in Terry County, Texas in 1990 and 1991 (n = 12). Vertical bars are standard error of mean.

Photosynthesis and leaf conductance exhibited similar diurnal patterns, and were both related to leaf-air vapor pressure deficit. For example, in 1990, the daily maximum leaf-air vapor pressure deficit was linearly correlated with daily average photosynthesis ($P < 0.0001$, $r = -0.84$, $n = 24$), and with daily average stomatal conductance ($P < 0.0001$, $r = -0.91$, $n = 24$) at the exterior of the stand. As leaf-air vapor pressure deficit increased in the afternoon, photosynthesis and stomatal conductance decreased (Fig. 2–3). Thus, photosynthesis and stomatal conductance were also susceptible to leaf-air vapor pressure deficit. As stomata closed in response to increased leaf-air vapor pressure deficit, water loss was curtailed and the plants were able to maintain a relatively stable xylem water potential (Fig. 4). Franco et al. (1994) observed that when predawn xylem water potential was > -2 MPa in *Larrea tridentata* (D.C.) Cov. the leaf-air vapor pressure deficit gradient had a large impact on photosynthesis and leaf conductance. In saltcedar, predawn xylem water potential was well above -2 MPa (Fig. 4), and photosynthesis and stomatal conductance were a function of leaf-air vapor pressure deficit which is consistent with observation reported by Franco et al. (1994).

Intercellular CO_2 concentration (Ci) was significantly lower during most of the growing season in 1991 than in 1990 (Fig. 5a–5c). Therefore, mesophyll conductance (A/Ci) was significantly higher in 1991 than in 1990. This suggested that photosynthesis was limited by the non-stomatal component, i.e., by the photosynthetic biochemistry. A low intercellular CO_2 concentration indicated a higher mesophyll assimilation rate. Intercellular CO_2 concentration often increases in dehydrated leaves (Lauer and Boyer 1992, Epron and Cornic 1993) because the photosynthetic apparatus is unable to fix CO_2 fast enough to deplete intercellular CO_2 concentration. A higher intercellular CO_2 concentration in dehydrated leaves indicates that the demand for CO_2 diminishes since metabolism is inhibited. During a dry growing season, even a phreatophyte like saltcedar had dehydrated, or wilted, leaves with low turgor as observed in this study (xylem water potential ranged from -2.5 to -3.5 MPa), which resulted in reduced assimilation rates and high intercellular CO_2 concentration.

In a controlled environment, Gallardo et al. (1994) reported that lupin (*L. cosentinii* Guss. cv. Eregulla) with a well-established root system can utilize localized supplies
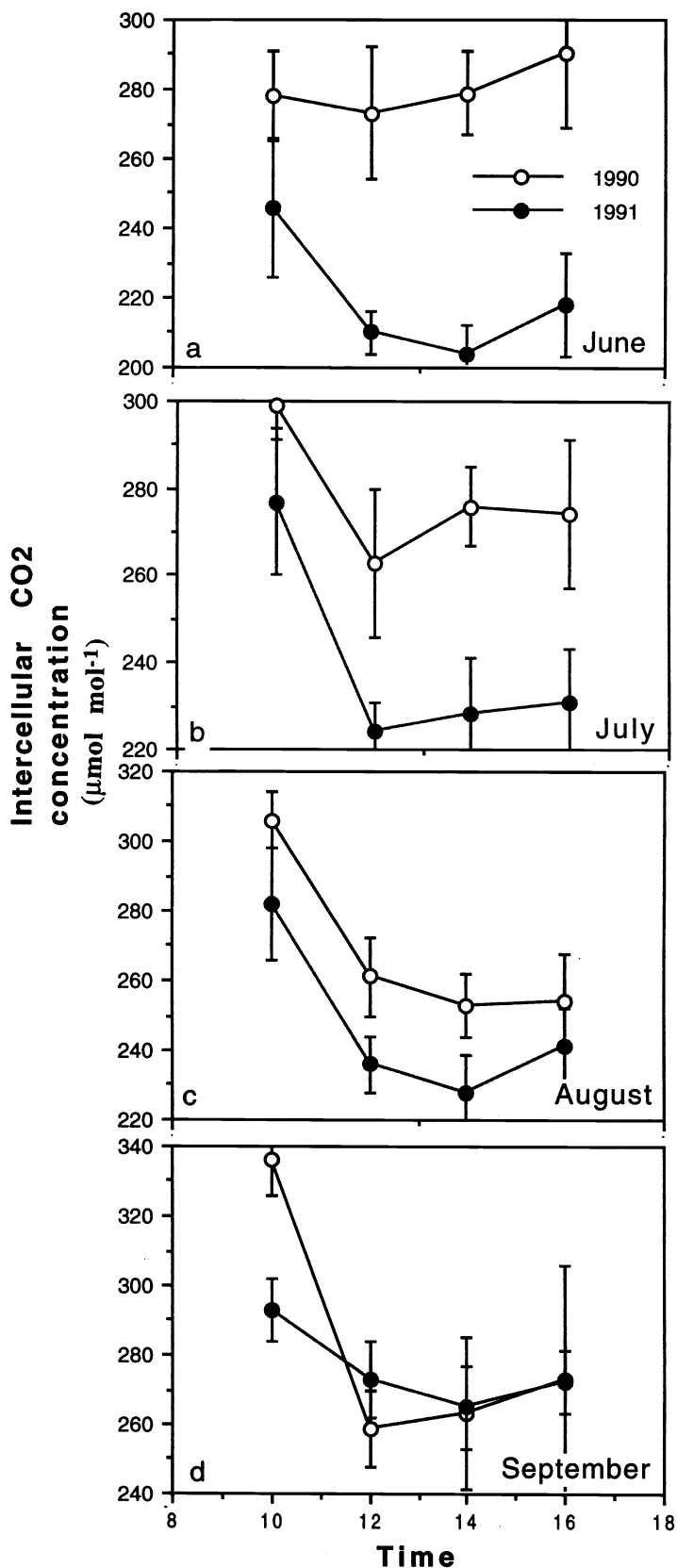
the facultative phreatophyte *Prosopis* exhibited 62% higher daily stem flow when surface soil was wet than when surface soil was dry.

Phreatophytes, by definition, are a group of deep-rooted trees and shrubs that obtain dependable water supply from the saturated water table. The predawn xylem water potential was similar between the 2 years (Fig. 4), indicating that drought in the 1990 growing season had limited effects on plant water status early in the morning due to absorption of the groundwater by the deep roots. There was a large variation in transpiration rate at the leaf level, therefore, no significant difference in transpiration was shown between the 2 years (data not presented). The roots with access to a water table could supply a large portion of the water requirements when surface soil was dry (Burgess et al. 2000) and transpiration rate was, to a large extent, regulated by leaf-air vapor pressure deficit. Our results, however, suggest that even in *T. gallica* trees growing in soil with a shallow water table, surface soil drying can substantially reduce photosynthesis and stomatal conductance.

Fig. 5. Diurnal patterns of intercellular CO_2 concentration (μmol CO_2 mol^{-1}) of saltcedar trees growing in Terry County, Texas in 1990 and 1991 (n=24). Vertical bars are standard error of mean. Intercellular CO_2 concentration was lower in 1991 than in 1990 (P < 0.05) in 5a-5c.

of available soil water to maintain leaf gas exchange despite appreciable portion of the root system being in dry soil. They speculated that the increased water uptake by deep roots may have diluted any abscisic acid (ABA) produced by the roots in the dry soil. However, other studies (Zhang and Davies 1989, Henson et al. 1989, Ali et al. 1998) reported that partial soil drying reduced stomatal conductance and leaf growth due to root-borne chemical signals in the dry soil. Photosynthesis is closely related to the extent of leaf hydration (Kaiser 1982) which depends on water uptake and hydraulic conductance of the root system. Graham and Nobel (1999) showed that under field conditions the entire root system of *Agave deserti* (Engelm.) must be rewetted for maximal carbon gain to occur rapidly. In west Texas where potential evapotranspiration can reach as high as 16–18 mm per day during a drought period (Wan et al. 1998), water uptake by saltcedar from the deep water source was unlikely to be available in quantities large enough to completely relieve leaf water deficit as indicated by sharply reduced leaf conductance (Fig. 3) and leaf wilting. Burgess et al. (2000) showed that in the woody pheatophyte *Banksia prionotes* (Proteaceae) relative contribution of the taproot to total water uptake during a dry period was 80%, which declined steadily to 45% with increased rainfall and increased availability of water to lateral roots. In the wet year (1991), when water availability to lateral roots increased, the entire root system of saltcedar was probably actively involved in water uptake, leading to rapid leaf hydration and higher photosynthesis.

As a phreatophyte, saltcedar plants have maximum root development in the capillary fringe above the water table and are able to tolerate drought (Anderson 1982, Cleverly et al. 1997). However, in this experiment gas exchange and stomatal conductance was shown to be quite susceptible to a summer drought. Since saltcedar is a deep-rooted plant, a summer drought may only represent a mild water stress as indicated by predawn xylem water potential. Yet, photosynthesis and leaf conductance declined in response to this mild water stress. Furthermore, the response of saltcedar to partial soil drying was not different from that of several relatively shallow-rooted crop species such as wheat, lupin and sunflower (Zhang and Davies 1989, Henson et al. 1989, Ali et al. 1998). This suggests that the dual root system makes saltcedar a highly opportunistic water user: it can effectively use soil water

wherever it is available. When the surface soil is wetted by rainfall, water uptake from the upper soil profile contributes greatly to plant water consumption, while the plants depend mainly on the deep roots for water supply during a drought. The ability of saltcedars to closely regulate photosynthesis and leaf conductance during drought increases its survivability in arid and semiarid rangelands. The rapid response of saltcedar to summer rainfall enhances photosynthetic production and competitiveness against the obligate pheatophytes that depend only on groundwater source for growth.

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Effects of nitrogen availability on the growth of native grasses exotic weeds

PETRA N. LOWE, WILLIAM K. LAUENROTH, AND INGRID C. BURKE

Authors are Research Associate, Shortgrass Steppe Long Term Ecological Research Project, Department of Forest Sciences, Colorado State University, Fort Collins, Colorado 80523, Professor, Rangeland Ecosystem Science Department, Colorado State University, Fort Collins, Colo. 80523, Professor Department of Forest Sciences, Colorado State University, Fort Collins, Colo. 80523 respectively. At the time of the research, senior author was graduate research assistant, Rangeland Ecosystem Science Department, Colorado State University, Fort Collins, Colo.

Abstract

Many studies have shown that high nitrogen availability encourages the community dominance of exotic, weedy species. Other researchers have attempted to reduce existing exotic species infestations by reducing soil nitrogen availability. We tested the hypothesis that exotic weeds and native species differ in their response to nitrogen availability, predicting that the exotics would have a much more positive response than the natives at high nitrogen levels but that natives would better tolerate low nitrogen levels. To test this hypothesis, we conducted a greenhouse experiment investigating the aboveground biomass, belowground biomass, height, and aboveground tissue nitrogen concentration response of 2 North American native plant species, blue grama (*Bouteloua gracilis* H.B.K. Lag.) and western wheatgrass (*Pascopyrum smithii* (Rybd.) A. Love), and 4 exotic species, cheatgrass (*Bromus tectorum* L.), leafy spurge (*Euphorbia esula* L.), Canada thistle (*Cirsium arvense* L.), and Russian knapweed (*Centaurea repens* L.), to 5 levels of nitrogen availability, 0 g N/m^2, 1 g N/m^2, 4 g N/m^2, 7g N/m^2, and 10 g N/m^2. We grew single individuals of each species from seed in 3 liter pots in the greenhouse for 75 days. The exotics and natives did differ in their response to nitrogen availability, but not in the predicted manner. The exotics did not have a more positive response to nitrogen availability than the native species, and the species with the poorest response was an exotic. There were no differences between the exotic and native species at any level of nitrogen availability in root:shoot ratios, total biomass, or percent leaf tissue nitrogen, but the native species as a group gained more height than the exotics at every level of nitrogen availability. Our data do not show a generalizable relationship between exotic or native plant groups and growth response to nitrogen.

Key Words: nutrient response, *Bromus tectorum*, *Cirsium arvense*, *Centaurea repens*, *Euphorbia esula*, greenhouse

Resumen

Muchos estudios han demostrado que la alta disponibilidad de nitrógeno promueve el dominio de la comunidad por especies de plantas exóticas y malezas. Otros investigadores han intentado reducir la infestación de especies exóticas reduciendo la disponibilidad de nitrógeno del suelo. Probamos la hipótesis de que las malezas exóticas y las especies nativas difieren en su respuesta a la disponibilidad de nitrógeno, prediciendo que las exóticas tendrían una respuesta mucho mas positiva que las nativas a los altos niveles de nitrógeno, pero que las nativas tolerarían mejor los bajos niveles de nitrógeno. Para probar esta hipótesis se condujo un experimento en invernadero investigando la respuesta de la biomasa aérea y subterránea, la altura de planta y la concentración de nitrógeno en los tejidos aéreos de dos especies nativas de Norte América "Blue grama" (*Bouteloua gracilis* H.B.K. Lag.) y "Western wheatgrass" (*Pascopyrum smithii* (Rybd.) A. Love) y cuatro especies exóticas "Cheatgrass" (*Bromus tectorum* L.), "Leafy spurge" (*Euphorbia esula* L.), "Canada thistle" (*Cirsium arvense* L.) y "Russian knapweed" (*Centaurea repens* L.) a 5 niveles disponibilidad de nitrógeno: 0 g N/m^2, 1 g N/m^2, 4 g N/m^2, 7g N/m^2 y10 g N/m^2. Plantas individuales de cada especie provenientes de semilla crecieron durante 75 días en 31 macetas en el invernadero. Las exóticas y nativas difirieron en su respuesta a la disponibilidad de nitrógeno, pero no en la manera predicha. Las exóticas no tuvieron una respuesta mas positiva a la disponibilidad de nitrógeno que la nativas y la especie con la respuesta mas pobre fue una exótica. En ningún nivel de disponibilidad de nitrógeno se detectaron diferencias entre las especies exóticas y nativas respecto a la relación tallo:raíz, biomasa total o porcentaje de nitrógeno en el tejido foliar, pero las especies nativas como grupo ganaron mas altura que las exóticas en cada nivel de disponibilidad de nitrógeno. Nuestros datos no muestran una relación generalizable entre grupos de plantas exóticas y nativas y la respuesta del crecimiento al nitrógeno.

Non-native, invasive weed species are theorized to share a host of specific life history traits that contribute to their success as invasives; one of those characteristics is a rapid growth response to nutrient enrichment (Grime 1977, Baker 1986). Conversely, fast growing plant species, many but not all of which are exotic weeds, are thought to fare poorly under low nutrient conditions

(Grime 1977, Chapin 1980, Shipley and Keddy 1988, Carson and Pickett 1990). The spread and persistence of invasive exotic weeds is of major concern to both land owners and conservationists as exotic plant invasion can reduce biodiversity (Huston 1994) and alter ecosystem function (Vitousek 1986).

High nitrogen availability has been shown to encourage the spread and dominance of exotic invasive weeds (Hobbs and Atkins 1988, Huenneke et al. 1990, Milchunas and Lauenroth 1995). Other researchers have attempted to reduce exotic species by reducing nitrogen availability, hypothesizing that native

species have a competitive advantage over exotics under low nitrogen conditions (McLendon and Redente 1992, Wilson and Gerry 1995, Morghan and Seastedt 1999, Paschke et al. 2000). Several exotic species, such as cheatgrass (*Bromus tectorum* L.), leafy spurge (*Euphorbia esula* L.), Canada thistle (*Cirsium arvense* L.), and Russian knapweed (*Centaurea repens* L.), have become of particular concern in western rangelands of the United States because of their aggressive invasion of large areas. Empirically testing the response of these species to varying nitrogen levels can help predict the impact of nitrogen additions or reductions on systems where these noxious weeds occur.

The objective of this study was to test the hypothesis that fast growing exotic weeds have a different response to both low and high levels of nitrogen availability than native species. We predicted the exotic species would have a greater response than the natives to nitrogen at high levels of availability, but the natives would better ability to tolerate the low levels of nitrogen. Additionally, we tested the common assumption that exotic species are strongly responsive to nitrogen inputs.

Methods

We set up the experiment in the greenhouse as a completely randomized design with 6 species at 5 levels of nitrogen availability. We had 5 replicates of each species at each level of nitrogen availability for a total of 150 pots. Two of the plants were native species and 4 were invasive, exotic species. The native species were blue grama (*Bouteloua gracilis* H.B.K. Lag.) a warm season perennial grass, and western wheatgrass (*Pascopyrum smithii* (Rydb) A. Love), a cool season perennial grass. Blue grama was chosen because it dominates a large portion of the shortgrass steppe, an ecosystem that has not been significantly invaded by exotic weeds (Kotanen et al. 1998). Western wheatgrass is a native species that has some weedy characteristics (sensu Baker 1986), for example, it grows readily in disturbed areas such as roadsides (Stubbendieck et al. 1981). The exotic, invasive weed species selected for study were cheatgrass, (*Bromus tectorum*), leafy spurge (*Euphorbia esula*), Canada thistle (*Cirsium arvense*), and Russian knapweed (*Centaurea repens*). Blue grama and western wheatgrass seeds were obtained from Pawnee Buttes Seed Inc. (Greeley, Colo.). Cheatgrass seeds were collected by hand

at the Central Plains Experimental Range (CPER, 40°49' N latitude, 107°46' W longitude), which is 61 km northeast of Fort Collins, Colo., USA. The seeds for the other exotic species were collected from open field sites in Fort Collins, Colo.

We sowed 10 seeds of each species into each of 25, 15-cm x 16.5-cm plastic pots with a substrate of 60% vermiculite, 40% washed sand by volume and a surface area of 191 cm^2. Ten days after first emergence, we thinned the seedlings to 1 plant per pot.

A nitrogen gradient was established with 5 levels of nitrogen the equivalent of 0 g N/m^2, 1 g N/m^2, 4 g N/m^2, 7 g N/m^2, and 10 g N/m^2. Nitrogen availability across the Great Plains of the United States, where the species tested here would grow, and potentially compete, ranges from 1.5 g/m^2 to 10.5 g/m^2 (Burke et al. 1997). We applied the nitrogen treatments as a solution of ammonium nitrate in stages: 10% of the total ammonium nitrate application was applied on the 20th day after germination, and every 2 weeks thereafter we added dosages of 25%, 30%, 20%, and 5%. We applied all micro- and macro-nutrients, except nitrogen, to the pots with a modified Hoagland's solution at a rate of 100 ml every week. We maintained the pots near field capacity by watering every day or every other day, depending upon need. We maintained the pots in an unshaded greenhouse from 8 July to 21 Sept. 1999, about 75 days.

At the end of the experiment, we harvested aboveground biomass by clipping each plant just above the root crown and drying the plant material at 55°C for 48 hours. We washed the root system of each plant carefully to remove as much of the potting material as possible. Root biomass is reported on an ash free basis. We measured plant height in centimeters for each plant at the end of the experiment, before biomass harvesting. We ground the dried aboveground material in a ball mill and analyzed a 0.1 g subsample for nitrogen content in a LECO CHN-1000 analyzer (St. Joseph, Mich.).

We analyzed the data in 2 ways. First,

we analyzed the aboveground biomass at the end of the experiment versus nitrogen availability using regression in SAS 1999 (SAS Institute, Cary, N.C.) to compare response slopes. Secondly, we used one-way analysis of variance utilizing a general linear model in SAS to determine differences between root:shoot ratios of the individual species at different nitrogen levels, and the differences between total biomass, height, and percent tissue nitrogen of the grouped average response of the 4 exotics and the 2 natives. We used Fisher's least significant difference (LSD) procedure (P = 0.05) to compare all treatment means and slopes.

Results

There was a significant positive relationship between aboveground biomass and nitrogen availability for each species, but the responses differed significantly (Table 1). The most positive relationships were for the exotics *Cirsium arvense* and *Bromus tectorum* and the native *Bouteloua gracilis*. The species with the least positive relationship between aboveground biomass and nitrogen availability was the exotic *Euphorbia esula*.

Root:shoot ratios did not differ between species at different nitrogen levels, but did differ at different nitrogen levels for each species (Table 2). All species with the exception of *Euphorbia esula* showed a decrease in the root:shoot ratio with the increase of nitrogen availability from 0 to 1 g N/m^2, but showed no further decrease after this level.

There were no significant differences between total biomass gain at any level of nitrogen availability between native and exotic species (Fig. 1a). There were significant differences between natives and exotics for plant height, with the average height of the native species being significantly taller at every level of nitrogen availability than the average height of the exotics (Fig. 1b). Percent leaf nitrogen increased for both exotic and native

Table 1. Regressions for 6 plant species of nitrogen availability versus aboveground biomass gain over 75 days when grown from seed in the greenhouse.

Species	Native/Exotic	Slope	Y-Intercept	R^2	n
Cirsium arvense	Exotic	0.417[*a]	0.008	0.788	16
Bromus tectorum	Exotic	0.403[*a]	0.190	0.905	23
Bouteloua gracilis	Native	0.375[*a]	0.255	0.715	23
Centaurea repens	Exotic	0.264[*b]	0.019	0.880	21
Pascopyrum smithii	Native	0.227[*b]	0.285	0.667	21
Euphorbia esula	Exotic	0.044[*c]	0.017	0.399	24

Slopes significantly different from zero are indicated with *(P = 0.05). Slopes with the same letter are not significantly different at P = 0.05.

TABLE 2. Mean root:shoot ratios (± one standard error of the mean) of 6 different plant species grown at different nitrogen levels from seed in the greenhouse for 75 days.

Nitrogen Level	PASM	BOGR	BRTE[*]	CERE[*]	CIAR[*]	EUES[*]
0 g/m^2	8.8±3.1^a	13.8±4.9^a	9.5±3.8^a	20.5±10.2^a	11.6±8.3^a	6.67±2.7^a
1 g/m^2	4.9±3.9^b	2.03±0.9^b	3.4±1.6^b	3.5±1.2^b	1.9±0.4^b	2.43±1.0^a
4 g/m^2	0.76±0.1^b	0.99±0.08^b	1.4±0.3^b	0.43±0.08^b	0.73±0.3^b	4.5±2.6^a
7 g/m^2	0.79±0.09^b	0.95±0.7^b	0.70±0.1^b	0.50±0.04^b	0.57±0.03^b	2.67±1.0^a
10 g/m^2	1.02±0.3^b	0.44±0.1^b	0.70±0.1^b	0.45±0.08^b	0.38±0.02^b	2.8±1.6^a

PASM=*Pascopyrum smithii*. BOGR= *Bouteloua gracilis*. BRTE= *Bromus tectorum*. CERE=*Centaurea repens*. CIAR=*Cirsium arvense*. EUES=*Euphorbia esula*. Means within the same column with the same letter are not significantly different at P=0.05. [*]Denotes an exotic species.

species as nitrogen availability increased but there were no significant differences between the percent leaf nitrogen of the exotic and native species at any level of nitrogen availability (Fig. 2).

Discussion

Our data support the hypothesis that exotic and native species differ in response to nitrogen availability, but not in the way we predicted. We predicted that the exotic species would have higher growth than the natives at high nitrogen levels, as both theoretical (Grime 1977, Baker 1986) and field studies have either predicted or shown this result (Huenneke et al. 1990, McLendon and Redente 1991, Milchunas and Lauenroth 1995). Conversely, we predicted that the native species would grow better than the exotics at low levels of nitrogen availability, as has been predicted by Chapin (1980) and shown by others (Wedin and Tilman 1990, Redente et al. 1992).

If our original prediction was correct, comparing the regression slopes of above-ground biomass to nitrogen availability (Table 1) should show the exotic species with more positive responses to nitrogen availability than natives; however, this did not occur. The responses were mixed, with the 2 native species having the same response to increasing nitrogen availability as 3 out of the 4 exotic species. Additionally, there were no differences in total biomass gain between averages of the 2 native species and the 4 exotic species at any level of nitrogen availability (Fig. 1a), and the average plant height of the native species had a greater response to increasing nitrogen availability than the exotics (Fig. 1b), which is very different from the predicted results.

We also tested the assumption that exotic species have a strong response to nitrogen inputs. Our data show that some exotics have a strong response to nitrogen

inputs while others do not. The species with the weakest response was *Euphorbia esula*, a species that has invaded 3 million acres in 29 of the 50 states in the U.S. (Sheley and Petroff 1999). Growth response to nitrogen availability can not explain the competitive success of all exotics, other factors such as response to water availability, temperature, or her-

bivory may be influencing competition.

Fast growing species, such as many exotic weeds, are predicted to have a higher root:shoot ratio at low nutrient availability and a lower ratio at higher availability than slow growing species from infertile habitats, such as many native grassland species (Chapin 1980). This is predicted to occur because fast growing species from fertile habitats are thought to have greater plasticity in allocation than species from stressful low fertility environments (Grime 1977). In our study, there were no statistical differences in the root:shoot ratio of the different native and exotic species at any level of nitrogen availability. At the low levels of nitrogen availability (Table 2), all species except *Euphorbia esula* had a lower root:shoot ratio as nitrogen availability increased.

Our results are similar to results found by Padgett and Allen (1999), who compared the growth response of 3 exotic
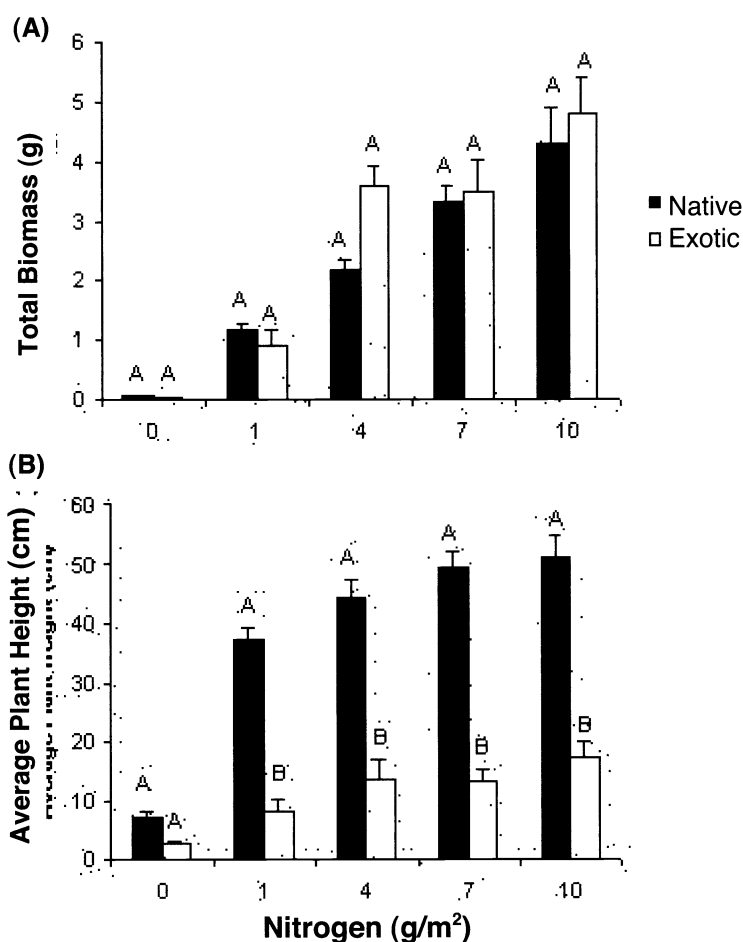

Fig. 1. Averaged total biomass gain (A) and plant height (B) response of 2 native species (*Bouteloua gracilis* and *Pascopyrum smithii*) and 4 exotic species (*Bromus tectorum, Centaurea repens, Cirsium arvense,* and *Euphorbia esula*) grown from seed in the greenhouse for 75 days, to a gradient in nitrogen availability. Error bars are one standard error of the mean. Bars with the same letter are not significantly different at *P* = 0.05.
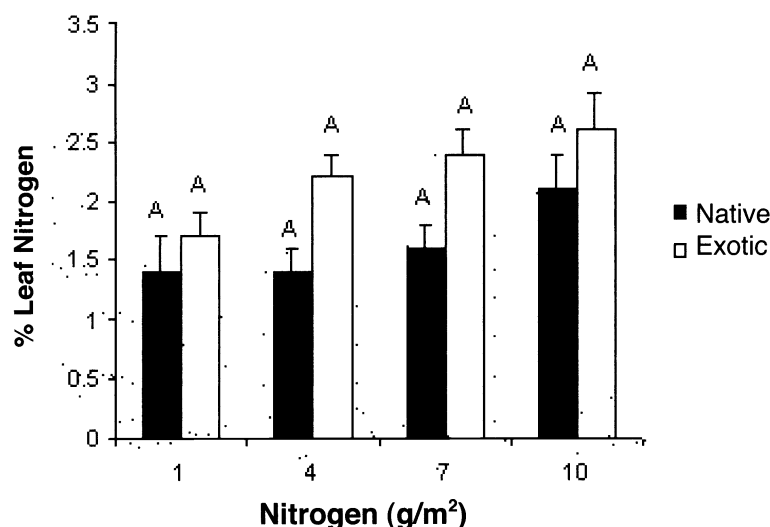
Fig. 2. Averaged % leaf nitrogen response of 2 native species (*Bouteloua gracilis* and *Pascopyrum smithii*) and 4 exotic species (*Bromus tectorum, Centaurea repens, Cirsium arvense*, and *Euphorbia esula*) grown from seed in the greenhouse for 75 days, to a gradient in nitrogen availability. Error bars are one standard error of the mean. Bars with the same letter are not significantly different at $P = 0.05$.

annuals and 3 shrubs to a gradient in nitrogen availability. They found that native species had a much stronger response to increasing nitrogen availability than predicted, showing a greater relative yield response than all 3 exotics in the study. Redente et al. (1992) grew 4 native species and 1 fast growing exotic species, Russian thistle [*Salsola iberica* (Sennen)], under 7 different nitrogen levels, and found the growth of Russian thistle was significantly reduced at low levels of available nitrogen while the slow growing native species performed comparatively better. We found no differences in the growth of the exotics and natives we tested at low nitrogen levels.

Management Implications

Several researchers have attempted, with varying levels of success, to reduce existing exotic weed populations by reducing nitrogen availability, hypothesizing that native species are better adapted to low nitrogen environments and therefore have a competitive advantage over exotics under low nitrogen conditions (McLendon and Redente 1992, Morgan 1994, Seastedt et al. 1996, Wilson and Gerry 1995, Morghan and Seastedt 1999). McLendon and Redente (1992) were successful in reducing the canopy cover of 2 fast growing exotic weeds, Russian thistle, and kochia (*Kochia scoparia* (L.) Schrad.) by reducing soil nitrogen content with the addition of sucrose to a disturbed sagebrush system in northwestern Colorado. By contrast, Seastedt et al. (1996) and

Morghan and Seastedt (1999) were unable to reduce the density of 2 exotic invasive plants, field alyssum (*Alyssum minus* (L.) Rothm.), and diffuse knapweed (*Centaurea diffusa* Lam.) when they reduced soil nitrogen with additions of sucrose and sawdust to a disturbed mixed grass community in Colorado. Restoration efforts attempting to reduce exotic weed species by reducing nitrogen availability rely on the differential responses of exotic and native species to nitrogen, specifically that exotic weed species will be at more of a disadvantage at low nitrogen levels than native species. Our results show, for the species tested, that there is no generalizable relationship between life history (weedy exotic versus non-weedy native) and growth response to nitrogen. From these results, we predict that the success of restoration efforts using nitrogen reduction to control exotic species may significantly depend on the species composition of the site to be treated.

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Intermediate wheatgrass and Russian wildrye responses to defoliation and moisture

J. R. HENDRICKSON AND J. D. BERDAHL

Authors are Rangeland Scientist and Research Plant Geneticist, respectively, Northern Great Plains Res. Lab, USDA-ARS, Box 459 Mandan, N.D.

Abstract

Perennial forage grasses in the Northern Great Plains are often grazed under water-limiting conditions. The effects of defoliation and soil moisture dynamics on herbage yield, tiller recruitment and number of crown positions for 2 perennial forage grasses were evaluated in a greenhouse experiment at Mandan, N.D. Intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkw. & D.R. Dewey] and Russian wildrye (*Psathyrostachys juncea* (Fisch.) Nevski] were grown at 75, 50, or 40% of field capacity and left as undefoliated controls or defoliated at 10-day intervals to an 8- or 4-cm stubble height. Cumulative herbage yield exhibited defoliation level by soil moisture ($P = 0.0001$) and species by defoliation ($P = 0.007$) interactions. Yield decreased with increasing defoliation intensity at 75 and 50% of field capacity, but at 40% of field capacity only the most intense defoliation level was significantly affected. Russian wildrye produced more herbage (1.97 g plant^{-1}) than intermediate wheatgrass (1.36 g plant^{-1}) under severe defoliation level. Increased defoliation intensity ($P = 0.0001$) but not water availability ($P > 0.05$) decreased tiller numbers. Pooled across all treatments, Russian wildrye produced 10 tillers per plant and intermediate wheatgrass produced 7 ($P = 0.0001$). This may partially explain Russian wildrye's greater grazing tolerance. The number of crown positions (potential axillary bud sites in the bottom 20mm of the plant) was similar between species suggesting that increased tiller numbers in Russian wildrye occurred because its axillary buds were more readily activated than intermediate wheatgrass. Moderate and severe defoliation reduced the number of crown positions on parent seedlings to only 62 and 50% of the number of crown positions of control seedlings, respectively. Water stress decreased ($P = 0.004$) number of crown positions at 40% of field capacity but only when crown positions of both parent and daughter tillers were pooled. In this experiment, defoliation had a greater effect than water stress. Moisture level mainly affected tiller size not numbers. The interaction between defoliation and water stress should be examined in field studies to foster improved management of these 2 grasses.

Key Words: (*Psathyrostachys juncea*), (*Thinopyrum intermedium*), Biomass, Tiller recruitment, Axillary buds,

Resumen

Los pastos perennes en las Grandes Planicies del Norte (Northern Great Plains) son a menudo pastoreados bajo condiciones de escasez hídrica. Los efectos de la defoliación y de la dinámica de la humedad del suelo sobre la producción de forraje, reclutamiento de macollas y el número de posiciones en la corona se evaluaron en un experimento en invernaderos en Mandan, Dakota del Norte. Se cultivó *Thinopyrum intermedium* ((Host) Barkw & D.R. Dewey) y *Psathyrostachys juncea* ((Fisch.) Nevski) a 75, 50, o 40% de la capacidad de campo y se dejaron como controles sin defoliar o defoliados, a intervalos de 10 días a 8- 4- cm de altura. La producción herbácea acumulativa mostró interacciones entre el nivel de defoliación y la humedad del suelo ($P = 0.0001$) y entre especie y defoliación ($P = 0.007$). La producción disminuyó con el aumento en la intensidad de la defoliación al 75 y 50% de la capacidad de campo, pero al 40% de la capacidad de campo, sólo el nivel más severo de defoliación tuvo un efecto significativo. *P. juncea* produjo más hierba (1.97 g planta^{-1}) que *T. intermedium* (1.36 g planta^{-1}) en condiciones de defoliación severa. El aumento en la intensidad de defoliación ($P = 0.0001$) y no la disponibilidad de agua ($P > 0.05$) produjo una reducción en el número de macollas. Combinando todos los tratamientos, *P. juncea* produjo 10 macollas por planta mientras que *T. intermedium* produjo 7 ($P = 0.0001$). Esto puede explicar parcialmente la mayor tolerancia al pastoreo de *P. juncea*. El número de posiciones en la corona (posiciones potenciales de yemas axilares en los 20 mm basales de la planta) fue similar entre las especies, lo que sugiere que el mayor número de macollas en *P. juncea* ocurrió debido a que sus yemas axilares fueron activadas más fácilmente que las de *T. intermedium*. La defoliación moderada y severa redujo el número de posiciones en la corona en las plantas progenitoras sólo en un 62 y 50% del número de posiciones en la corona en las plantas usadas como control, respectivamente. El estrés hídrico disminuyó ($P = 0.004$) el número de posiciones en la corona en el 40% de la capacidad de campo, pero sólo cuando se combinaron las posiciones en la corona de la macolla madre con las de la hija. En este experimento la defoliación tuvo mayor efecto que el estrés hídrico. El nivel de humedad afectó especialmente el tamaño de las macollas pero no el número de ellas. La interacción entre la defoliación y el estrés hídrico debería ser examinada en estudios de campo para ayudar en el mejoramiento del manejo de estas 2 especies de pasto.

Perennial forage grasses in the Northern Great Plains are often grazed when moisture is limiting. If apical or intercalary meristems are removed by grazing, production of new tillers through activation of axillary buds is crucial to reestablish the photosyn-

thetic canopy (Jewiss 1972). Limiting axillary bud production by a stress, such as drought, may adversely affect canopy regrowth and subsequent stand persistence (Busso et al. 1989). Understanding the interaction of drought and defoliation is paramount to development of viable grazing management guidelines for perennial forage grasses.

The ability to establish new tillers is an important trait associated with grazing tolerance in grasses. A comparative study of the grazing-sensitive bluebunch wheatgrass [Pseudoroegneria spicatum (Pursh) A. Löve] and the grazing-tolerant crested wheatgrass [Agropyron desertorum (Fisch. ex Link) Schult.] indicated ability to activate axillary buds was the primary mechanism affecting greater grazing tolerance of the latter (Caldwell et al.1981). Tiller recruitment from recently developed axillary buds contributed more to population persistence than did existing bud banks in sideoats grama [Bouteloua curtipendula (Michx.) Torr.] (Hendrickson and Briske 1997). Bud banks were considered to be buried viable populations of axillary buds in the soil (sensu Harper 1977 p. 109). However, axillary bud numbers are important, because, as a source of new tillers, they set a meristematic limit for future yields in perennial grasses, (Murphy and Briske 1992). Grazing and drought may adversely affect the ability of these axillary buds to initiate new tillers, and negatively affect stand persistence (Busso et al. 1989).

Intermediate wheatgrass [Thinopyrum intermedium (Host) Barkw. & D.R. Dewey] and Russian wildrye [Psathyrostachys juncea (Fisch.) Nevski] are 2 perennial forage grasses planted in the Northern Great Plains. Intermediate wheatgrass will not tolerate frequent grazing and haying (Lawrence and Ashford 1966). Russian wildrye can withstand heavy utilization (Smoliak 1968), is drought tolerant (Asay et al. 1996) and maintains its nutritional value with advancing maturity (Knipfel and Heinrichs 1978). The objective of our greenhouse study was to determine the mechanisms affecting their different responses to grazing and moisture by evaluating the effects of 3 moisture levels and 3 defoliation levels on herbage yield and tiller and axillary bud numbers.

Methods

Plastic bags (61 x 66 cm) were inserted into circular plastic pots with a radius of 11 cm and a height of 25 cm. The pots were filled with 7,800 g of a mix of 8 parts soil, Parshall fine sandy loam (coarse-loamy, mixed Pachic and Haploborolls) to 1 part vermiculite and 1 part peat moss. Field capacity of the soil was determined by hydrating the mix in 1,000 ml graduated cylinders and then drying hydrated soil at 70° C and subtracting the dry weight from the hydrated weight. Soil was considered hydrated when the wetting front reached within 2.5 cm of the cylinder's bottom. Twelve seeds of either 'Mankota' Russian wildrye (Berdahl et al. 1992a), or 'Reliant' intermediate wheatgrass (Berdahl et al. 1992b) were placed at a depth of 2.5 cm in each pot on 13 February 1997. The greenhouse was kept at 21 ± 3° C with 16 hours of light and 8 hours of darkness. Supplemental lighting was used to extend the light period. Pots were thinned to 9 plants after 2 weeks. Pots were watered to field capacity at the start of the experiment and were kept well watered until initial defoliation to ensure plants were generally at a morphological stage of Haun 3.5 (Haun 1973) at initial defoliation. Treatments were replicated 4 times in a factorial arrangement with 3 levels of defoliation and 3 levels of soil moisture. Defoliation treatments were: no defoliation (Control), defoliation to 8 cm stubble (Moderate) and defoliation to 4 cm stubble (Severe). Soil moisture treatments were 75, 50, and 40% of field capacity. Pots were weighed daily and watered as needed to maintain the appropriate moisture. Leaf water potentials were measured weekly on each species with a pressure chamber (Soil Moisture Corporation, Santa Barbara, Calif.[1]).

Of the 9 seedlings in each pot, the 3 in the center were identified as target seedlings prior to imposition of treatments. Target seedlings were defoliated and the remaining seedlings were not. In control treatments, target seedlings were not clipped until the end of the experiment. Defoliation began when plants had reached the 3.5 Haun stage (Haun 1973). Intermediate wheatgrass was more vigorous and reached the 3.5 Haun stage faster than Russian wildrye. Intermediate wheatgrass was initially clipped on 14 March 1997, about 2 weeks before Russian wildrye, and defoliations were repeated at approximately 10-day intervals thereafter. Prior to clipping, tiller numbers were recorded on the target seedlings, and newly emerging tillers were marked with color-coded wires. All herbage removed during defoliation was stored in a paper bag and dried at 55° C for 3 days. Senescent plant material was also included with the harvested biomass. Plant material was considered senesced when it was detached or the leaf blade appeared dead. Senescent material from the control pots was removed at final harvest.

Defoliated treatments were clipped 6 times. After the final clipping, the 3 target seedlings were removed, the potting soil washed from their crowns and roots, and the above-ground herbage stored in plastic bags. Roots were removed from the crowns of 2 seedlings and the herbage was dried at 55° C for 3 days before weighing. Roots were not included in the herbage determination. The third seedling was dissected in the laboratory. After dissection, all herbage, excluding roots, was dried and weighed like the other 2 seedlings.

In the crown region of grasses are compressed phytomers, each of which consists of a node, internode, leaf, and axillary bud (Briske 1991) (Fig. 1). Removing leaves from the crown area often results in leaf scars. These are marks or scars on the crown where the sheath was attached to crown base. Not all leaf axils contain buds (Mueller and Richards 1986), so leaf scars are important because they indicate the position of a potential bud when there are no visible bud scars. By counting the number of leaf scars, axillary buds and emerged tillers in the crown region (bottom 20 mm of the seedling), we were able to estimate the number of potential axillary bud sites or crown positions. The crown positions that did not develop into new tillers were classified as: 1) buds, i.e. developed axillary buds; 2) missing buds, i.e. axillary buds that were lost during processing, and 3) leaf scars.

Following dissection, seedling crowns were placed into 2,3,5-triphenyl tetrazolium chloride (TTC) solution for 22 hours at room temperature, which made buds more visible and improved the assessment of their viability. After removing the crowns from the stain, crown positions on the parent seedling and daughter tillers were counted using a dissecting microscope.

The experiment was analyzed as a randomized complete block with 2 species, 3 levels of defoliation and 3 levels of moisture availability in a factorial arrangement of treatments using SAS GLM procedures (SAS 1990). An experimental unit was a pot and the 3 target seedlings within a pot. Herbage yields and tiller numbers were log transformed to correct for heterogene-
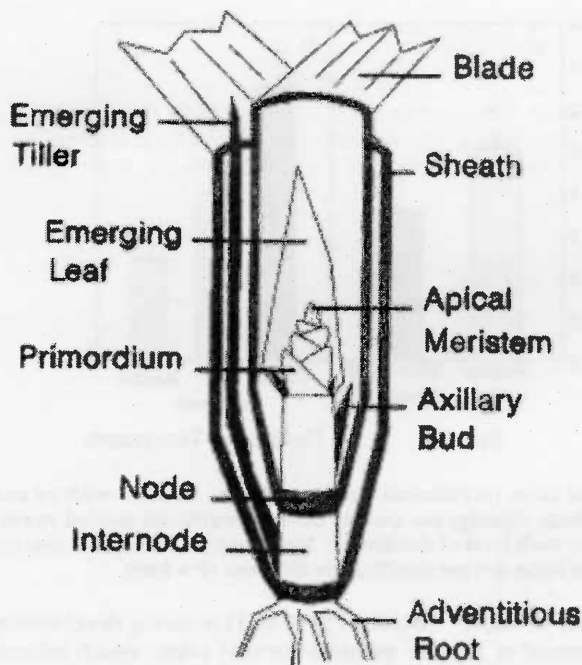
Fig. 1. Longitudinal view of a grass tiller showing the crown area. Note the node, internode, leaf and axillary bud that make up a phytomer. Emerging tillers begin as axillary buds. Crown positions were considered as to be sites where there was an axillary bud or emerging tiller. Identifying leaf scars or the areas where the leaf sheath was attached to the crown facilitated locating these positions (Figure redrawn from Murphy and Briske 1992).
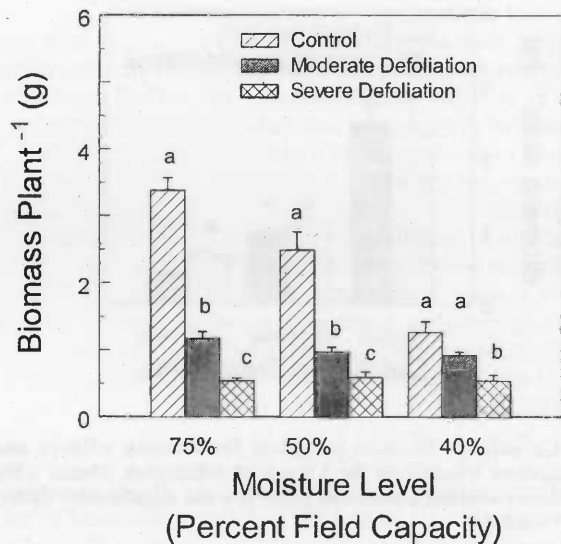

Fig. 2. Cumulative biomass per plant for three defoliation levels under 3 levels of water stress. Biomass was averaged across species and represents the total yield over time. Means within a cluster sharing a common letter are not significantly different (P > 0.05).

ity of variance. Herbage yield was expressed as cumulative biomass from all harvest dates including senesced material but excluding roots. Tiller numbers were expressed as cumulative number of tillers emerged per seedling including parent and daughter tillers. Results are presented with untransformed values for clarity. Analysis of the number of crown positions on the parent seedling (parental crown positions) and on the parent seedling and its daughter tillers (combined crown positions) did not detect heterogeneity of variances, so transformation was not required. Mean separation for all variables employed LSD procedures (P ≤ 0.05).

Results

Herbage Yields

Mean leaf water potentials pooled across time and defoliation treatments for both species are found in Table 1. Russian wildrye water potentials were consistently more negative than intermediate wheatgrass.

Herbage yield exhibited both defoliation by water availability (P = 0.0001) and species by defoliation (P = 0.007) interactions. Yields decreased with increasing

defoliation intensity at 75 and 50% of field capacity but not among control and moderately defoliated plants at 40% of field capacity (Fig. 2). Yields of undefoliated plants at 40% of field capacity were similar to moderately defoliated plants at 75% of water holding capacity. Under severe defoliation, Russian wildrye produced more biomass (P < 0.05) than intermediate wheatgrass generating a species x defoliation interaction (Fig. 3).

Tiller Numbers

Tiller numbers were affected by species (P = 0.0001) and defoliation level (P = 0.0001) but not by moisture treatments (P = 0.112). There were no significant interactions (P > 0.05). Russian wildrye seedlings averaged 10 tillers per plant (P < 0.05) compared to 7 for intermediate wheatgrass (Fig. 4A). Tillers per plant decreased (P < 0.05) with increasing defo-

liation (Fig. 4B). Control plants produced 2.7 times more tillers as severely defoliated plants and 1.6 times more tillers than moderately defoliated plants.

Crown Positions

Both grasses had similar (P = 0.213) numbers of crown positions. Most crown positions on intermediate wheatgrass were primarily axillary buds (51%) and new tillers (41%). Axillary buds comprised 38% and new tillers 61% of the crown positions on Russian wildrye. The remaining crown positions (8 and 1% for intermediate wheatgrass and Russian wildrye respectively) were either leaf scars or missing buds.

Crown positions of the parent seedlings were affected by defoliation (P = 0.0001) but not by moisture level (P = 0.214) (Fig. 5A and 5B). Moderate and severe defoliation treatments had fewer parental crown positions than the control treatments. The number of crown positions on a parent seedling and its daughter tillers (combined

Table 1. Mean water potential and standard errors (n = 32) for Russian wildrye and intermediate wheatgrass pooled across time and defoliation treatments.

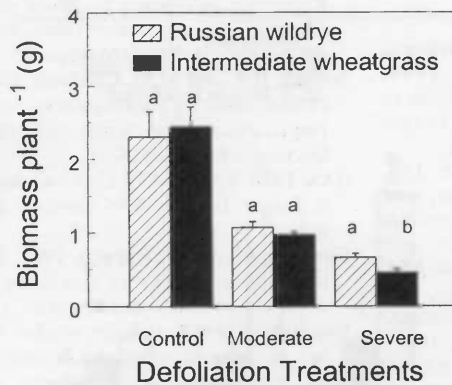| Species	Moisture level (Percent of field capacity)		
	75%	50%	40%
	------------------ (Mpa) ------------------		
Russian Wildrye	−0.75 ± 0.02	−1.12 ± 0.11	−1.60 ± 0.13
Intermediate Wheatgrass-	−0.64 ± 0.11	−1.00 ± 0.16	−1.12 ± 0.13

Fig. 3. Cumulative biomass per plant for Russian wildrye and intermediate wheatgrass for 3 levels of defoliation. Means within a cluster sharing a common letter are not significantly different (P > 0.05).
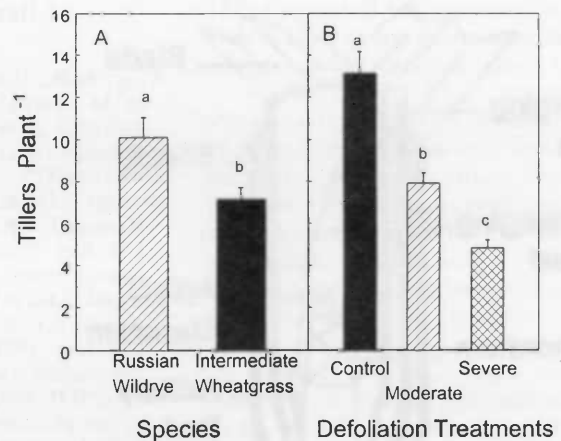

Fig. 4. Total tiller recruitment per plant for A) Russian wildrye and intermediate wheatgrass and B) tiller recruitment pooled across species for each level of defoliation. Means within each panel sharing a common letter are not significantly different (P > 0.05).

crown positions) was affected by defoliation (P = 0.0001) and moisture level (P = 0.004) but not species (P = 0.372). There were no significant (P > 0.05) interactions for the combined crown positions. Combined crown positions were reduced at 40% but not at 50 and 75% of field capacity (Fig. 5C). The number of combined crown positions decreased as defoliation level increased (Fig. 5D).

Discussion

The level of defoliation had a greater effect on plant response than moisture level in our study. Control plants generally produced more herbage, more tillers and more crown positions than defoliated plants and both herbage yield and tiller numbers decreased as the level of defoliation increased.

An earlier study of drought and defoliation effects in Russian wildrye and crested wheatgrass, 2 grazing tolerant grasses, found lightly defoliated plants produced more herbage than controls (Mohammed et al. 1982). In our study, herbage yield decreased with increasing level of defoliation in both grasses. Russian wildrye, which is known for its ability to persist under heavy grazing (Smoliak 1968) and drought (Asay et al. 1996), produced significantly more biomass with severe defoliation than intermediate wheatgrass.

With our driest treatment, biomass was similar between moderately defoliated and undefoliated plants. Mean leaf water potentials in our study were not as negative than those reported for 2 tropical C_4 grasses (Simones and Baruch 1991) (–3.0

to –3.5 MPa) but were similar to those (–1.3 to –1.6 MPa) of Mohammad et al. (1982) in Russian wildrye and crested wheatgrass. Our plants were defoliated sooner and at shorter intervals than in Mohammad et al.'s (1982) study, which may partially explain the differences between our results and theirs. Our moderate defoliation (8 cm stubble height) approximated the light defoliation treatment (7 cm stubble height) of Mohammad et al. (1982).

Water stress has been shown to decrease the effect of defoliation in grasses (Fennema and Briede 1990, Simones and

Baruch 1991) by 1) reducing development of moisture stressed plants which reduces defoliation intensity 2) slowing the onset of water stress in defoliated plants, 3) suspension of leaf aging and 4) an interaction of all of these (Simones and Baruch 1991). In our study, herbage yield of control plants declined when water was limiting but yields of moderately and severely defoliated plants were approximately the same regardless of moisture level. As a result, yields of control and moderately defoliated plants were similar at 40% of field capacity. The decline in biomass across moisture levels for control plants
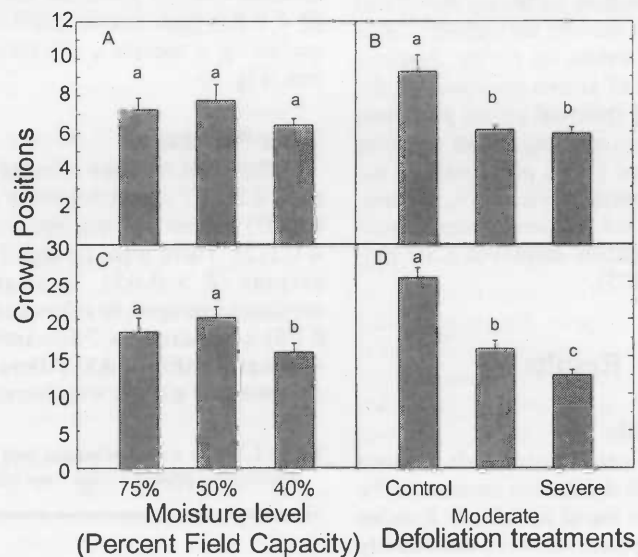

Fig. 5. Number of crown positions per parent seedling as affected by moisture level (A) and defoliation (B) and combined parent seedling and daughter tillers as affected by moisture level (C) and defoliation (D). Means within each panel sharing a common letter are not significantly different (P > 0.05).

supports Simones and Baruch's (1981) speculation that reduction in yield of water stressed plants effectively reduces defoliation intensity.

Defoliation had a greater effect on tiller recruitment than water stress. Except for the crown positions on the parent and daughter tillers (combined crown positions) at 40% of field capacity, water stress did not affect current tiller recruitment or the number of crown positions. Our reduced yields, therefore, were simply a product of smaller tillers. Defoliation, however, decreased both realized and potential tiller recruitment via depression of axillary bud numbers. Axillary buds probably set a meristematic limit on future yields because they are the source of new tillers (Murphy and Briske 1992) and defoliation probably has a larger impact on potential yields than water stress.

Rapid development of new tillers is a common characteristic of grazing-tolerant grasses (Caldwell et al. 1981, Nowak and Caldwell 1984). Russian wildrye can withstand heavy grazing (Smoliak 1968) and, in our study, produced approximately 3 more tillers per plant than the grazing-sensitive intermediate wheatgrass. The number of crown positions did not differ between species so Russian wildrye simply had a greater ability to activate new tillers.

Our findings help explain some of the dynamics observed in intermediate wheatgrass and Russian wildrye pastures. We noted that reduced moisture levels lowered herbage production but did not affect realized or potential tiller recruitment in these grasses. Severe defoliation, however, retarded both tiller recruitment and development of axillary buds necessary for subsequent growth. The greater tiller recruitment of Russian wildrye potentially explains its greater grazing tolerance compared to the more grazing sensitive intermediate wheatgrass. Regardless of the species, we suggest that managers protect the productive potential of their pastures by not severely defoliating their forages. This research suggests that proper grazing management is important regardless of the moisture situation. More research is needed on these grasses, however, to evaluate the effects of grazing management and drought on well-established plants in applied circumstances.

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Book Review

Post-Cowboy Economics: Pay and Prosperity in the New American West. By Thomas M. Power and Richard N. Barrett. 2001. Island Press, Washington, DC. 185p. US$25.00 paper. ISBN 1-55963-821-4.

The American West has occupied and continues to occupy a special place in the American imagination. The home of the cowboy, this region is known not only for espousing a distinct kind of rugged individualism but also for its extensive reliance on natural resource industries such as logging, mining, and ranching. Lately, the American West hasn't been doing very well economically. This book studies the genesis, the causes, and the consequences of this economic stagnation. Specifically, the authors use the 8 chapters of this book to challenge the belief that the American West's economy "has been strangled by restrictive environmental policies, particularly those of a federal government unresponsive to local needs" (p. xviii).

Chapter 1 explains that the term "cowboy economics" refers to a particular way of comprehending the economy of and public economic policy in the American West. The authors point out that this way is deeply rooted in the belief "that the very future of the region and its communities are at risk because of environmental regulation" (p. 3). It is noted that although this belief is a popular one, it is flawed. Laying the groundwork for their alternate perspective on the economy of the American West, the authors forcefully argue that salaries and income in this region have actually followed trends established in the U.S. economy. Although this is a nice introductory chapter, on occasion, the authors are methodologically sloppy. For an example, on p. 10, *without* any supporting evidence, the authors assert that a "substantial body of research has confirmed that some industries tend to pay higher wages than others for workers with the same qualifications and doing the same type of job."

The purpose of Chapter 2 is to explain certain puzzles related to incomes and salaries in the American West. Although this is an informative chapter, it would have profited from a more complete accounting of the analytic methods that are employed. Here are 2 examples of what I have in mind. First, the authors seek to gain a better understanding of the economic well-being of people in this region. To do this, they analyze the fall in pay per job. Why *only* look at the fall in pay per job? In particular, why not study alternate measures such as per capita income? Although the authors recognize that the fall in pay metric "is incomplete and [hence] can be misleading..." (p. 40), they do *not* provide a comprehensive analysis of the many components that constitute economic well-being. Second, on p. 37, the authors provide a somewhat misleading equation of the relationship between pay per job and pay per worker. What the authors should have done is to index the total number of jobs (say n) with a subscript (say i) and then stated that the annual pay per worker is the summation of the earnings in all the n jobs.

Chapter 4 asks a salient question: were shifts in industrial structure responsible for the dramatic changes in the level and the distribution of wages in the American West? As the chapter points out, the available evidence indicates that the answer is no. In the course of demonstrating this, the chapter rightly notes that the "reason declining employment in natural resources or goods production played such a small part in the fall in average pay per job is that pay was declining everywhere, and particularly sharply in natural resources and goods production" (p. 77). As with Chapter 2, once again, one can question aspects of the employed method-

ology. In particular, in analyzing the impacts of the change in industrial structure in the American West, what are the *complete* implications of the admittedly simplistic division of the economy into sets of just 2 sectors? This question is inadequately addressed by the authors.

The implications for the American West of being trapped in images from the past are explored in Chapter 6. Here, the authors contend that the American West is very clearly connected to the U.S. economy by the mobility of capital, goods, and labor. Consequently, it is *erroneous* to think that the economic problems of this region are local in nature and that they can be solved by changes in local policy. Further, the view that rural areas in this part of the country "depend for their existence on the exploitation of natural resources..." (p. 127) is patently false. Unfortunately, even though there is no truth in this view, many residents of the American West continue to be vehemently opposed to the activities of the federal government. This point is certainly a salient one and it has been made by others in recent times (see my review of Debra Donahue's *The Western Range Revisited* in this journal, Vol. 53, No. 1, 2000). Finally, the authors properly point out that this "intense hostility toward government spills beyond the confines of politics, pervading the social and personal lives of communities and creating a niche from which socially toxic hate groups can operate" (p. 127).

What are apposite public economic policies for the American West? This question is addressed in Chapter 7. The authors argue that if local economic policy is to be effective, then its design and implementation must be informed by 3 fundamental principles. First, the aspirations of policy should be modest and realistic. Second, "it is important to know who the winners and losers are supposed to be and whether the policy will really affect the right people in the right way" (p. 140). Third, when choosing between people and places, policymakers should realize that the choice between these 2 criteria comes down to the issue of mobility. Following this, the authors convincingly point out that once policymakers appreciate these 3 principles, they will realize that the "mobility and [the] openness of the local economy severely limit the range of governmental action..." (p. 153).

Despite a few errors of commission and omission, in general, this is a fine book. Its principal accomplishment is that it successfully debunks the popular but flawed "cowboy economics" view of the American West. As such, I recommend this book to readers who would like to understand contemporary economic events in the American West as they should be understood.—*Amitrajeet A. Batabyal*, Rochester Institute of Technology, Rochester, New York.

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