Journal of Range Management

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Are Namibia's grasslands desertifying?

DAVID WARD AND BEN T. NGAIRORUE

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Abstract

We compared the herbage standing crop on 31 farms along a rainfall gradient in Namibia (southwestern Africa) in 1997 with the results attained for the same gradient by Walter (1939). We found that the slope for the regression of herbage yield on mean annual rainfall in 1997 was 5.93, i.e. 5.93 kg herbage was produced per hectare for every 1 mm increase in rainfall along the gradient. This regression slope is considerably lower than that in Walter's (1939) study (slope = 10.34). Thus, current grassland productivity per unit of rainfall in Namibia is about half that of 50 years ago. There is no evidence of a change in annual rainfall over this period, nor is there any evidence that either short-term (current) or longer-term (11 years) stocking densities affect current herbage yield. We conclude that, while desertification has taken place, grazing over the last decade has not been the cause of this reduced productivity.

Key Words: Africa, rangelands, historical records, grazing, rainfall

Resumen

Se comparó el cultivo de pastoreo estable en 31 fincas a lo largo de un gradiente de precipitación en Namibia (sudoeste de Africa), en 1997, con los resultados obtenidos para el mismo gradiente por Walter (1939). Encontramos que la pendiente en la regresión para la producción de pasto en relacion con la precipitación media anual en 1997 fue 5.93, i.e. 5.93 kg de pasto es producido por hectarea en cada incremento de 1 mm en la precipitación a lo largo del gradiente. Esta linea de regresión es considerablemente más baja a la del estudio realizado por Walter (1939), (pendiente = 10.34). De este modo, la actual productividad por unidad de precipitación en las praderas de Namibia es cercana a la mitad de la productividad hace 50 años. No hay evidencias de un cambio en la precipitación anual en este periodo de tiempo, ni hay alguna evidencia de que la densidad de la ganaderia a corto-plazo (actualmente) o a largo-plazo (11 años) afecten la producción de pastos. Concluimos que, mientras la desertificación ha tomado lugar, el pastoreo en la ultima decada no ha sido la causa de esta reducida productividad.

There is widespread concern over desertification (i.e. a long-term decline in productivity) of the semi-arid grasslands of the world (Schlesinger et al. 1990, 1996, Hall and Scurlock 1991, Strohbach 1992, Parton et al. 1995). However, it is often difficult to unequivocally determine whether desertification has occurred, because different types of information (e.g. on soil quality, carbon isotopes, vegetation quality and quantity) may give conflicting results (Hoffman et al. 1995, Parton et al. 1995, Parsons et al. 1997). Also, logistical problems such as variability in annual rainfall cause great natural fluctuations in herbage growth, making it difficult to differentiate pattern in declining productivity from noise caused by random or event-driven fluctuations (Hoffman and Cowling 1990, Sullivan 1996, Hoffman 1997, Ward et al. 1998, Ward et al. 1999). Long-term cycles in rainfall can further exacerbate this problem. For example, Hoffman and Cowling (1990) and Hoffman (1997) have shown that Acocks' (1953) claim that desertification was rampant in the semi-arid Karoo region of South Africa was probably caused by the long dry period in the 1950's. When one compares photographs of the vegetation taken in 1925 by I.B. Pole Evans with photographs taken at the same sites by Hoffman in 1993, it appears that vegetation cover has declined. However, if one compares Pole Evans' photographs to those taken in 1989, one sees that no long-term change has occurred, since the 1920's and 1980's were similarly wet periods (Hoffman 1997).

Another major problem in assessing whether desertification has occurred is that few long-term data exist to define the past condition of grasslands. The grasslands of Namibia are notable exceptions to this. Walter (1939) examined the relationship between herbage production and average annual rainfall in Namibia (southwestern Africa) over a rainfall gradient of 100–500 mm. These data represent a baseline that can be used to make comparisons between production 58 years ago with the present day. Furthermore, because these data represent the relationship of grassland production with rainfall along a rainfall gradient, we can compare past productivity with that of today without having to concern ourselves with possible differences in rainfall between the sampling periods because the effects of variance in rainfall can be controlled by regression analysis. For these reasons, we attempt here to assess whether there have been significant changes in the productivity of Namibia's grasslands from the time of Walter's (1939) study and the present day.

We thank Japhet Karamata and Immanuel Kapofi for their assistance. We also thank the 31 farmers, the technicians at the Namibian weather bureau for their assistance, and the Namibian department of veterinary services for the provision of long-term stocking data. This study was funded by grant TA-MOU-94-C13-149 from the U.S. Agency for International Development to David Ward, Uriel Safriel and Mary Seely. This is publication number 287 of the Mitrani Department for Desert Ecology and publication number 88 of the Ramon Science Center.

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Materials and Methods

Study sites

In 1997 we studied herbage yield on 31 commercial farms in 3 clusters of 11, 10, and 10 farms, each within a 100 km radius of Otjiwarongo, Windhoek and Keetmanshoop, respectively (Fig. 1). All the farms were commercial and not communal farms, i.e. the possibility that the farms were in poor state due to the 'tragedy of the commons' (sensu Hardin 1968) or similar mechanism is unlikely. These 3 towns were chosen as the centers of our study for 2 important reasons: (1) long-term rainfall data exist, and (2) they are found along the length of a rainfall gradient from the dry southern part of Namibia (Keetmanshoop: mean ± S.E. annual rainfall = 141.98 ± 9.82 mm), through central Namibia (Windhoek: mean + S.E. annual rainfall = 361.15 ± 13.71 mm) to the more mesic north (Otjiwarongo: mean + S.E. annual rainfall = 449.63 + 18.04 mm) (Fig. 1). The vegetation in the northern region of this study is thornbush savanna, with varying degrees of dominance of thorn trees (mostly *Acacia* species) and perennial grasses (Van der Merwe 1983). Central Namibia is open dry savanna, also dominated by *Acacia* trees with a mixture of annual and perennial grasses. Southern Namibia is covered by dwarf shrub savanna and open dry grasslands dominated by annual grasses. The only criterion for choosing farms within each of these regions was that long-term rainfall records were available for each farm from the Namibian national weather service. Stocking density for each farm was obtained either directly from the farmers (1997 season) or from the Namibian Department of Veterinary Services (long-term data). Long-term data are collected once a year for each by the Namibian Department of Veterinary Services for the purposes of disease control.

Herbage measurements

We used a point-frequency frame to measure herbage height (Mueller-Dombois and Ellenberg 1974) on the 31 farms. Note that we use the term 'herbage' here to denote all plant species that are not predominantly woody. In the main, these are grasses, but not entirely so. The study was done from the end of February to the middle of April 1997, the peak of the wet season in Namibia. On each farm, herbage height was measured at 3 points 20 m apart along the length of a gradient at 100, 200, 300, 500, and 1,000 m from stock watering points. This ensured that herbage height was measured from the worst to the best places on each farm as degradation around water points did not extend as far as 1,000 m from water on any farm (Ngairorue and Ward, Personal communication). Average herbage height from all these points was used to derive a single herbage height data point for each farm. Herbage height was converted to herbage mass (kg ha^{-1}) from a regression where we measured herbage height using the point-frequency frame and herbage mass by cutting, drying, and weighing herbage from a 1 m^2 quadrat placed under the point-frequency frame. At each farm, sampling sites were chosen at random. The relationship between herbage mass and herbage height was defined by the equation:

Herbage Mass (kg ha^{-1}) = 10 * (4.17 * Herbage Height - 2.02); ($r^2 = 0.88$, $P < 0.001$).

Soil quality

We measured the following soil variables: organic carbon, total nitrogen, total phosphorus, pH, conductivity, water-holding capacity. Soil was collected at 10–30 cm depth at the same 3 points used for the herbage biomass measurements, i.e. 20 m apart at each of the 5 distances from the waterpoints. These 3 samples were mixed to give a single value for each distance from the waterpoint. Organic carbon was measured as percentage mass loss on ignition at 400°C for 16 hours in a muffle furnace (Nelson and Sommers 1996). Total nitrogen was measured by conventional Kjeldahl techniques (Bremner 1996), and total phosphorus was measured with the Olsen technique (Olsen and Sommers 1982). Conductivity and pH were measured using pH and conductivity meters. Water-holding capacity was recorded as the percentage increase in mass of 10 g of dry soil when distilled water was added until the saturation point was reached. We also used radishes (*Raphanus sativus* Linneaus 1758) cv. Sparkler as a bioassay (total dry weight after 3 weeks) of soil nutrients (Olsvig-Whittaker and Morris 1982).

Statistical analyses

We used conventional least-squares regressions to determine the relationships between herbage mass and rainfall. Residuals from these regressions were used to assess the effects of stocking density on herbage mass after the effects of rainfall differences among farms were removed. Multiple regressions were used to determine the effects of several independent variables such as soil nutrient parameters on herbage mass. Analyses of

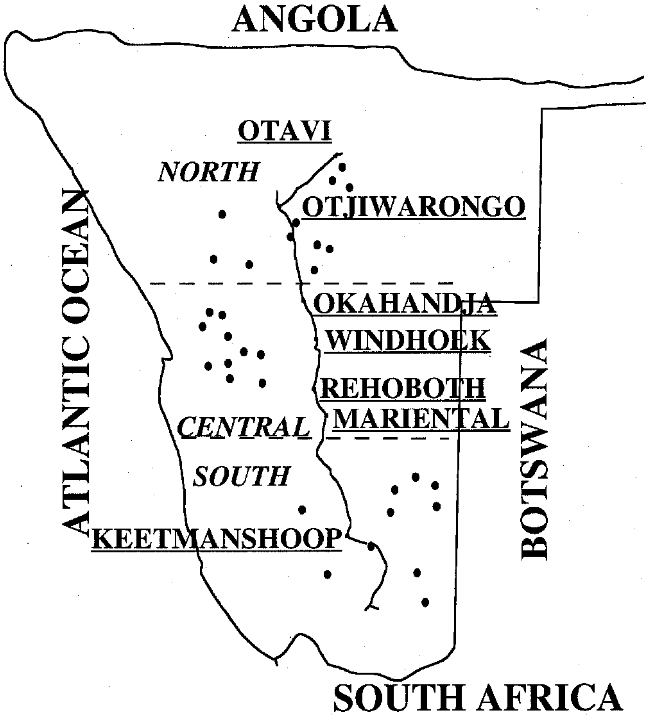

Fig. 1. Study sites on 31 farms in Namibia. Black circles indicate farm positions.

covariance were used to compare intercepts of regressions. Paired t-tests were used for paired data.

In addition to using least-squares regressions to determine the relationship between herbage mass and rainfall, we also examined the maximal relationship between herbage mass and rainfall. In any relationship between productivity and a controlling environmental variable, one might expect that an 'envelope effect' exists (*sensu* Goldberg and Scheiner 1993). That is, there is a maximal (theoretical) relationship between herbage production and rainfall but in any single site a plethora of factors (not least of which is grazing) may skew this relationship downwards. No upwards skew can occur because there is a constraint placed by rainfall on herbage production over which additional herbage cannot be produced. We therefore expect an 'envelope' that describes a triangular cluster of data points below the regression line (Fig. 2). Such a relationship violates the assumption of conventional least-squares regression that there is homogeneity of variance (by definition, an 'envelope' results in greater variance at higher values of the independent variable). Thomson et al. (1996) describe a simple statistical test for an 'envelope effect': One first takes the positive residuals from the least-squares regression of the dependent and independent variables in question. These positive residuals are then regressed against the independent variable. The positive residuals of this new regression are taken and regressed against the original independent variable. This process is continued until the regression slope is no longer significantly different from zero. If there is indeed an 'envelope effect', the uppermost regression line (Fig. 2) will describe the upper limit to the 'envelope' (Thomson et al. 1996). If there is no envelope, the positive residuals will not be significantly related at any stage to the independent variable.

To test for possible cyclicity in long-term rainfall patterns, we used autocorrelation analyses. This is a statistical index that reveals the extent of the correlation between the residuals. The first-order autocorrelation is the conventional Pearson correlation of a series of numbers with the same series shifted by 1 year. This is then repeated for second-order (series shifted by 2 years), third-order (series shifted by 3 years), and further autocorrelations for as many years as there are in the series. Each correlation is tested for significance at the conventional level of α (0.05).

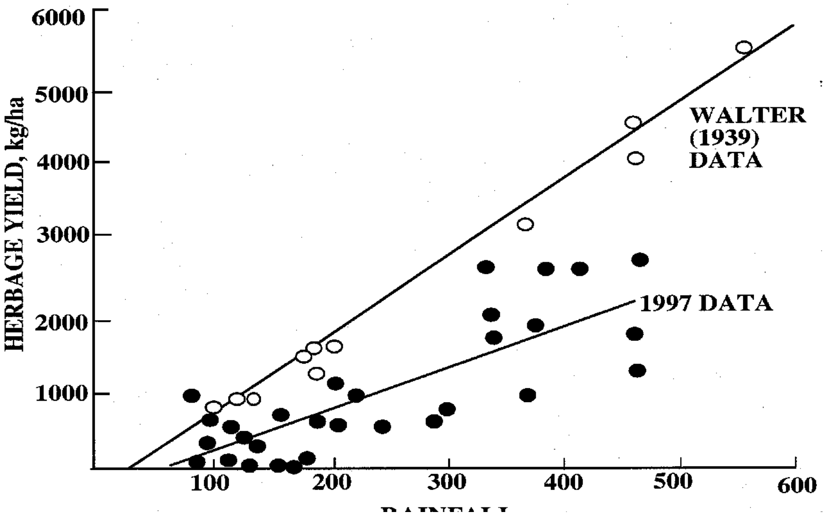

Fig. 3. Relationship between herbage yield (kg/ha) and mean annual rainfall (mm) on 31 farms in Namibia. Walter's (1939) regression formula is: herbage yield = 10.34 average annual rainfall - 401.3 (Rutherford 1980). Our regression for 1997 is: herbage yield = 5.93 average annual rainfall - 328.55.

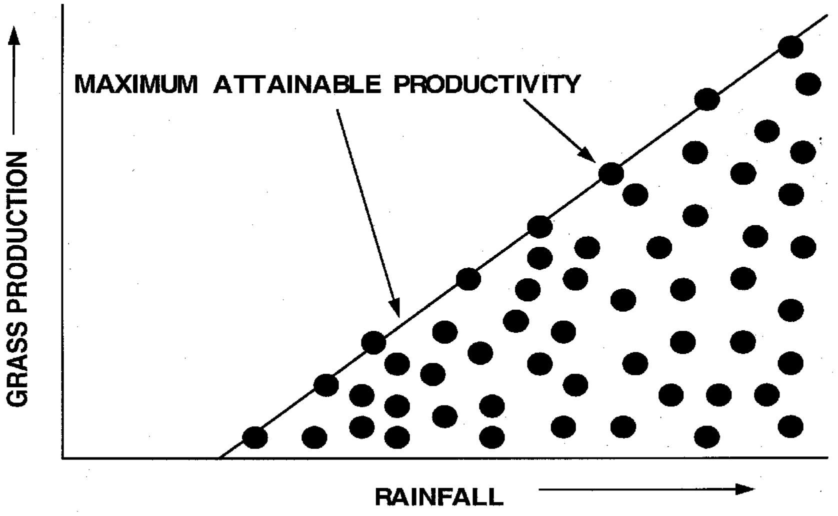

Fig. 2. The 'envelope' effect in regression. Dots indicate individual data points, all of which are below the regression line that constrains the relationship. Note the heterogeneity of variance in the relationship; there is more variability on the right side of the x-axis than on the left.

Results

Herbage Yield

The slope of the regression of current (1997) herbage yield per hectare on long-term average rainfall (herbage yield = 5.93 average annual rainfall - 328.55) is far lower than that reported by Walter (1939) (herbage yield = 10.34 average annual rainfall - 401.3) (following Rutherford 1980) (Fig. 3). More of the variance in average herbage yield is explained by variance in average annual rainfall (r^2 = 0.64, F = 52.406, P < 0.0001, error d.f. = 29) than is explained by variance in the current season's rainfall (r^2 = 0.49, F = 27.796, P < 0.0001, error d.f. = 29).

We also regressed maximal herbage yield (i.e. where there was no grazing effect at a distance of 1,000 m from the waterpoint) against average annual rainfall at each site. The slope was steeper (herbage yield = 6.618 average annual rainfall - 504.126, r^2 = 0.58, F = 40.028, P < 0.0001, error d.f. = 29) than that for average annual rainfall, although this difference was not significant (ANCOVA: F = 0.822, P = 0.368, error d.f. = 59). Indeed, there was no significant difference between herbage yield at 1,000 m from waterpoints and the herbage yield averaged over all distances from waterpoints on all the farms (paired t-test: t = 1.671, P = 0.105, error d.f. = 30).

Studies such as these could be biased by the logistical difficulties involved in sampling all sites simultaneously. For example, if all farms with high herbage yield were sampled at the end of the season after grazing, wind and other effects have reduced herbage yield, a significantly lower slope would be recorded for the herbage yield:rain regression. To test for bias produced by sampling date, we examined the correlation between the residuals of the regression of average herbage yield against average annual rainfall and sampling date. Because there was no significant correlation (r^2 = 0.01, F = 0.339, P = 0.565, error d.f. = 29), no effect of sampling date on the results is presented here.

It is possible that Walter's regression line represents a maximal relationship between herbage yield and rainfall (Rutherford 1980), and therefore our current regression line will lie through the average of the points below Walter's regression. We performed the procedure outlined above for testing for an 'envelope' effect and found that no such effect exists (r^2 = 0.034, F = 0.212, P = 0.661, error d.f. = 6).

We also calculated the slope for maximal herbage yield against rainfall by regressing herbage yield for the two farms with the most positive residuals in the original least-squares regression against the independent variable (long-term average rainfall). In doing so, we created the maximal regression for our 1997 data. This regression (herbage yield = 8.49 average annual rainfall - 110.87) was still 20% lower than that of Walter (1939).

Stocking densities

To test for the effects of grazing pressure on herbage yield, we took the residuals from the regression between herbage height and average annual rainfall (Fig. 3) and regressed them against current stocking densities [expressed in Large Stock Units (LSU) per hectare][1]. This regression removed the effect of variance in rainfall, and allowed us to directly examine the effects of stocking density on herbage yield. There was no significant relationship between these two variables (r^2 = 0.006, F = 0.181, P = 0.674, error d.f. = 29), nor between the residuals of herbage height and long-term stocking densities (data from 1986–1996) (r^2 = 0.013, F = 0.384, P = 0.540, error d.f. = 29—Fig. 4).

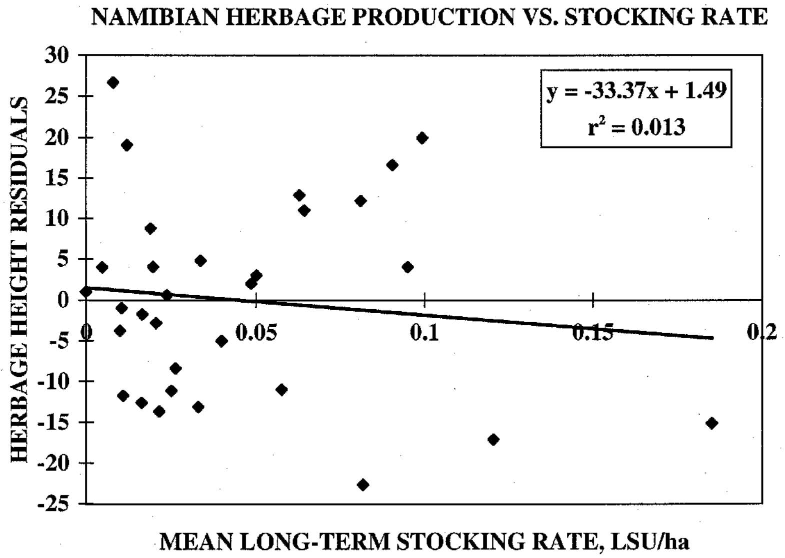

Fig. 4. Relationship between residuals of herbage height vs. mean annual rainfall and mean long-term stocking rate (LSU/ha).

Soil variables

We tested for the effects of variance in soil variables on herbage yield after the confounding effect of average annual rainfall was removed. We used a multiple regression with the residuals of herbage yield as the dependent variable and organic carbon, total nitrogen, total phosphorus, water-holding capacity, pH, conductivity, and total dry mass of radishes from the bioassay as independent variables. There was no significant effect of any of the soil variables on herbage yield (F = 0.856, P = 0.554, error d.f. = 23).

Changes in rainfall over time

Our study was conducted in an average rainfall year for the region. Mean ±S.E. % of seasonal (1996/1997) rainfall was 231.8 ± 29.61 mm (c.v. = 0.72) while long-term average rainfall for all 31 farms was 240.4 + 21.94 mm (c.v. = 0.52). Thus, 1996/1997 season rainfall was 96.4% of the long-term average. This difference was not significant (paired t-test, t = 0.524, P = 0.604, error d.f. = 30).

We tested whether long-term rainfall changes might have led to the decline in production that we recorded compared to Walter (1939). There was no significant change in rainfall at any of the 3 long-term rainfall stations (Otjiwarongo, Windhoek (Fig. 5) and Keetmanshoop). Declines could potentially be recorded because measurements were made at the low point in a rainfall cycle. We tested for the presence of rainfall cycles by autocorrelation analyses. Only at the Windhoek station was there any evidence of a cycle (P < 0.05), and this cycle is just 2-years long. Hence, the results we have for herbage yield are not a result of being in the low point of a long-term rainfall cycle.

Discussion

There is currently much concern in Namibia about the effects of various agricultural practices on productivity of the land (Quan et al. 1994, Seely and Jacobson 1994, Bester 1995, Ward 1996, Aharoni and Ward 1997). Indeed, about 60% of northern Namibia suffers from bush encroachment, while up to 90% of southern Namibia is considered to be overgrazed (Quan et al. 1994). However, statistics such as these do not tell us whether these problems are leading to long-term degradation. Thus, results such as ours form an important baseline to determine whether land degradation, and hence desertification, is occurring.

Our conclusion clearly rests on the validity of Walter's (1939) data. In making such a comparison, it is necessary to ensure that all possible confounding variables are controlled, which we have

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[1] A Large Stock Unit is the equivalent of a single mature cow or 6 goats or sheep (Meissner et al. 1983).

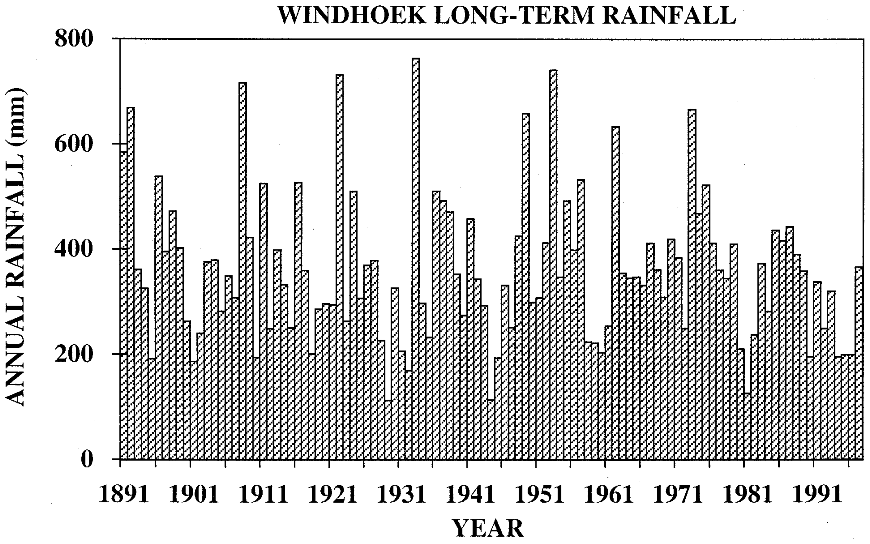

Fig. 5. Long-term rainfall patterns at Windhoek. There has been no significant change in rainfall over the period of measurement (r = 0.095, F = 0.938, P = 0.335, error d.f. = 103). Data from the Namibian National Weather Bureau.

attempted to do in our study. Importantly, we have demonstrated that variation due to soil type and grazing regime over the last 11 years was not correlated with herbage height (and by inference with biomass) on the 31 farms. Furthermore, we have shown that more of the variance in herbage yield can be explained by long-term average rainfall than by seasonal rainfall. Thus, it is appropriate that we and Walter (1939) used long-term average rainfall as the independent variable in the regression with herbage yield. This conclusion is inconsistent with Rutherford's (1980) claim that annual rainfall has a greater effect on grassland productivity than long-term average rainfall. Rutherford (1980) concluded that only annual grasslands should have been used in Walter's (1939) study to allow for a direct relationship with annual rainfall. We consider this point to be unnecessarily restrictive because grasslands tend to change from annual to perennial grasses with increasing rainfall (Shmida 1985), thereby precluding appropriate comparison along the rainfall gradient in Namibia. Additionally, annual grasses tend to replace perennial grasses in desertified grasslands, especially those suffering from heavy grazing (Kelly and Walker 1977, Frost et al. 1986, O'Connor 1991, O'Connor and Pickett 1992, Seely and Jacobson 1994, Parton et al. 1995, Parsons et al. 1997).

A possible reason for the reduced productivity (identified by the lower regression slope of herbage yield:rainfall) in our data compared with that recorded by Walter (1939) is that Walter's regression line represents a maximum, rather than an average relationship as suggested by Rutherford (1980). Indeed, Whittaker and Marks (1975) found the low variance in Walter's relationship "remarkable". We note the very low variance about the regression line (Fig. 3). We consider it parsimonious to conclude that some degree of data "smoothing" was done by Walter (1939). We tested whether the reduced productivity in 1997 was due to comparison of our average regression relationship with a possible maximal relationship described by Walter (1939). We did this by regressing herbage yield for the 2 farms with the most positive residuals (in the herbage yield: average rainfall regression) against rainfall to produce a maximum slope. We still found that our data lay below those of Walter (1939). We believe, therefore, that even "smoothing" of the data by Walter cannot account for the lower slope of the regression in the current data. We noted that the maximal slope in our data (8.49) is very similar to Deshmukh's (1984) regression compiled for data from a wide range of sites in eastern and southern Africa, viz. herbage yield = 8.488 * rainfall - 195.768. This similarity in slopes suggested to us that Namibian herbage production may once have been similar to that described by Deshmukh (1984), but that it has now declined to an average slope of 5.93 (Fig. 3).

Desert-grassland transition

Rutherford (1980) used Seely's (1978a, b) data to justify a claim that a slope of about 5 was "normal" for southern African grasslands [Seely's regression equation was: Plant Production (kg ha^{-1}) = 5.48 * Seasonal Rainfall (mm) - 113.0], and also for his claim that it is only appropriate to use this year's rainfall and annual grasses. However, Seely's data are at the low end of the rainfall scale (< 100 mm rain per annum), and annual grasses only occur there. We believe that it is prudent to consider there to be a piecewise regression relationship (rather than a linear one) between herbage production and rainfall. That is, from 20 mm up to about 100 mm of annual rainfall, herbage production (annual grasses only) increases by about 5 kg/ha for every 1 mm increase in annual rainfall (because 5.48 = slope of Seely's equation). Above 100 mm annual rainfall, the perennial grass component increases as rainfall increases. This increase in the proportion of perennial grasses produces an increase in the standing crop of grasses per unit of rainfall because perennial grasses remain in the grassland even in low rainfall years. Thus, the slope of the herbage yield:rainfall regression should become steeper with annual rainfall exceeding 100 mm. In undegraded situations, we tentatively suggest that this slope should be about 8 kg ha^{-1} for every 1 mm increase in average annual rainfall, i.e. the slope (8.488) derived by Deshmukh (1984) for a wide range of undisturbed eastern and southern African sites. From our results, it appears logical to consider long-term average annual rainfall as the major factor affecting herbage production above 100 mm annual rainfall and actual annual rainfall below this amount. Thus, we consider both Walter (1939) and Seely (1978a, b) to be correct in their choices of the independent variables, and therefore disagree with the choice advocated by Rutherford (1980).

We therefore return to our original question: Are Namibia's grasslands desertifying? We conclude in the affirmative. The level of productivity per unit rainfall is considerably lower than that previously measured. Identification of the causes for this decline in productivity is needed so that appropriate management strategies can be developed for the sustainable use of these rangelands, especially because current stocking densities do not seem to have an effect.

O'Connor (1985) analyzed long-term experiments in southern Africa on the effects of rainfall and grazing on state variables but he found no evidence that changes in rainfall patterns have caused a major change in any system. Cyclic changes in grassland composition have followed rainfall cycles, i.e. grassland composition has been nearly constant for any particular rainfall condition and all species eliminations have been of a temporary nature only. He concluded that long-term rainfall variability, independent of rainfall regime, has an overriding effect on grassland compositional trends. The cumulative effects of grazing, however, do influence the rate of rainfall-induced compositional changes (O'Connor 1985). This conclusion is consistent with Bester's (1995) claim that the major cause of rangeland degradation in Namibia is the overestimation of the annual forage production, resulting in overutilization of the rangeland.

Our data on short-term (current season) and longer term (11 years) stocking densities are inconsistent with these claims. We found no evidence for changes or long-term cycles in rainfall, and no effects of stocking densities on biomass. This result does not mean that grazing has not affected the botanical composition of the rangelands. Grazing may affect botanical composition in semi-arid and arid rangelands (Landsberg et al. 1997, 1999). Milchunas and Lauenroth (1993) found that there was a positive correlation between the degree of grazing-induced change in botanical composition and mean annual rainfall, although increasing evolutionary history of grazing produced increasing dissimilarity in species composition between grazed and ungrazed sites regardless of the level of precipitation. A grazing-induced change in botanical composition may cause an indirect decline in productivity if the original species had higher biomasses than the current species. However, if this were the case, it would still be possible to detect a decline in productivity by the regression approach we used. Furthermore, due to the absence of such data in Walter's (1939) study, no comparison can be made between the botanical composition along this environmental gradient in 1939 and the composition in our study.

We suggest that while stocking densities have been the cause of the lowered herbage production in Namibia, this effect is very gradual and takes more than the 11 years to manifest itself. In another study in the central part of the rainfall gradient in Namibia, Ward et al. (1998) found that 10-fold differences in stocking rates over the short- to medium-term (1–50 years) did not cause detectable differences in herbage yield or soil quality. However, a decline in herbage productivity was discerned when comparing sites known to have had heavy grazing for the last 150 years with similar sites that have experienced only 5–10 years of heavy grazing. Wiegand and Milton (1996) have shown by spatially-explicit modeling in the arid Karroo of South Africa that simulated overgrazing of a rangeland in good initial condition only became obvious 40 or 50 years after the initiation of heavy grazing, and after 70 years the mean vegetation state eventually reached that of an overgrazed rangeland. Both Wiegand and Milton's (1996) and our (Ward and Kapofi 1999, Personal communication) results point to the extremely long-term nature of declining productivity or desertification brought about by heavy grazing in such arid habitats. It is clearly necessary that future research programs establish long-term sampling plots along the rainfall gradient in Namibia to determine whether slow long-term degradation is occurring, as appears to be the case from the results presented here.

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Ungulate herbivory on Utah aspen: Assessment of long-term exclosures

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Abstract

The role of livestock grazing and big-game browsing in the decline of aspen (*Populus tremuloides* Michx.) in the Intermountain West has long been questioned.All known aspen exclosures (n=8) on the Dixie and Fishlake National Forests in south-central Utah were measured during late summer of 1995 and 1996 to determine aspen stem dynamics, successional status, and understory species composition. Five of the exclosures were of a 3-part design with a total-exclusion portion, a livestock-exclusion portion, and a combined-use portion which permitted the effects of deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) herbivory to be measured separately from those of livestock. Aspen within all total-exclusion plots successfully regenerated and developed multi-aged stems without the influence of fire or other disturbance. Aspen subjected to browsing by wildlife, primarily mule deer, either failed to regenerate successfully or regenerated at stem densities significantly lower (2,498 stems ha^{-1}) than that on total-exclusion plots (4,474 stems ha^{-1}). On combined wildlife-livestock-use plots, most aspen failed to regenerate successfully, or did so at low stem densities (1,012 stems/ha^{-1}). Aspen successfully regenerated on ungulate-use plots only when deer numbers were low. Similarly, ungulate herbivory had significant effects on understory species composition. In general, utilization by deer tended to reduce shrubs and tall palatable forbs while favoring the growth of native grasses. The addition of livestock grazing, however, tended to reduce native grasses while promoting introduced species and bare soil. Thus, communities dominated by old-age or single-age trees appear to be a product of ungulate browsing, not a biological attribute of aspen as has been commonly assumed. There was no evidence that climatic variation affected aspen regeneration. Observed differences are attributed to varied histories of ungulate herbivory.

Key Words: *Populus tremuloides* communities, reproduction, decline, cattle grazing, deer browsing, elk browsing, undergrowth.

Resumen

El papel del apacentamiento del ganado y el ramoneo de la fauna silvestre mayor en la disminución del "Aspen" (*Populus tremuloides* Mitch.) en la región intermontañosa del oeste has sido ampliamente cuestionado. A fines de los veranos de 1995 y 1996 se midieron todas las exclusiones conocidas (n=8) de "Aspen" en los Bosques Nacionales Dixie y Fishlake situados en la región sur-central de Utah. Las mediciones realizadas en estas exclusiones fueron para determinar la dinámica de tallos, el estado sucesional y la composición de especies herbáceas. Cinco de las exclusiones estuvieron dentro de un diseño de tres factores: exclusión total, exclusión contra el ganado y uso combinado, el cual permitía medir separadamente los efectos de la herbívora de venados (*Odocoielus hemonius*) y alces (*Cervus elaphus*) de la del ganado. El "Aspen" se regeneró exitosamente dentro de las exclusiones, y sin la influencia del fuego u otro factor de disturbio, desarrollo una estructura de tallos de diferentes edades. El "aspen" sujeto al ramoneo de la fauna silvestre, principalmente venado, fallo en regenerarse exitosamente o se desarrollo con densidades de tallos significativamente menores (2,498 tallos ha^{-1}) que el "aspen de las parcelas totalmente excluidas (4,474 tallos ha^{-1}). En las parcelas de uso combinado, ganado-fauna, la mayoría del aspen no se regeneró satisfactoriamente o lo hizo con bajas densidades de tallos (1,012 tallos ha^{-1}). El "Aspen" se regeneró exitosamente en las parcelas utilizadas por ungulados solo cuando el número de venados fue bajo. En forma similar, la herbívora de los ungulados tuvo efectos significativos en la composición del estrato herbáceo. En general, la utilización por el venado tendió a reducir los arbustos y las hierbas altas palatables mientras que favoreció el crecimiento de los zacates nativos. Por otra parte, la adición del apacentamiento de ganado domestico, tendió a reducir los zacates nativos y promovió el desarrollo de especies introducidas y de suelo desnudo. Así, las comunidades dominadas por arboles viejos o de una sola edad parecen ser el producto del ramoneo por los ungulados y no un atributo biológico del "Aspen" como comúnmente se ha asumido. No hubo evidencia de que la variación climática afectara la regeneración del "Aspen". Las diferencias observadas se atribuyeron a diferentes historiales de herbívora de los ungulados.

Aspen (*Populus tremuloides* Michx.) in the western United States does not commonly grow from seed because of its demanding seed bed requirements (Kay and White 1995, McDonough 1979). Because individual trees are relatively short-lived (< 150 years), long-lived aspen clones are often dependent on periodic disturbance such as fire to stimulate vegetative regeneration via root suckering, and to reduce conifer competition (Bartos and Mueggler 1981, Shepperd and Smith 1993).

Aspen has been declining throughout the Intermountain West since shortly after European settlement (Kay 1997a, Bartos and

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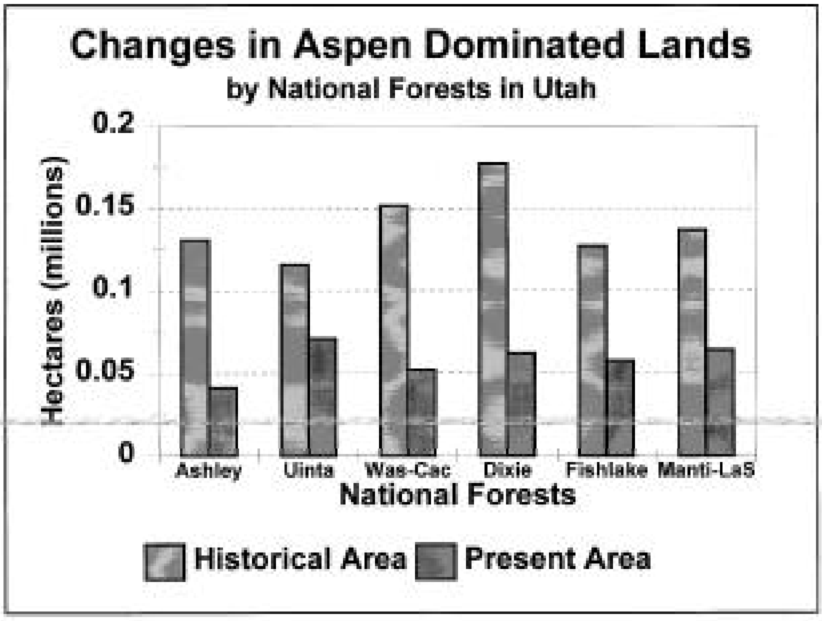

Fig. 1. The decline of aspen on National Forests in Utah. Unpublished forest inventory data, Rocky Mountain Research Station, USDA Forest Service, used with permission.

Campbell 1998). On the Fishlake and Dixie National Forests in Utah, for example, there were historically over 304,000 ha of aspen; today there are only approximately 120,000 ha (Fig. 1). Furthermore, many aspen stands contain old-age or single-age trees and have not successfully regenerated for 80 years or longer (Mueggler 1989).

Several hypotheses have been advanced to explain this decline. These include fire suppression (Houston 1973, Despain et al 1986), climate change (Despain et al. 1986, Romme et al. 1995), livestock grazing (Sampson 1919, Baker 1925), and browsing by mule deer (*Odocoileus hemionus*) and/or elk (*Cervus elaphus*) (Olmstead 1979, Shepperd and Fairweather 1994).

To test the ungulate herbivory hypotheses, we measured all of the long-term, aspen-containing exclosures on the Fishlake and Dixie National Forests in south-central Utah. These exclosures, established during the 1930s to 1970s, were built to study the effect of livestock and/or wildlife use on aspen communities (Young 1956, Laycock 1969).

Methods

Laycock's (1975) list of range reference sites in Utah was first checked for aspen-containing exclosures on the Fishlake and Dixie National Forests. Forest Service employees on both national forests were then contacted to see if these exclosures still existed and if additional aspen-containing exclosures were present on the 2 forests. These potential study sites were subsequently field-checked to see if the exclosures were still functional. We tried to locate in agency files all previous vegetation data, written description of permanent vegetation sampling schemes, and any old photographs.

Some of the exclosures were of a 2-part design where an inside area was fenced to exclude livestock, primarily cattle, but deer and elk had access. Adjacent unfenced outside plots were grazed by both wild and domestic ungulates. Other exclosures were of a 3-part design where 1 area was fenced to exclude all ungulates (treatment 1), another was fenced to exclude livestock (treatment 2), and outside areas were open to wild and domestic ungulates (treatment 3).

At each exclosure, any permanent aspen plots previously established by the agencies were resampled and permanent photopoints rephotographed. Sampling was done during late summer of 1995 and 1996. Next, 2 x 30 m belt transects were placed in representative aspen communities within each of the various parts of each exclosure (Kay 1990). The varied size of exclosures did not always allow sampling with an equal number of transects (Table 1). Each treatment at the following exclosures were sampled by 3 belt transects: Pot Holes, Blind Lake, Riddle Swale, and Hancock. Each treatment on Park Pasture was sampled by 4 transects, and Parker Mountain by 6. At Woodchuck, treatments 1 and 2 were sampled by 3 transects and treatment 3 by 2; at Grindstone, treatments 1 and 2 were also sampled by 3 transects, but treatment 3 by 4. To facilitate recording data, each 30 m transect was subdivided into 3 segments and the number of live aspen stems was recorded using the following size classes within each segment: (1) stems less than 2 m tall, (2) stems greater than 2 m tall but

Table 1. Location and description of aspen containing exclosures in south-central Utah, compiled in 1995–1996.

Exclosure	Land Ownership[1]	Location			Year established	Size (m)		Elevation	Main aspect	Vegetation type[2]
		Township	Range	Section		Livestock exclusion	Total exclusion			
								(m)		
Pot Holes	DNF	30S	3E	27	1958	62x63	None	2743	NW	A,S/G
Park Pasture	DNF	31S	5E	22	1957	88x94	None	2652	NE	A,G
Blind Lake	DNF	30S	4E	24	1958	44x117	None	2984	SE	A,G
Riddle Swale	DNF	33S	1W	19	1957	65x76	65x113	2554	N	A,S/G,C
Woodchuck	DNF	31S	2 1/2W	33	1947	63x63	63x63	2804	S	A,S/G
Grindstone	FNF	29S	4W	29	1934	46x63	46x63	2816	S	A,C
Hancock	FNF	26S	1E	11	1962	61x61	61x61	3054	SE	A,C
Parker Mountain	UT	28S	1W	26	1974	100x100	100x100	2804	E	A,S/G

[1] DNF = Dixie National Forest, FNF = Fishlake National Forest, UT= Utah State School Trust Lands.

[2] Vegetation types within the exclosures. A = aspen, S/G = sagebrush/grasslands, G = grasslands, and C = conifers

less than 5 cm diameter at breast height (DBH), (3) stems between 6 and 10 cm DBH, (4) stems between 11 and 20 cm DBH, and (5) stems greater than 21 cm DBH. Ages of aspen within each size class were determined by coring the larger and cutting the smaller stems and counting annual rings.

The number and species of conifers were recorded on the 2 x 30 m belt transects using the same size classes. While a 2 x 30 m belt transect is adequate to measure aspen stem dynamics and conifer seedlings (Bartos et al. 1994), a plot of that size tends to underestimate the more widely spaced conifers. To overcome this problem, the total percent conifer canopy cover was estimated in each aspen stand following Mueggler (1988).

Aspen and conifer stem counts on each of the 2 x 30 m belt transects were used to produce a mean number of stems per hectare by size classes for each treatment at each site. The treatment means of the various aspen size class data were then compared using repeated measures analysis of variance. Each site was considered an experimental unit for this analysis.

Frequency and canopy-cover of understory plants, bare soil, and rock were recorded from 0.1 m^2 plots at 1 m intervals to the right of each of the belt-transect's centerline (Daubenmire 1959). Readings from all the 0.1m^2 understory plots were averaged within each treatment and then compared using Student's t-test.

Other information recorded at each study site included: Universal Mercator Grid coordinates, elevation, aspect, old and new bark damage, highlining, and sucker browsing. The last 3 items provided an estimate of past ungulate use. Elk and moose (*Alces alces*) strip-off and eat the bark of aspen. Such bark damage usually occurs during winter when other foods are in short supply. Mule deer do not strip aspen bark, but mule deer, elk, and moose all browse aspen when the plants are available.

To determine the effects of deer herbivory on Indian paintbrush (*Castilleja miniata* Dougl.) we measured the height, crown diameter, total number of flower stalks, and the number of grazed flower stalks. These measurements were made just at the Hancock site.

Results

Many of the aspen-containing exclosures listed by Laycock (1969) for south-central Utah no longer exist or were not maintained. Thus, only 8 exclosures containing aspen were evaluated (Table 1). Prior data were found for the Grindstone Flat exclosure. Photographs showing the originally enclosed aspen communities were found for 4 exclosures (Pot Holes, Park Pasture, Grindstone Flat, and Parker Mountain).

Pot Holes

With protection from cattle grazing, the aspen stand successfully established new stems without fire or other disturbance, and increased in size inside the exclosure as evidenced by photographs. The new suckers established in the early 1970s when mule deer numbers were low (Fig. 2). Later when deer numbers expanded the animals consumed all the lower branches from the newly grown aspen, termed highlining, and prevented new suckers from exceeding 1 m in height. The aspen stand inside the exclosure is now composed of multi-sized, multi-aged stems, while little regeneration has occurred outside the exclosure (Table 2).

The largest live aspen were 28 cm DBH and 85+ years old. The 6–7 cm DBH stems were 20–21 years old and the 4 cm stems were 10–12 years old. There was fresh deer sign within the exclosure in August 1995. At this elevation (2,799 m), the conifers are mostly ponderosa pine (*Pinus ponderosa* Lawson) with a few Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco).

Major differences in understory species composition inside and outside this exclosure were significant (P<0.05). Shrubs, such as rabbitbrush (*Chrysothamnus* spp. Nutt.) had lower frequency and canopy cover inside the exclosure, while needle-and-thread grass (*Stipa comata* Trin. & Rupr.) was more frequent inside the fenced plot, as was total grass canopy cover. Indian paintbrush (*C. linariaefolia* Benth.) was more frequent where live-

Table 2. Mean aspen stem densities by size classes and estimated conifer canopy cover inside and outside exclosures in south–central Utah in 1995–96.

Exclosure	Mean aspen stem density by size classes					Conifer canopy cover
	<2m tall	2m tall to 5cm DBH	6 to 10cm DBH	11 to 20cm DBH	>20cm DBH	
	- - - - - - - - (stems ha^{-1}) - - - - - - - -					(%)
Pot Holes						
Livestock exclusion	7,348	3,791	2,221	618	333	<1
Outside	9,018	668	0	55	55	<1
Park Pasture						
Livestock exclusion	1,221	4,676	3,758	1,378	250	<1
Outside	459	835	835	0	584	<1
Blind Lake						
Livestock exclusion	9,574	8,684	3,228	1,057	556	<1
Outside	8,963	6,568	167	55	668	<1
Riddle Swale						
Total exclusion	7,228	4,670	2,780	1,890	168	<1
Livestock exclusion	8,613	2,446	834	0	449	<1
Outside	1,890	0	111	0	222	5
Woodchuck						
Total exclusion	5,177	4,787	2,394	1,169	390	None
Livestock exclusion	946	0	56	779	390	None
Outside	2,088	0	0	1,086	0	None
Grindstone Flat						
Total exclusion	NA[1]	2,505	3,396	1,614	333	30
Livestock exclusion	NA	0	222	835	668	50
Outside	NA	0	0	167	752	60
Hancock						
Total exclusion	5,288	7,738	1,225	557	445	11
Livestock exclusion	2,728	0	0	0	557	31
Outside	4,676	0	0	0	500	30
Parker Mountain						
Total exclusion	974	2,672	1,308	84	500	None
Livestock exclusion	4,509	389	0	0	84	None
Outside	1,030	28	0	0	306	None
Means						
Total Exclusion	4,668a[2]	4,474a	2,221a	1,063a	734a	–
Livestock Exclusion	4,991a	2,498b	1,289ab	583a	822a	–
Outside	4,018a	1,012b	139b	170a	772a	–

[1] NA = Stems less than 2m tall were not counted because most had been consumed by a recent fire – see text.

[2] Means within columns followed by the same letter are not different at P<0.08 by analysis of variance on means.

stock had been excluded, while *Antennaria microphylla* Rydb. was more prevalent outside the exclosure. There was also more bare soil and less litter outside the exclosure than inside.

Park Pasture

When the Park Pasture exclosure was erected on the east side of Boulder Mountain, the area was a heavily used sheep-cattle allotment. Sheep were eliminated in 1963 and cattle herbivory subsequently reduced (U.S. Forest Service 1995). Historically, the area was also grazed by high numbers of mule deer, but that herd has since declined (Fig. 2). When the exclosure was built elk were rare, but they are now common. In fact, several fresh elk beds were observed inside the exclosure when the site was visited during August 1995.

There were no young aspen stems in 1957, but with exclusion of livestock, aspen regenerated and spread inside the exclosure (Fig. 3). This exclosure is also on an aspen-grassland ecotone with few conifers. Ponderosa pine, Douglas-fir, spruce (*Picea* spp. A. Dietr.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) are the most common species in the immediate area. The largest aspen were 38–40 cm DBH and were 105–115 years old. Inside the exclosure there were numerous 10–15 cm DBH stems that were 25–30 years old, but there were none outside (Table 2). These began growth during the mid-1960's when combined high deer and cattle grazing apparently prevented aspen regeneration outside the exclosure. When deer numbers declined during the early to mid-1970s (Fig. 2), aspen regenerated both inside and outside the exclosure, but trees were about 5-times more numerous where cattle also were excluded (Table 2). The 6–10 cm DBH stems were all approximately 20 years old. Rebounding deer populations during the 1980s highlined the regenerated aspen and prevented new suckers from growing taller. Little difference, however, existed in understory species composition or frequency.

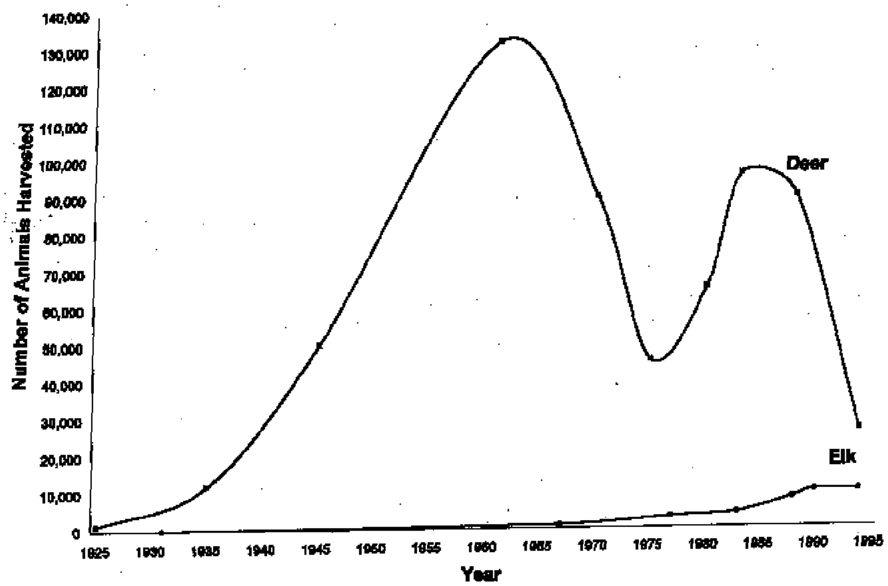

Fig. 2. The number of deer and elk harvested by hunters in Utah from 1925 to 1995. (Utah Div. of Wildlife Resources' Annual big Game Reports—data smoothed to show historical trends.)

Blind Lake

The Blind Lake exclosure on the north side of Boulder Mountain is in an area comprised primarily of aspen and small meadows. Aspen stems inside the exclosure are multi-sized and multi-aged, and began regenerating shortly after the exclosure was erected (Table 2). The elimination of cattle grazing reduced browsing on the aspen suckers and allowed them to grow into the larger size classes. Aspen outside the exclosure regenerated approximately 20 years ago when deer populations plummeted (Fig. 2), despite continued access by cattle. The largest aspen were 30–38 cm DBH and 95–105 years old, while the 4–5 cm DBH stems were 18–25 years of age. Photographic evidence indicates that the aspen clone inside the exclosure has increased in area displacing a largely grassland community.

There was significantly less snowberry (*Symphoricarpos oreophilus* Gray) (P<0.01) and lovage (*Ligusticum porteri* Coult. & Rose) (P<0.01), and significantly more bare soil (P<0.01) and dandelion (*Taraxacum officinale* Weber ex Wiggers) outside the exclosure. In general, there were more palatable forbs (U.S. Forest Service 1937, Nelson and Leege 1982, Wallmo and Regelin 1981) inside than outside the exclosure, while less palatable and non-native forbs were more common outside than inside. There was also more vegetative cover inside than outside the exclosure (P<0.01).

Riddle Swale

Riddle Swale is a 3-part exclosure with a total-exclusion portion, a livestock-exclusion portion, and an outside plot open to both wildlife and cattle. The site is located on the west side of Escalante Mountain at the ecotone between aspen, sagebrush, and pinyon-juniper. A few Utah juniper (*Juniperus osteosperma* (Torr.) Little), pinyon pine (*Pinus monophylla* Torr. & Frem. In Frem.), ponderosa pine, and Douglas-fir are found both inside and outside the exclosure.

Inside the total-exclusion part aspen began regenerating shortly after the exclosure was constructed in 1957; the stems are now multi-sized and multi-aged (Table 2). In the livestock-exclusion portion of the exclosure, aspen only regenerated when deer numbers declined around 20 years ago (Fig.2). As the deer recovered, however, they highlined all the previous aspen regeneration inside the livestock exclosure and prevented any new aspen suckers from growing more than 1 m tall. Where both cattle and deer grazed, few aspen stems attained more than 2 m in height (Table 2). The largest aspen at this site were 23–26 cm DBH and 72–78 years old. The 8–10 cm DBH stems were 20–25 years old, and the 3–5 cm stems were 14–20 years old.

There were also major differences in understory species composition. Deer use only and combined use eliminated Indian paintbrush, while combined big game and cattle use significantly (P<0.01) reduced the canopy cover of native grasses compared to the exclosures. Conversely, sagebrush increased under deer use, but more so under combined use. Bare soil and rock were not apparent where ungulate herbivory was absent, but increased to 6.4% cover where only wildlife grazed and to 27.2% cover with combined deer-cattle use (P<0.01).

Woodchuck

Woodchuck is a 3-way exclosure built on the northeast slope of Mount Dutton. Although this exclosure is at over 2,800 m

Fig. 3. Photographs of the Park Pasture exclosure: (a) taken in September 1958 shortly after the exclosure was constructed and showing no aspen regeneration; and (b) in August 1995 showing spread of aspen inside the exclosure.

in elevation, it is surrounded by extensive sagebrush-grasslands and lacks conifers. Cattle have used this allotment historically, and deer numbers have also been high. Elk have recently become common on Mount Dutton but do not appear to use this isolated patch of aspen.

Aspen within the total-exclusion part is multi-sized and multi-aged (Table 2), and began regenerating shortly after the exclosure was constructed in 1947. No new aspen stems have attained heights of 2 m or more in the livestock-exclusion or combined-use areas. The deer at this site have not allowed aspen to regenerate even where cattle have been excluded. The largest aspen were 25–30 cm DBH and 100+ years old, while aspen in the 15–16 cm size class were 65–70 years of age. Apparently, some event in the late 1920s and early 1930s allowed some aspen regeneration in this stand before it was enclosed.

Deer use significantly reduced wild rose (*Rosa woodsii* Lindl.), snowberry, lupine (*Lupinus caudatus* Kellogg), and Indian paintbrush, but favored the growth of native grasses, especially needle and thread (all $P<0.01$). The addition of cattle grazing significantly reduced native grass cover (<0.01) and significantly increased the amount of bare soil ($P<0.01$). The canopy cover of introduced Kentucky bluegrass (*Poa pratensis* L.) increased from 1.9% in the total exclusion area, to 23.7% under deer only use ($P<0.01$), and to 50.9% with the addition of cattle grazing ($P<0.01$). Total vegetative understory cover declined significantly ($P<0.01$) from 95.9% in the non-grazed area to 77.7% in the wildlife only area to 63.7% with combined use.

Grindstone Flat

The 3-part exclosure at Grindstone Flat (Table 1) was evaluated during the 1950s (Young 1956), and then remeasured by the U.S. Forest Service in 1975 (Mueggler and Bartos 1977). Part of the site was originally clear-cut prior to exclosure construction, but 1/3 of each exclosure, as well as all of the outside aspen, were left uncut. Only the uncut areas were analyzed to maintain comparability with the other sites.

Aspen regenerated inside the total-exclusion area, while deer use prevented aspen regrowth in the livestock-exclusion area, as well as the outside area (Table 2). Spruce and subalpine fir have heavily invaded the area (Mueggler and Bartos 1977) .

During late June 1996 the exclosure and much of the surrounding lands were burned by the Pole Creek wildfire. Much of the vegetation inside the exclosure complex was burned, and the old exclosure pole-fence destroyed. The total-exclusion and livestock-exclusion areas were completely consumed by flames, as was the surrounding outside aspen. In contrast, the cut total-exclusion area was largely unburned while the cut livestock-exclusion area did not burn at all.

Since this is 1 of only 2 long-term exclosures on the Fishlake National Forest containing aspen, the Forest Service rebuilt the exclosure fences in 1997. We were able to measure aspen stem densities in September 1996 because the larger-sized live stems were too green to be consumed by the fire. Aspen stems less than 2 m tall, however, were not quantified because many of those were removed by the fire. Understory species composition was not measured for the same reason.

Of most relevance in this exclosure comparison is that aspen in the total-exclusion area successfully regenerated and produced a multi-aged stand prior to the 1996 fire, while aspen in the livestock exclosure and outside combined use areas produced no new stems greater than 2 m tall. Conifer cover in the total-exclusion area was less than in the areas accessible to either deer or cattle (Table 2).

The largest aspen trees were 38–44 cm DBH, but age determination was difficult because of extensive heart rot. In 1975, Mueggler and Bartos (1977) recorded a 41 cm DBH aspen that was 175 years old, so the few remaining, unburned trees were likely approaching or near the maximum age (200 years) recorded for aspen in the Intermountain West (Jones and Schier 1985).

Hancock

This 3-part exclosure is located above Doctor Canyon, approximately 3 km southeast of Hancock Flat and 1 km northeast of Rust Spring. Unlike the other exclosures in this study, Hancock has been a sheep allotment and mule deer were the most abundant wild ungulate.

Aspen in the total-exclusion portion began regenerating shortly after the exclosure was constructed and today is multi-sized and multi-aged despite invasion by conifers (Table 2). Aspen has not regenerated successfully in either the wildlife-only or the combined-use areas; all of the aspen suckers that occur have been repeatedly browsed by deer and/or sheep. When this site was measured in July, mule deer had already browsed many of the new aspen suckers in the livestock-exclusion portion of the exclosure. The largest aspen stems were 30 cm DBH and 105+ years old. Spruce canopy cover appeared greater on the grazed portion than on the ungrazed portion of the exclosure.

Deer grazing and combined use created major differences in understory species composition. Both deer grazing and combined use significantly (P<0.01) reduced Indian paintbrush, dandelion, and total vegetative cover, and significantly (P<0.01) increased cover of grass, yarrow (*Achillea millefolium* L.), rock, bare soil, and litter. Deer grazing also significantly (P<0.01) reduced height, crown diameter, and number of flower stalks of individual Indian paintbrush plants. Deer had already grazed 63% of the Indian paintbrush flower stalks inside the livestock-exclusion portion of this exclosure when it was sampled in July.

Parker Mountain

When this site was fenced (1974) there was concern that browsing by jackrabbits (*Lepus* spp.) might effect aspen regeneration. To monitor this, each of the total-exclusion and livestock-exclusion areas were partitioned with additional fencing to prevent entry by lagomorphs on half of these areas.

The exclosure is on a joint cattle-sheep allotment where mule deer and antelope (*Antilocapra americana*) have been abundant. In recent years, however, the deer population has declined and most of the present wildlife use is by elk. The exclosures are also near the lower elevation of aspen and the site is surrounded by sagebrush-grasslands.

Exclusion of lagomorphs had no effect on aspen regeneration or understory composition so the 2 data sets were pooled. When protected from ungulates, aspen successfully regenerated on this site producing a multi-aged stand (Table 2). Aspen successfully regenerated in the livestock-exclusion part and on outside plots, especially after deer declined, but at significantly lower (P<0.05) densities than on the total exclusion plot. The increasing elk population, however, highlined those stems and inflicted extensive bark damage (Krebill 1972) on the unprotected aspen. The largest aspen were 26–28 cm DBH and 90–95 years of age. Photographic evidence indicates that aspen in the total-exclusion part of this exclosure has spread into sagebrush-grasslands, an indication that climate had not limited expansion at this site.

Although this exclosure had been in place for only 22 years, there were significant (P<0.05) differences in understory species composition. Indian paintbrush and littleflower penstemon (*Penstemon procerus* Dougl. ex Graham) had greater frequency and canopy cover in the total-exclusion area than on the wildlife exclusion area, and they were virtually eliminated by combined wildlife-livestock use. Conversely, native grasses were most abundant in the total-exclusion part (54%), were halved by wildlife-only use, and reduced to only 16% under combined use. The addition of livestock grazing also increased (P<0.05) the amount of bare soil.

Discussion

Aspen Stem Dynamics

Aspen within all total-exclusion exclosures regenerated successfully without disturbance and developed multi-sized, multi-aged stems, even where the stand had been heavily invaded by conifers (i.e., the Hancock exclosure). Aspen subjected to browsing only by wildlife, primarily mule deer, either failed to produce new stems greater than 2 m tall, or regenerated at stem densities lower than on the total-exclusion plots. On combined wildlife-livestock use plots, most aspen failed to regenerate successfully, or did so at stem densities lower than on the livestock-exclusion plots. Aspen regenerated successfully on livestock-exclosed and combined-use plots only when mule deer populations were low.

Mule deer have been the most prevalent wild herbivore in south-central Utah since at least the 1930s. Moose were only recently transplanted into the area, and elk populations were very low until the 1980s. Deer numbers in Utah generally peaked during the early 1960s, but declined precipitously by 1975 (Fig. 2). This reduced the browsing pressure on aspen suckers, and many stands in southern Utah were able to regenerate successfully if livestock use was not excessive. An increase in deer during the 1980s prevented new aspen suckers from increasing in height, and the deer also consumed the lower branches from aspen that had regenerated earlier (Fig. 4). In the mid-1990s, mule deer populations again declined, but few aspen stands were able to regenerate successfully because increasing numbers of elk were foraging on the young suckers (Fig. 2). Thus, in some areas of Utah, deer browsing has been replaced by elk browsing. Elk also seem to have a greater preference for aspen than mule deer (Kay 1997b, Shepperd and Fairweather 1994). Episodes of aspen regeneration have been observed in other areas when mule deer (Julander and Low 1976, Olmstead 1979) or elk (Olmstead 1979, Kay and White 1995) numbers were low.

Understory Species Composition

Understory species composition of aspen stands was significantly affected by ungulate herbivory. In general, utilization by mule deer tended to eliminate palatable

Fig. 4. Highlining by mule deer in a 2-age class aspen stand on the Dixie National Forest.

Table 3. Mean frequency (Freq.) and canopy cover (C.C.) of undergrowth species on total–exclusion (wild & domestic ungulates), partial exclusion (livestock), and no–exclusion plots. (Means are based on only those sites where the species occurred; "n" = number of sites where species occurred; summation of cover values therefore are meaningless.)

	TOTAL EXCLUSION			*PARTIAL EXCLUSION*			*NO EXCLUSION*		
	n	Freq.	C.C.	n	Freq.	C.C.	n	Freq.	C.C.
		- - - - - (%) - - - - -			- - - - - (%) - - - - -			- - - - - (%) - - - - -	
TREES									
Picea engelmannii Parry ex Engelm.	1	18	10.6	2	45	30.3	2	23	14.8
SHRUBS									
Artemisia tridentata Nutt.	3	20	7.7	4	24	12.2	4	25	11.3
Artemisia tripartita Rydb.	1	3	0.4	2	2	0.2	2	15	4.5
Chrysothamnus nauseosus (Pallas) Britt.	1	1	0.1	2	4	1.1	2	8	2.1
Chrysothamnus viscidiflorus (Hook.) Nutt.	1	0	0. 0	2	15	4.8	2	20	8.1
Juniperus communis L.	0	0	0	1	0	0.0	1	1	0.4
Juniperus osteosperma (Torr.) Little	1	7	3.3	1	0	0. 0	1	8	5.9
Potentilla fruticosa L.	0	0	0	1	4	0.3	1	5	0.7
Purshia tridentata (Pursh) DC.	1	0	0.0	1	0	0. 0	1	2	1.9
Ribes spp. L.	0	0	0	1	8	2.9	1	4	1.4
Rosa woodsii Lindl.	3	2	0.9	4	3	0.8	4	4	0.8
Symphoricarpos oreophilus Gray	3	17	8.0	5	19	8.4	5	11	3.3
GRAMINOIDS									
Agropyron caninum (L.) Beauv.	3	28	4.0	3	16	2.4	3	8	0.7
Bromus ciliatus L.	4	28	5.6	6	15	1.7	6	10	1.0
Carex spp. L.	2	18	0.1	1	17	4.2	1	0	0.0
Festuca idahoensis Elmer	2	1	0.1	3	42	9.7	3	39	6.5
Festuca thurberi Vasey	2	40	13.4	4	23	5.2	4	31	6.2
Koeleria cristata (L.) Pers.	1	4	0.5	1	35	4.2	1	24	2.6
Muhlenbergia wrightii Vasey ex Coult.	0	0	0	2	1	0.1	2	16	3.4
Poa interior (NY)	1	7	1.1	1	0	0.0	1	8	0.8
Poa pratensis L.	2	8	2.8	4	22	15.4	4	42	18.8
Sitanion hystrix (Nutt.) J. G. Sm.	3	18	2.6	5	19	3.0	5	18	2.5
Stipa columbiana Macoun	1	4	1.8	1	0	0.0	1	0	0.0
Stipa comata Trin. & Rupr.	3	42	11.7	6	46	14.1	6	30	4.1
Stipa lettermanii Vasey	1	17	2.3	1	11	2.2	1	0	0.0
FORBS									
Achillea millefolium L.	2	10	0.8	3	34	2.7	3	25	14.6
Antennaria microphylla Rydb.	0	0	0	1	0	0	1	54	11.9
Aquilegia coerulea James	1	8	2.3	1	3	0.2	1	0	0
Aster spp. L.	1	13	2.4	1	9	0.9	1	9	0.7
Castilleja linariaefolia Benth.	3	28	3.9	4	6	1.1	4	1	0.1
Castilleja miniata Dougl. ex Hook.	1	56	29.5	1	6	0.4	1	2	0.2
Fragaria virginiana Duchesne	0	0	0	1	16	1.2	1	3	0.2
Galium spp. L.	1	38	3.9	1	28	3.6	1	0	0. 0
Ligusticum porteri Coult. & Rose	0	0	0	2	42	12.3	1	0	0. 0
Lupinus argenteus Pursh	1	37	14.2	2	6	1.5	2	29	6.7
Lupinus caudatus Kellogg	1	82	40.4	1	0	0.0	2	18	4.4
Penstemon procerus Dougl. ex Graham	1	18	3.7	1	0	0.0	1	0	0.0
Phlox spp. L.	1	0	0.0	1	22	4.3	1	6	1.2
Potentilla glandulosa Lindl.	1	40	8.0	1	45	5.5	1	10	1.0
Potentilla gracilis Dougl. ex Hook.	0	0	0	1	2	1.3	1	0	0.0
Senecio spp. L.	1	10	2.0	1	0	0	1	0	0
Taraxacum officinale Weber ex Wiggers	1	29	4.6	3	14	2.6	3	31	8.7
Vicia americana Muhl.	0	0	0	1	83	25.2	1	72	26.5
ROCK	4	1	0.3	7	8	3.1	7	9	3.1
BARE SOIL	4	3	0.6	7	13	2.0	7	30	9.4
LITTER	4	63	25.3	7	66	26.8	7	69	28.9

tall forbs and shrubs while favoring the growth of native grasses and unpalatable forbs (U.S. Forest Service 1937, Nelson and Leege 1982, Wallmo and Regelin 1981) (Table 3). Indian paintbrush in particular was harmed by mule deer herbivory. The addition of livestock, primarily cattle, significantly reduced the native grass cover at most sites, while introduced grasses and bare soil increased. It is clear that the combined level of ungulate use at all sites has not only altered the age structure of aspen stands but also altered understory species composition. It is equally clear that wildlife can dramatically affect the structure of aspen communities. Earlier open-range grazing studies have reported similar findings (Baker 1925, Weatherill and Keith 1969, Julander and Low 1976, Mueggler 1988, Smith et al. 1972).

Numerous hummingbirds were observed feeding on Indian paintbrush inside the total-exclusion area at the Hancock exclosure, but not inside the livestock-exclusion area or on outside plots. Thus, grazing-induced reduction of this flowering forb alone may have major effects on species not normally considered in range-wildlife studies.

Other Aspen Exclosure Studies

Aspen exclosure studies throughout the western United States and Canada depict similar findings. Coles (1965) and Mueggler and Bartos (1977) report similar results in central Utah. Kay (1990) measured 14 aspen exclosures in the Yellowstone Ecosystem where elk are the major herbivore. He found that all protected stands regenerated and developed multi-aged stands and that protection completely altered the composition of the undergrowth: shrubs and palatable forbs dominated inside the exclosures, whereas non-native grasses resistant to grazing dominated outside. In 3 out of 4 exclosures in Colorado's Rocky Mountain National Park, where deer and elk are the primary herbivores, aspen developed multi-aged stands while areas outside did not (Hess 1993, Baker et al. 1997). In South Dakota, aspen in Custer State Park expanded into grasslands where wildlife were excluded (Hoffman and Alexander 1987), and aspen in Wind Cave National Park develop multi-size class stands after exclusion of wild ungulates (Kay 1990).

From study of 4 exclosures in Alberta's Elk Island National Park where elk and moose are the major herbivores, Milner (1977) concluded that not only was aspen regeneration restricted by browsing, but palatable shrubs were more abundant under protection. Trottier and Fehr (1982), evaluating exclosures in Canada's Banff National Park, concluded that aspen regeneration was limited by elk browsing and that protected plots had both greater shrub density and more diverse height than the unprotected plots. Comparing repeat photographs taken of an exclosure (after 50 years protection) near Banff, Kay et al. (1994) observed that a dense multi-aged aspen stand had grown up inside the exclosure while no aspen stems had regenerated successfully outside. These same authors also reported that aspen regenerated successfully where protected for approximately 10-years within the game-proof fenced Trans Canada Highway right-of-way through Banff's lower Bow Valley, but did not where elk were free to browse.

The consensus of all of these studies is that deer and elk can significantly hinder aspen regeneration and change understory species composition. Moreover, livestock use has an additive negative effect on aspen regeneration and understory composition. Excessive use by wildlife tends to reduce woody species and palatable forbs. Utilization by mule deer favors native grasses. Excessive elk use has a negative effect on grasslands because elk utilize a broader array of forages than deer (Nelson and Leege 1982). Excessive use by cattle also tends to reduce the abundance of native grasses and increase the amount of non-native species and bare soil.

Climate Change

The exclosures also demonstrate that climatic variation has had little effect on reproduction in aspen communities compared to that imposed by ungulates. Since the exclosure fence usually bisects a single aspen clone, differences between protected and open areas cannot be a product of either genetics or climate. The more abundant vegetation inside the exclosures, especially on total-exclusion plots, alters the microclimate, but that is an incorporated variable caused by the plant's response to the elimination of ungulate browsing, not the cause of the vegetation's response. Such microclimatic conditions would prevail in any aspen stand not subject to heavy ungulate use, whether in an exclosure or not.

If climatic variation is having an overriding effect on aspen community dynamics as proposed by others (Romme et al. 1995), we would expect aspen inside exclosures in south-central Utah to show signs of stress, especially since many of the exclosures are situated at the lower elevation of aspen or at grassland-aspen ecotones. However, no signs of physiological stress were observed during this study. In fact, the area occupied by aspen has increased inside exclosures at the expense of grasslands (Fig. 3). Baker et al. (1997) reported no correlation between climatic variation and aspen regeneration, while Kay (1990) reported that enclosed aspen in the Yellowstone Ecosystem replaced grasslands even on south-facing hillsides. White et al. (1998) and Kay (1997b) similarly reported no correlation between climate and aspen regeneration in the Canadian Rockies.

Conclusions

1. Browsing by native and domestic ungulates has hindered aspen regeneration throughout south-central Utah.

2. Aspen need not always be burned or clear-cut to regenerate successfully.

3. Wild ungulates, primarily mule deer, can have a major effect on aspen stem dynamics and understory composition.

4. Livestock grazing, as historically practiced in southern Utah, has had widespread effects on aspen communities, including changes in understory species composition.

5. Combined wildlife-livestock use most severely alters aspen community dynamics.

6. Aspen stands in the Rocky Mountain west dominated by old or single-age trees are most likely a product of excessive ungulate browsing.

7. Managers should quantify the level of ungulate herbivory before treating aspen stands with fire or cutting, because developing suckers may be subject to repeated browsing. If ungulate browsing is excessive, treatment of aspen stands may only hasten their demise.

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Herpetofaunal responses to brush management with herbicide and fire

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Abstract

We examined how native herpetofauna of the Cross Timbers in Oklahoma, USA, were influenced by vegetation types derived from combinations of herbicide applications and prescribed burning. Brush management treatments consisted of tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3,4-thiazol-2-y-1]-N,N'-dimethylurea)-only, tebuthiuron + fire, and untreated pastures of mature hardwood forest (no herbicide or fire). A total of 292 individuals representing 30 species was captured in 1994 and 1995 using time-constrained searching and drift-fence arrays on 3 replicates of the 3 treatments. Relative total abundance and species richness of herpetofauna were similar on all 3 treatment types. However, differences were apparent by taxonomic group. In general, amphibians were most abundant in untreated and tebuthiuron-only pastures, lizards were most abundant on the untreated pastures, and snakes were most abundant on pastures treated with tebuthiuron + fire. Maintenance of a mosaic of habitats in the Cross Timbers may enhance diversity of the native herpetofauna.

Key Words: reptiles, amphibians, brush management, tebuthiuron, prescribed burning, Cross Timbers, Oklahoma.

Resumen

Examinamos como la herpetofauna nativa de los Cross Timbers de Okla., USA, fue influenciada por los tipos de vegetación derivados de combinaciones de tratamientos de herbicida y quemas prescritas. Los tratamientos de manejo de mata fueron tebuthiuron (N-[5-(1,1-dimethylethyl)-1, 3, 4-thiazol-2-y-1]-N, N'-dimethylurea)-sólo, tebuthiuron + quema, y pastizales no tratados de bosque caducifolio maduro (no herbicida ni quema). Un total de 292 individuos representantes de 30 especies fueron capturados en 1994 y 1995 por medio de búsquedas de tiempo-restringido y matrices de cercas de desvío en tres réplicas de los tres tratamientos. La abundancia relativa total y la riqueza de las especies de la herpetofauna fueron parecidas en los tres tipos de tratamiento. Sin embargo, se vieron diferencias por grupo taxonómico. Por lo general, los anfibios fueron más abundantes en los pastizales no tratados y los de tebuthiuron-sólo, las lagartijas fueron más abundantes en los pastizales no tratados, y las culebras fueron más abundantes en los pastizales tratados de tebuthiuron + quema. El mantenimiento de un mosaico de hábitat en los Cross Timbers puede fomentar la diversidad de la herpetofauna nativa.

The Cross Timbers is a western extension of the oak-hickory ecoregion and contains about 19 million ha of upland hardwood forest and tallgrass prairie in the central United States (Garrison et al. 1977, Soil Conserv. Serv. 1981). Livestock production in these oak-dominated rangelands is relatively limited because of low production of herbaceous forage (Scifres 1980). Brush management can increase production of herbaceous forage by selectively removing woody overstory species; this benefits livestock production (Scifres and Mutz 1978, Stritzke 1980, McCollum et al. 1987) and economic returns (Bernardo and Engle 1990, Bernardo et al. 1992).

There are no published studies that directly address effects of brush management on native herpetofauna, but a few studies from the western United States have revealed that abundances of lizards and snakes were reduced in areas that were either grazed by livestock or modified by humans (Busack and Bury 1974, Berry 1978, Jones 1981, 1988, Szaro et al. 1985, Bock et al. 1990). Our research in the Cross Timbers of central Oklahoma showed that modification of this habitat with herbicides and fire can have both deleterious and favorable effects on native biota. Generally, eastern cottontail rabbits (*Sylvilagus floridanus*—Lochmiller et al. 1991, 1995), cotton rats (*Sigmodon hispidus texianus*—McMurry et al. 1994), and white-tailed deer (*Odocoileus virginianus*—Soper et al. 1993a, 1993b, Leslie et al. 1996) responded positively to annual burning as part of the brush management prescription. Conversely, occurrence and numbers of some avian species [e.g., Louisiana waterthrush (*Seiurus motacilla*), tufted titmouse (*Parus bicolor*)] were impacted negatively by habitat alterations associated with brush control (Schultz et al. 1992a, 1992b).

Landowners likely will continue to convert the Cross Timbers into grasslands (Boren et al. 1996), so it is important to understand effects of such conversion on wildlife populations. Our objective was to determine effects of derived habitat types resulting from brush management with herbicide and fire on populations of reptiles and amphibians in the Cross Timbers.

Study Area and Methods

We conducted our study on the Cross Timbers Experimental Range (CTER), located about 12 km southwest of Stillwater, Okla. (36°02'40" to 36°04'20"N, 97°09'30" to 97°11'39"W). The

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CTER is a 648-ha research facility that lies near the western edge of the Cross Timbers ecoregion (Kuchler 1964). Upland forest of the CTER is dominated by post oak (*Quercus stellata* Wangenh.) and blackjack oak (*Q. marilandica* Muenchh.) in the overstory, interspersed with a mosaic of tallgrass prairie (Ewing et al. 1984). The understory is predominantly eastern redcedar (*Juniperus virginiana* L.), American elm (*Ulmus americana* L.), redbud (*Cercis canadensis* L.), poison ivy (*Rhus radicans* L.), and rough-leaf dogwood (*Cornus drummondii* Meyer). The predominant herbaceous ground cover is little bluestem [*Andropogon scoparius* (Michx.) Nash], but rosette panicgrass (*Panicum oligosanthes* Schultes), indiangrass [*Sorghastrum nutans* (L.) Nash], and western ragweed (*Ambrosia psilostachya* D.C.) occur in varying amounts throughout the CTER. Bottomland forest is restricted to intermittent stream drainages that transect the study area (Ewing et al. 1984).

The CTER was established in 1983 to evaluate responses of livestock and vegetation to various brush management techniques. It was divided into 20, 32.4-ha (0.41 x 0.79 km) fenced experimental pastures that represented 4 replicates of 5 treatments comprising 2 herbicides and prescribed burning. Herbicide + fire treatments were burned annually for 3 years starting in 1985 and then on a 3-year rotation starting in 1990. Both herbicides were effective, although pastures treated with tebuthiuron (N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-N,N'-dimethylurea) resulted in the greatest tree kill of 52–99% (Stritzke et al. 1987) and increased herbaceous production (Engle et al. 1991, Stritzke et al. 1991). Untreated habitats had a dense woody canopy, little herbaceous cover, and moderate amounts of woody understory (Engle et al. 1991, Stritzke et al. 1991). Treatments with fire had reduced cover of eastern redcedar (Stritzke et al. 1991), although other woody species were not greatly reduced by fire alone.

All experimental pastures were grazed by beef cows in 1984 and by yearling beef cattle in summer in 1985 and after. Stocking was adjusted annually on individual pastures on the basis of the residue of previous year's end-of-season herbage and expected forage production during the following year with the goal of 50% utilization of annual forage production (Stritzke et al. 1991).

In 1994 and 1995, we evaluated herpetofaunal communities on 3 of the 5 experimental treatments: (1) soil-applied tebuthiuron herbicide applied at 2 kg a.i. ha^{-1} in March 1983; (2) tebuthiuron + fire in spring; and (3) untreated (no herbicide or burning). We chose those treatments because they represented the maximal range of habitats available on the CTER relative to overstory cover and composition of the vegetation (Ewing et al. 1984). Untreated pastures were mature upland oak forest (Fig. 1a); tebuthiuron + fire treatments were open, park-like prairie with a scattering of eastern redcedar (Fig. 1b); and the tebuthiuron-only treatments were a mixed-brush type dominated by eastern redcedar (Engle et al. 1991, Stritzke et al. 1991; Fig. 1c)—a derived habitat that was structurally and compositionally similar to dense stands of eastern redcedar that now occur on former prairies and hardwood forests through the south-central Great Plains due to fire supression. Production of grasses and forbs in 1994 and 1995 averaged 20 kg/ha in the untreated pastures, 680 kg/ha in the tebuthiuron-treated pastures, and 1,250 kg/ha in the tebuthiuron + fire pastures (Engle, unpublished data). Canopy cover of woody plants in the upland forests was greatest in the untreated pastures and least in the tebuthiruon + fire pastures (Stritzke et al. 1991; Fig. 1). Woody vegetation in the treated pastures was less spatially homogenous than in the untreated pastures and understory production and composition reflected that variability (Fig. 1). Three of the 4 replicates of each of the 3 selected treatments (9 pastures) were chosen at random prior to sampling for reptiles and amphibians. Sampling was conducted only on those areas of experimental pastures that were upland forest prior to herbicide application.

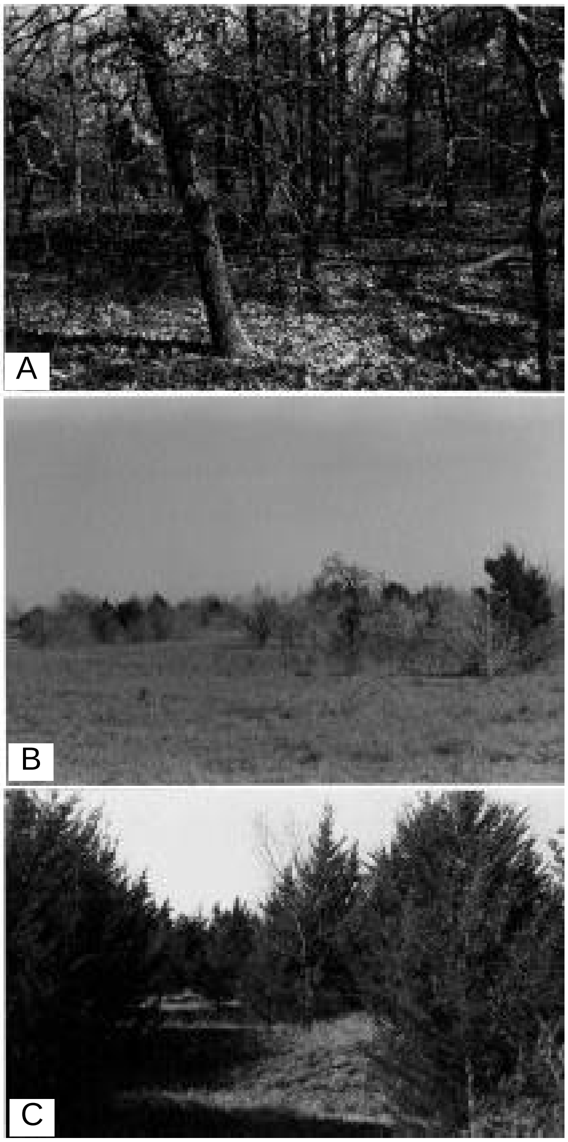

Fig. 1. Habitats in which herpetofauna were studied at the Cross Timbers Experimental Range resulting from the following treatments: a) untreated (no herbicide or fire), b) tebuthiuron + fire, and c) tebuthiuron only.

Herpetofauna were sampled monthly from mid-May through early October, 1994, and late-March through early October, 1995. Two capture techniques were used to assess abundances of reptiles and amphibians. During the sampling period in 1994, we performed time-constrained, search-and-seizure techniques (Scott 1994). For sampling in 1995, we used both time-constrained searches and drift-fence arrays with funnel traps. Use of drift-fence arrays is a standard effective method of sampling reptiles and amphibians (Scott 1994). Use of standardized drift fences, in combination with search-and-seizure techniques, to assess relative abundance and species richness of reptiles and amphibians facilitates comparisons of experimental units (Enge and Marion 1986, Jones 1986, Bury and Corn 1987). Time-constrained searching allowed counting of species not readily caught in drift-fence arrays or funnel traps (Bury and Corn 1987, Scott 1994).

One drift-fence array was installed on each of the 9 pastures. Each array consisted of 3, 15.2-m x 30.5-cm lengths of galvanized metal flashing emanating from a central point and radiating out at 120º angles. One edge of the flashing was buried about 6 cm below the ground surface, and the fence was stabilized on both sides with 2.5- x 60-cm wooden stakes placed near the ends and at 5-m intervals. We buried a 19.0-l plastic drop can flush with the soil surface at the center of the array and at the end of each arm (Campbell and Christman 1982, Vogt and Hine 1982, Corn 1994). When drift fences were not in use, we placed lids on drop cans to prevent entry of animals. To reduce mortality during trapping sessions, lids were propped 10–12 cm above the drop can to provide shade and ventilation. To avoid confounding treatment effects, drift-fences were placed ≥ 100 m from treatment boundaries and ≥ 200 m from permanent water sources. We also placed one double-ended funnel trap constructed of aluminum window screening on each side of each array arm (*n* = 6 funnel traps per array). Funnel traps were 66 cm long and 16 cm in diameter with an inside funnel opening of 7 cm in diameter and were primarily intended for the capture of snakes. Thin rubberized floor mats were cut 30 cm x 45 cm and were placed over the center of these traps to provide captured animals shelter from the weather. Traps were unbaited, which is standard for herpetofaunal studies.

Monthly drift-fence sampling periods in 1995 lasted 10 days. We checked arrays every second or third day during cool weather (daily high temperature <25°C) and every other day during hot weather (daily high temperature >25°C). Captured animals were identified to species, permanently marked by toe or scale clipping, and released at the point of capture. Recaptures were rare and were not included in data tabulations. Time-constrained searching was conducted in 1994 and 1995; each replicate received about 3.5 person-hours of active searching in 1994 and 2.5 person-hours in 1995. Random encounters and opportunistic observations of reptiles and amphibians also were recorded during monitoring periods if they occurred ≥ 100 m from pasture boundaries and ≥ 200 m from permanent water.

Herpetofaunal taxonomic groups were not lumped together because of their differential responses to habitat structure based on their physiological and behavioral capabilities (Jones 1986). Because our data were not normally distributed and sample sizes of some species were small, we used chi-square analyses (SAS 1985) to assess frequencies of captures among treatments by taxonomic group (amphibian and reptile; the latter subdivided into turtle, lizard, and snake) and pooled data across the 3 pasture replicates in each treatment to maximize sample size. We used Kruskal-Wallis tests to evaluate treatment effects on individual species (Anderson et al. 1991). Significance was set at $P \leq 0.10$.

Results and Discussion

We captured 292 animals representing 30 species during 2 years of study (Table 1). Thirty-six individuals of 16 species were documented during 32 hours of time-constrained searching in 1994 (1.1 captures per person-hour). Time-constrained searching during the 1995 season yielded 48 captures of 14 species during 21.5 hours of active searching (2.2 captures per person-hour). The 9 drift-fence arrays and associated funnel traps produced 199 captures during 60 nights of effort (540 array-nights) between late March and early October, 1995 (0.4 captures per array-night). Nine additional individuals were recorded as chance encounters in 1995.

Herpetofaunal abundance (summed over all 3 replicates) was greatest in untreated pastures (n = 110), less in tebuthiuron + fire pastures (95), and least in tebuthiuron-only pastures (87) (Table 1). Species richness (summed over all 3 replicates) was similar among pastures: tebuthiuron + fire (22), tebuthiuron-only pastures (21), and untreated pastures (20). Of 30 species, 3 each were unique to untreated pastures and pastures treated with tebuthiuron + fire, and 2 species were found exclusively on tebuthiuron-only pastures (Table 1). Considering individual species, only numbers of the 5-lined skink (*Eumeces fasciatus*) varied among treatments, being more common on untreated pastures (Kruskal-Wallis W = 5.45, 2 df, P = 0.07).

Numbers of captures of reptiles and amphibians differed among treatments (Table 1). Both taxonomic groups were about equally common on untreated pastures, but amphibians were least common on pastures with tebuthiuron + fire, and reptiles were least common on tebuthiuron-only pastures. Reptile taxa (snakes, turtles, and lizards) also differed significantly among treatments (Table 1). Lizards were more abundant on untreated pastures and were less abundant on tebuthiuron-only plots. Snakes were most abundant in pastures treated with tebuthiuron + fire. Turtles were captured too infrequently for definitive conclusions about their habitat associations.

Amphibians were most abundant on untreated and tebuthiuron-only pastures. They were less common on the most open park-like pastures created with tebuthiuron + fire. Those open pastures were exposed to more insolation and were likely drier, which are conditions generally unfavorable for amphibians. Reptiles, like amphibians, were common on untreated pastures but were more abundant on tebuthiuron + fire pastures than on the dense mixed-brush pastures created by tebuthiuron-only. For the most part, reptiles tolerate drier conditions and bask more than amphibians. Nevertheless, reptile taxa were not uniform in their habitat affiliations. Lizards were least common on the brushiest pastures and were most common on untreated pastures. Skinks, a subgroup of lizards, were most common in untreated pastures, followed by tebuthiuron + fire, and then tebuthiuron-only ($X^2 = 24.00$, 2 df, $P < 0.01$). Snakes were most common in open park-like pastures and least so in untreated pastures. Prairie snakes such as the eastern yellowbelly racer (*Coluber constrictor*) were found exclusively on tebuthiuron + fire treatments. Rough earth snakes (*Virginia striatula*) also were most abundant on the prairie-like pastures that were treated with either tebuthiuron or tebuthiuron + fire.

Our results indicate that modification of the Cross Timbers with tebuthiuron-only has a negative effect on reptiles in general and lizards in particular. The tebuthiuron-only treatment created the least heterogeneous habitats on the CTER and, 10 years post-treatment, was virtually an homogenous forest of eastern redcedar (J. F. Stritzke, pers. comm.), with little structural diversity. Changes in structural heterogeneity due to heavy grazing can reduce abundance and diversity of lizards (Jones 1981). Nevertheless, 2 species of snakes [speckled kingsnake (*Lampropeltis getulus*) and flathead snake (*Tantilla gracilis*)] occurred exclusively on the tebuthiuron-only treatment, although both were represented by a single capture.

We could not analyze the effect of cattle grazing because all the experimental plots were grazed at similar intensity. Other research similar to ours focused on the direct effect of livestock grazing, which in most cases was negative for reptiles and amphibians (Reynolds 1979, Ballinger and Jones 1985, Bock et al. 1990, Fleischner 1994).

Table 1. Numbers of captures of amphibians and reptiles on untreated and experimental pastures treated with tebuthiuron-only and tebuthiuron + fire at the Cross Timbers Experimental Range, Oklahoma, 1994–1995.

			Treatments		
Category	Common name	Scientific name	Tebuthiuron-only	Tebuthiuron + fire	Control
Frogs/toads	American toad	*Bufo americanus*	6	6	19
	Cricket frog	*Acris crepitans*	5	2	7
	Spotted chorus frog	*Pseudacris clarkii*	0	1	1
	Strecker's chorus frog	*Pseudacris streckeri*	1	0	1
	Great Plains narrowmouth toad	*Gastrophryne olivacea*	7	9	6
	Bullfrog	*Rana catesbeiana*	2	4	1
	Southern leopard frog	*Rana utricularia*	30	16	21
Salamanders	Smallmouth salamander	*Ambystoma texanum*	0	3	0
Total number of amphibians (%)[1]			51 (35.2)	38 (26.2)	56 (38.6)
Turtles	Red-eared slider	*Trachemys scripta*	0	0	1
	Eastern box turtle	*Terrapene carolina*	3	1	3
	Ornate box turtle	*Terrapene ornata*	1	1	0
Total number of turtles (%)[2]			4 (40.0)	2 (20.0)	4 (40.0)
Lizards	Slender glass lizard	*Ophisaurus attenuatus*	1	1	0
	Northern prairie lizard	*Sceloporus undulatus*	3	7	3
	Five-lined skink	*Eumeces fasciatus*	2	7	26
	Great Plains skink	*Eumeces obsoletus*	0	0	1
	Ground skink	*Scincella lateralis*	7	8	12
	Six-lined racerunner	*Cnemidophorus sexlineatus*	5	6	0
Total number of lizards (%)[2]			18 (20.2)	29 (32.6)	42 (47.2)
Snakes	Eastern yellowbelly racer	*Coluber constrictor*	0	4	0
	Ringneck snake	*Diadophis punctatus*	0	2	1
	Eastern hognose snake	*Heterodon platyrhinos*	1	0	1
	Speckled kingsnake	*Lampropeltis getula*	1	0	0
	Coachwhip	*Masticophis flagellum*	2	2	1
	Rough green snake	*Opheodrys aestivus*	0	1	1
	Brown snake	*Storeria dekayi*	1	1	0
	Flathead snake	*Tantilla gracilis*	1	0	0
	Western ribbon snake	*Thamnophis proximus*	1	3	0
	Rough earth snake	*Virginia striatula*	6	12	2
	Smooth earth snake	*Virginia valeriae*	0	1	0
	Copperhead	*Agkistrodon contortrix*	0	0	1
	Timber rattlesnake	*Crotalus horridus*	1	0	1
Total number of snakes (%)[2]			14 (29.2)	26 (54.2)	8 (16.7)
Total number of reptiles (%)[1]			36 (24.5)	57 (38.8)	54 (36.7)
Total number of captures			87	95	110
Total number of species			21	22	20

[1] 2 x 3 chi-square comparison of amphibians and reptiles among treatments = 6.409, 2 df, $P < 0.05$.

[2] 3 x 3 chi-square comparison of turtles, lizards, and snakes among treatments = 14.730, 4 df, $P < 0.01$.

Management Implications

Herbicides and prescribed fire are common range management tools, and we expect to see more rangeland of the Cross Timbers modified in this manner in the future (Boren et al. 1996). Our results suggest that the Cross Timbers can be managed for both cattle and wildlife by providing a mosaic of habitat types (Leslie et al. 1996) with applications of herbicide and prescribed fire in a spatially diverse pattern leaving some areas with unmodified mature upland forest. Application of tebuthiuron followed by prescribed burning is the most profitable practice for managing hardwood forests of the Cross Timbers for cattle grazing (Bernardo and Engle 1990, Bernardo et al. 1992). Applying herbicide and burning treatments in a mosaic can increase carrying capacity of livestock and white-tailed deer and the profitability of livestock and lease hunting under multiple-use objectives in the Cross Timbers (Bernardo et al. 1992). The application scale for herbicide and burning treatments to optimize habitat for livestock and game species likely would be larger than the scale required for herpetofauna. Spot treatments, generally considered by rangeland managers as ill-advised because they lead to overuse by grazing animals, perhaps could be used to enhance herpetofauna habitat under carefully controlled livestock grazing.

No single habitat, derived or not, is universally beneficial to herpetofauna or other wildlife. Herbicide application without fire does not benefit most reptiles, whereas herbicide with fire appears to negatively affect most amphibians. Complete removal of mature oak forest would alter species composition of amphibians and reptiles, and it might cause disappearance of some woodland species [e.g., skinks, (*Eumeces* spp.) and the copperhead (*Agkistrodon contortrix*)]. On a broader scale, native prairies in the south-central Great Plains that are now dominated by eastern redcedar due to decades of fire suppression likely have a less rich herpetofauna compared with more structurally diverse habitats, but even those areas appear to provide important habitat for some species.

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N-alkane as an internal marker for predicting digestibility of forages

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Abstract

Independent digestion trials with 5 forages were conducted to compare n-alkane with indigestible acid-detergent fiber (IADF) as internal markers to predict in vivo dry matter digestibility (digestibility). Forages were mixed grasses from subirrigated meadow (meadow), meadow regrowth (regrowth), native range (range), mature mixed grass hay from meadow, and alfalfa (*Medicago sativa* L.) hay. Meadow, regrowth, and range diets were immature grasses harvested 0.5 hours before feeding. Feces from the meadow hay and alfalfa hay trials were divided to compare freeze drying and oven drying (60°C). All diets were subjected to in vitro fermentation for 0, 48, or 96 hours. N-alkane was separated from samples by 4.5-hour saponification with alcoholic KOH followed by extraction with n-hexane. Indigestible ADF was measured by 96-hour in vitro fermentation followed by ADF extraction. Digestibility estimated by markers was compared with in vivo digestibilities. N-alkane based digestibilities were lower ($P < 0.01$) than in vivo digestibility for all diets. N-alkanes provided higher estimates of digestibilities than IADF for meadow ($P < 0.01$), regrowth ($P = 0.06$), and alfalfa hay ($P = 0.06$), and lower digestibility for meadow hay ($P = 0.02$). Digestibilities calculated using n-alkanes for range tended to be higher ($P = 0.14$) than IADF values. Freeze drying increased ($P<0.01$) the amount of n-alkane extracted from alfalfa hay, but did not affect ($P = 0.1$) the amount extracted from meadow hay. N-alkane disappeared ($P < 0.001$) from residue collected after 48 hours of in vitro fermentation, but no additional disappearance ($P = 0.78$) was evident at 96 hours. Neither marker was completely recoverable, although recovery of n-alkane was higher than indigestible ADF for 4 of the 5 forages tested.

Key Words: indigestible, ADF, hydrocarbon, beef cattle

Resumen

Se condujeron ensayos individuales de digestibilidad con 5 forrajes para comparar el n-alcano con la fibra indigestible ácido-detergente (IADF) como marcadores internos para predecir la digestibilidad in vivo de la materia seca (digestibilidad). Los forrajes evaluados fueron: zacates mezclados de una pradera subirrigada (pradera), rebrote de la pradera (rebrote), pastizal nativo (pastizal), heno de zacates mezclados maduros de la pradera y heno de alfalfa (*Medicago sativa* L.). Las dietas de pradera, rebrote y pastizal consistieron de zacates inmaduros cosechados 0.5 horas antes de ofrecerlos como alimento. Las heces fecales de los ensayos de los henos de pradera y alfalfa se dividieron para comparar el secado por congelamiento y el secado en horno (600 C). Todas las dietas se sometieron a fermentación in vitro por 0, 48 y 96 horas. El n-alcano fue separado de las muestras mediante una saponificación de 4.5 horas con KOH alcohólico seguido por una extracción con n-hexano. La ADF indigestible se midió mediante una fermentación in vitro de 96 horas seguida por la extracción de ADF. La digestibilidad estimada por los marcadores se comparó con las digestibilidades in vivo. En todas las dietas, la estimación de la digestibilidad basada en n-alcano fue menor ($P < 0.01$) que la digestibilidad in vivo. Las estimaciones de digestibilidad obtenidas con n-alcanos fueron mayores que las obtenidas con IDAF, esto para pradera ($P < 0.01$), rebrote ($P = 0.06$) y heno de alfalfa ($P = 0.06$), y menor para heno de pradera ($P = 0.02$). Las digestibilidades del pastizal calculadas usando n-alcano tendieron a ser mayores ($P = 0.14$) que los valores obtenidos con IADF. El secado por congelamiento aumento ($P < 0.01$) la cantidad de n-alcano extraída del heno de alfalfa, pero no afecto ($P = 0.01$) la cantidad extraída del heno de pradera. El n-alcano desapareció ($P < 0.001$) del residuo colectado después de 48 horas de fermentación in vitro, pero no se evidencio una mayor desaparición de n-alcano en la fermentación de 96-horas. Ningún marcador fue completamente recuperable, aunque la recuperación de n-alcano fue mayor que la IADF en 4 de los 5 forrajes evaluados.

In vitro dry matter disappearance and internal markers such as indigestible acid-detergent fiber (IADF) and lignin are common methods for estimating forage digestibility in cattle. However, these methods often fail to accurately predict in vivo digestibility (Galyean et al. 1986). Mayes et al. (1986) proposed that long chained hydrocarbons (n-alkanes) may accurately predict in vivo digestibility.

Naturally occurring n-alkanes found in most pasture species contain odd-numbered carbon chains with 25 to 35 carbon atoms. Because fecal recovery of n-alkanes improves with increasing chain length, tritriacontane ($C_{33}H_{68}$) is commonly used to estimate digestibility (Mayes et al. 1986a). Tritriacontane and pentriacontane ($C_{35}H_{72}$) are not present in some tropical forages (Laredo et al. 1991). However, there is evidence that long chain n-alkanes disappear during gastrointestinal passage (Mayes et al. 1986). Mayes et al. (1988) determined in sheep that a site of disappearance of n-alkanes is from the small intestine. In contrast, with dairy cattle Ohajuruka and Palmquist (1991) estimated that 15% of a ruminally infused synthetic n-alkane marker disappeared in the rumen. To correct for incomplete recovery of n-alkane markers in the feces, Mayes et al (1986) proposed dosing

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animals twice daily with synthetic even-chained n-alkanes. However, for many studies on range or pasture, dosing of synthetic n-alkanes may not be practical. Little is known on how method of drying (i.e., oven vs. freeze drying) affects n-alkane extraction from samples. Objectives of this study were to: 1) identify which n-alkanes were present in sufficient quantities to be used as internal markers for range, meadow and alfalfa, 2) compare the effectiveness of n-alkane with IADF in estimating in vitro and in vivo digestibility when externally dosing an even-chain n-alkane is not practical because of pasture size and animal distribution, 3) determine if n-alkane disappearance occurs in the rumen, and 4) evaluate effects of different drying methods on n-alkane extraction.

Material and Methods

Animals and Feeding

Five yearling steers (body weight = 425 kg ± 13) were housed individually in 3 x 3 m pens for 5 independent digestion trials using immature mixed grasses from subirrigated meadow (meadow), meadow regrowth (regrowth), and native sandhills range (range), mature mixed grass hay from meadow, and alfalfa (*Medicago sativa* L.) hay. Meadow, range, and meadow regrowth trials were conducted in 1995 using vegetative grasses, beginning 1 June, 1 July, and 15 July, respectively, at the Gudmundsen Sandhills Laboratory located 11 km northeast of Whitman, Neb. The meadow hay and alfalfa hay trials were conducted in September 1996 at the West Central Research and Extension Center, North Platte, Neb.

Dominant vegetation for the meadow, meadow regrowth, and meadow hay was 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.). Other common 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).

The forage collected from the range site was dominated by warm-season grasses, including little bluestem [*Schizachyrium scoparium* (Michx.) Nash], prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], sand bluestem (*Andropogon hallii* Hack.), and switchgrass (*Panicum virgatum* L.). Other common species were blue grama [*Bouteloua gracilis*(H.B.K.) Lag. ex Griffiths], hairy grama (*Bouteloua hirsuta* Lag.), sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray], prairie junegrass [*Koeleria pyramidata* (Lam.) Beauv.], needleandthread (*Stipa comata* Trin. & Rupr.), western ragweed (*Ambrosia psilostachya* DC.), Schweinitz flatsedge (*Cyperus schweinitzii* Torr.), and sun sedge (*Carex heliophila* Mack.). More detail of meadow and range vegetation and soils is given by Adams et al. (1998).

Each trial consisted of a 10-day diet adaptation period followed by 5 days of total fecal collection. Each forage was limit-fed twice daily at 1.0% of body weight per feeding with the forage from meadow, meadow regrowth, and range harvested 0.5 hours before feeding. Feed samples were collected and frozen before each feeding. Refusals were collected and frozen before the morning feeding, and feces were collected and frozen twice daily.

Laboratory analysis

Diets, refusals, and feces from each trial were freeze dried and ground in a Wiley Mill to pass through a 1-mm screen. Samples were composited by dry weight across days on an individual animal basis. Feces from the meadow hay and alfalfa hay trials were subsampled and either freeze dried or dried in a forced air oven (60°C) to compare the effect of drying method on n-alkane extraction. Laboratory analyses included dry matter, organic matter (AOAC 1990), and IADF (Berger et al. 1979, Cochran et al. 1986) for all samples and NDF (Van Soest et al. 1991), ADF (Van Soest 1963), crude protein (AOAC 1990), and in vitro dry matter disappearance (Tilley and Terry 1963) using modified procedures as described by Hollingsworth-Jenkins et al. (1996) for the diet samples.

Hentriacontane disappearance in the rumen was examined by using a modified Tilley and Terry (1963) method for in vitro dry matter disappearance. Samples weighing 1.8 g were measured into three , 30-ml polypropylene in vitro tubes in 0.6 g increments, inoculated with a mixture of rumen fluid:McDougall's buffer (McDougall 1948), and incubated in a 39°C water bath for either 48 or 96 hours. The contents from the 3 tubes were filtered through filter paper (Whatman[1] 541), and the residues were combined to form a single sample and saved for later n-alkane analysis.

Alkane Analysis

Subsamples weighing either 1 g for feces or 2 g for forage were placed in a 75-ml tube (fitted with a screwcap and teflon liner) with 0.6 ml of a 1,000 $mg/liter^{-1}$ solution of dotriacontane ($C_{32}H_{66}$) n-hexane as an internal standard. Each tube was then placed in a 90°C water bath to saponify samples for 4.5 hours with 10 ml alcoholic KOH. After saponification, liquid-liquid extraction was performed by adding 7 ml of n-hexane and 2 ml of H_2O, shaking vigorously, centrifuging (1,000xg for 10 min), and transferring the n-hexane layer to a prepared column for solid phase separation. The column was prepared by first placing 2 g of silicic acid per column in a 110°C oven to activate the silicic acid. Then the silicic acid was suspended in solution using 10 ml of n-hexane and placed in an extraction column. The extract eluted from the column was evaporated to dryness, reconstituted with 2 ml of n-hexane, and placed into a glass vial for later analysis using gas chromatography. Ten samples from the meadow, meadow regrowth, and range trials selected randomly were reconstituted with 2 ml of a triacontane ($C_{30}H_{26}$) standard (0.3 mg per ml of n-hexane) to determine the recovery rate of dotriacontane during the extraction procedure.

Calculations and Statistical Analysis

In vivo DMD and estimated values of DMD using IADF and n-alkanes as internal markers were calculated following procedures outlined by Schneider and Flatt (1975). N-alkane concentrations were determined using the following formula with 0.6 mg representing 0.6 ml of a standard solution containing 1.0 mg of dotriacontane per ml of n-hexane:

$$\text{mg of n-alkane/kg sample} = \frac{\text{peak area of alkane}}{\text{peak area of internal standard}} \text{ X } \frac{0.6 \text{ mg x } 100}{\text{sample weight x DM}} \quad \textbf{(1)}$$

Dry matter digestibility coefficients and marker recovery for each trial and drying

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[1] Whatman Labsales, P.O. Box 1359, Hillsboro, Ore. 97123.

methods for the meadow hay and alfalfa hay trials were analyzed as a randomized complete block, with steers as blocks using the General Linear Model Procedure of SAS (1990).

Results

Because the n-alkane, tritriacontane, did not produce any detectable peaks using gas chromatography for the freshly harvested forages, the next smaller, odd-chained n-alkane, hentriacontane ($C_{31}H_{64}$), was used. The recovery of the dotriacontane internal standard averaged 82%. The chemical composition of the 5 diets are given in Table 1. For all 5 diets, digestibility estimates calculated using n-alkane ratio were lower ($P < 0.01$) than in vivo DMD (Table 2). Comparison of digestibilities estimated using the n-alkane ratios and IADF ratios showed that the n-alkane ratio predicted higher DMD for meadow ($P < 0.01$), meadow regrowth ($P = 0.06$), and alfalfa hay ($P = 0.06$), and lower DMD for meadow hay ($P < 0.02$). Forage digestibilities for native range using n-alkane ratio tended to be higher ($P = 0.14$) than IADF ratio values. Indirect comparisons between in vivo digestibility and digestibilities estimated using an n-alkane and IADF showed that for meadow, range, meadow regrowth, and alfalfa hay, n-alkane provided a better estimate of in vivo digestibility. Intake and fecal output estimates are shown in Table 3.

Although statistical comparisons between in vitro dry matter disappearance and the other methods of estimating digestibility were not possible because in vitro methods produce a single estimate that does not account for the variation between animals, in vitro dry matter disappearance appeared to produce estimates of digestibility comparable to the n-alkane ratio method for the immature, freshly harvested forages and higher estimates for the alfalfa and meadow hay.

Fecal recoveries of hentriacontane and IADF are shown in Table 4. While marker recoveries were not consistent across forages, n-alkane recoveries for the forages that were freshly harvested were higher ($P < 0.02$) than IADF recoveries. Both markers had similar recoveries for alfalfa hay ($P = 0.14$), and IADF recovery rate was higher for meadow hay ($P = 0.07$). The amounts of hentriacontane extracted from the meadow hay fecal samples were similar ($P > 0.10$) for freeze drying (0.235 g kg^{-1}) and oven drying (0.240 g kg^{-1}). However, freeze drying increased ($P < 0.01$) the amount of n-alkane extracted from alfalfa hay (0.316 g kg^{-1}) compared with oven drying (0.249 g kg^{-1}).

Hentriacontane amounts found in residues collected by filtration after a 48-hour in vitro fermentation period decreased ($P < 0.001$) over 0.1 g kg^{-1} (Table 5). However, samples incubated for 96 hours produced residues similar ($P = 0.78$) to those produced after 48 hours of incubation. In terms of hentriacontane recovery, an average of 18.8% was recovered for the residues obtained after 48 and 96 hours of incubation.

Table 1. Chemical composition of fresh harvested forage from subirrigated meadow, subirrigated meadow regrowth, native sandhills range, mature hay from subirrigated meadow and alfalfa hay diets.

Diet	Dry matter	Organic matter	NDF	ADF	Crude protein	Hentriacontane
	- - - - - - - -	- - - - - - - -	-(DM, %) - - -	- - - - - - - -	- - - - - - - -	($g\ kg^{-1}$ dm)
Fresh meadow forage harvested in June	96.1	91.4	62.8	33.0	10.3	0.076
Fresh native range forage harvested in July	96.7	93.5	70.0	32.7	11.3	0.081
Fresh meadow regrowth harvested in July	96.4	87.9	63.8	34.0	11.3	0.093
Alfalfa hay	96.2	87.8	54.3	36.3	19.1	0.162
Meadow hay	96.8	90.5	67.1	38.9	7.7	0.175
Standard error of means	0.1	0.1	0.3	0.3	0.3	0.008

Table 2. In vivo, hentricontane, indigestible ADF (IADF), and in vitro dry matter disappearance (IVOMD) calculations of apparent dry matter digestibiliy estimates of fresh harvested forage from subirrigated meadow, subirrigated meadow regrowth and native sandhills range, mature hay from subirrigated meadow, and alfalfa hay.

Diet	In vivo	Hentriacontane	p-value[a]	IADF	p-value[b]	In vitro DMD
	- - - - - - - -	- - - - - - - -	-(DM, %) - - -	- - - - - - - -	- - - - - - - -	- - - - - - - -
Fresh meadow forage harvested in June	67.5	62.9	0.004	57.2	0.001	61.5
Fresh native range forage harvested in July	70.5	61.8	0.004	58.3	0.14	58.3
Fresh meadow regrowth harvested in July	70.7	57.5	0.002	51.0	0.06	57.8
Alfalfa hay	60.2	50.0	0.01	43.8	0.06	58.2
Meadow hay	55.1	36.2	0.0001	42.6	0.01	47.1
Standard error of means	2.9	4.5		2.7		0.3

[a]Comparison between in vivo digestibility and digestibility predicted using hentriacontane.
[b]Comparison between digestibility predicted using hentriacontane and IADF.

Table 3. Fecal output of dry matter, actual dry matter intake, hentriacontane intake and dry matter intake predicted by hentriacontane used to calculate digestibilities[a].

	Intake		Fecal Output	
Diet	Hentriacontane predicted dry matter	Actual dry matter	Hentriacontane	Dry matter
	($kg\ day^{-1}$)	($kg\ day^{-1}$)	($g\ day^{-1}$)	($kg\ day^{-1}$)
Fresh meadow forage harvested in June	4.8	5.5	0.36	1.8
Fresh native range forage harvested in July	5.3	7.0	0.42	2.0
Fresh meadow regrowth harvested in July	5.8	8.5	0.50	2.4
Alfalfa hay	6.1	7.5	1.05	3.0
Meadow hay	5.6	8.0	1.09	3.6

[a]Data in table is for reader information, no statistics performed.

Table 4. Recoveries of indigestable acid detergent fiber (IADF) and hentriacontane from the feces of steers fed fresh harvested forage from subirrigated meadow, subirrigated meadow regrowth, native sandhills range, mature hay from subirrigated meadow, and alfalfa hay.

Diet	Alkane	IADF	p-value
Fresh meadow forage harvested in June	87.2	75.6	0.01
Fresh native range forage harvested in July	76.0	69.9	0.002
Fresh meadow regrowth harvested in July	67.6	57.9	0.02
Alfalfa hay	80.4	71.1	0.14
Meadow hay	70.5	78.4	0.07
Standard error of means	5.2	5.2	

Discussion and Conclusions

Although n-alkane recovery increases with increasing chain length (Mayes et al. 1986), hentriacontane was selected as the internal marker to estimate DMD because tritriacontane was not detected in the freshly harvested forages. The inability of tritriacontane to be detected in this study was attributed to lack of column sensitivity where n-alkane amounts less than 20 mg kg^{-1} are not detectable. This agrees with Casson et al. (1990) who suggested that odd chain n-alkane concentrations should be at least 50 mg kg^{-1} DM for accurate prediction of DMD. Additionally, Laredo et al. (1991) concluded that for some tropical forages tritriacontane was not present in sufficient quantity for intake to be estimated using dotriacontane: tritriacontane ratios.

Although hentriacontane consistently underestimated the in vivo digestibilities for all forages examined, it offered an improvement over digestibilities estimated with IADF for freshly harvested forages. The differences between digestibilities estimated with hentriacontane and IADF can be explained by examining fecal recoveries. An exception is that hentriacontane and IADF had similar fecal recoveries but different digestibility estimates for alfalfa hay. Fecal recoveries of hentriacontane for freshly harvested range and meadow forages were lower than those reported for hays. In contrast to freshly harvested forages, fecal recovery of hentriacontane for alfalfa and meadow hays were within ranges reported for other hays (Dove et al. 1989, Ohajuruka and Palmquist 1991). Differences between digestibilities predicted using hentriacontane and in vitro dry matter disappearance were small for meadow, meadow regrowth, and range.

Cochran et al. (1986) reported that fecal IADF recoveries from animals grazing immature forages are lower than for animals fed mature forages. However, hentriacontane recoveries appeared to be greater for the studies using freshly harvested forage. Additionally, Owens and Hanson (1992) stress that markers be chemically discrete with a specific method of analysis. When comparing the 2 markers, one benefit n-alkanes have over IADF is that n-alkanes meet this requirement, because their composition remains the same over a variety of forages. Another concern is IADF can have additional sources of error due to variations found among donor animals and handling of innoculum (Horton et al. 1980, Fahey and Berger 1988).

Replacing freeze-drying of fecal samples with oven drying would decrease the amount of drying time and increase the number of samples handled. While hentriacontane amounts in feces from steers fed meadow hay were not affected by drying method, oven drying reduced the amount of hentriacontane recovered from the feces of steers on an alfalfa hay diet by 20%. In a review of n-alkanes as markers, Dove and Mayes (1991) indicated drying method affects herbage n-alkane concentrations and that further research was needed to determine the effect of drying method on n-alkane concentrations in feces. During oven drying, the high temperatures may subject hentriacontane to either marker degradation or chemical reactions that make complete extraction difficult. Because hentriacontane concentrations vary with drying methods in both forage and feces, it is recommended that samples should be freeze dried for n-alkane analysis.

In vitro fermentation was used to determine if hentriacontane was degraded in the rumen. Filter paper rated to retain particles greater than 25µm was used to isolate the residue since Mayes et al. (1988) indicated that n-alkanes are associated with the particulate phase of digesta. Initial examination of the results indicated that hentriacontane is highly degraded in the rumen. However, the in vivo studies showed an average total tract recovery of 76.3%. Hentriacontane recovery in the residue left after in vitro fermentation was approximately 60 percentage units lower. While in vitro fermentation could degrade hentriacontane to a greater extent than gastrointestinal passage, large differences are unlikely. Because the hentriacontane amounts found in the residues remained unchanged between the 48-hour and 96-hour incubation times, we propose that the low recovery was due to association of the marker with the liquid phase, which was lost during filtration rather than degradation as suggested by Mayes et al. (1988). Further examination is recommended to determine which digesta phase hentriacontane associates with during gastrointestinal passage.

Locating the site of n-alkane disappearance is important when evaluating their use as potential internal markers. If disappearance is isolated to the lower tract, the marker may be used to estimate forage dry matter digestibility in the rumen. Faichney (1975) indicated that a marker needs to be intimately associated with the material it is marking. If n-alkanes are to be reliable as internal markers, it is important that the digesta phase association of n-alkanes be determined.

We concluded that digestibility was underestimated by n-alkanes and hentriacontane recovery was not consistent across forages. Freeze-drying should be used to dry fecal samples for n-alkane analysis. In grazing situations where internal markers are desired, naturally occurring n-alkanes may be a more reliable alternative than IADF for estimating DMD of immature forages.

Table 5. Hentriacontane in residue after 0, 48, and 96 hours of in vitro fermentation.

Time	Hentriacontane g/kg	SE[c]	p-value
Control, 0 hours	.184	61.8	
48 hours	.031	14.9	.0002[a]
96 hours	.038	10.9	.78[b]

[a] Comparison of control with 48-hour fermentation.
[b] Comparison of 48- and 96-hour fermentation.
[c] Standard error of means.

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Spatial distribution of economic change from Idaho ranches

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Abstract

Economic impacts from federal grazing policy frequently figure in public debate about federal land in the American West. The spatial and economic level of aggregation at which impacts are estimated is a significant issue, both politically and methodologically. We present an input/output model incorporating spatial detail at the sub-county level. Seven community-level economies are portrayed and contrasted with the aggregated 2-county economy. Our argument is that economic dependencies, notably dependencies on the range cattle industry, differ significantly between communities and that this differentiation is completely masked when the 2 county area is examined as 1 economy. The sub-county breakdown illustrates the degree to which communities are differentially vulnerable to reduced cattle prices and a reduction in available federal forage.

Key Words: Public land, grazing, input/output models

Resumen

Los impactos económicos de las políticas federales de apacentamiento frecuentemente figuran en los debates públicos acerca de las tierras federales del oeste Americano. El nivel de agregación espacial y económico al cual los impactos son estimados es un problema significativo, tanto político como metodológico. Aquí presentamos un modelo de entrada/salida en el que se incorpora detalles espaciales al nivel de sub-municipio. Siete economías a nivel de comunidad se describieron y contrastaron con el agregado de 2 economías de municipio. Nuestro argumento es que las dependencias económicas, dependencias notablemente en la industria ganadera de pastizal, difieren significativamente entre comunidades, y que esta diferenciación es completamente enmascarada cuando las 2 áreas municipales se examinan como una sola economía. La separación en sub-municipios ilustra el grado al cual las comunidades son diferencialmente vulnerables a los precios reducidos del ganado y a una reducción del forraje federal disponible.

The importance of the range cattle industry to communities in the western U.S. is a frequent topic for local people, policy makers, federal land managers, and the general discussion of public land management. The economic impact of changes in grazing policies on public lands continues to be an important issue. Typically, overall economic impacts are evaluated either with statistics about employment or earnings derived from an industry (Power 1996), with regional economic techniques (Lacy and Johnson 1990), or with econometrics (LaFrance and Watts 1995). Other studies focus on the impact of changes in grazing fees or other land management issues (Torell and Drummond 1997, Bartlett et al. 1979, Cook et al. 1980, Anderson et al. 1993, Torell and Doll 1991, Lambert 1987, Rowan and White 1994). All approaches to estimating economic impacts have limitations. Most approaches can only focus on ranches as a group or on a large region taken as a single area. Given this, a notable limitation of traditional impact studies is the absence of spatial economic detail. Estimation of local economic impacts on communities and their spatial distribution are beyond the capabilities of most methodologies and approaches.

The level of spatial and economic aggregation used to assess policy changes is a significant problem for impact assessment. It is not simply a methodological choice to use a state or county estimate, for example. The choice has implications for policy in that an impact may be very large for 1 county, but negligible for the state as a whole. Thus, how we approach aggregation frames the policy discussion about the estimated economic consequences of different policy choices. Even county level analysis can mask significant differentiation between community-level economies and this differentiation has direct implications for evaluating the range cattle industry and federal grazing policies.

We use input/output techniques to evaluate the spatial distribution of economic impacts from public land grazing across 7 communities in a 2 county area of central Idaho. Examining the importance of ranching at the 2 county, aggregate level portrays the local economy very differently from the disaggregated community economies of the area. We use this model to illustrate how economic change will be distributed across 7 communities when cattle prices decline or available federal grazing animal unit months (AUMs) are reduced.

Materials and Methods

Custer and Lemhi Counties in central Idaho are dominated by federal lands: both counties contain over 90% public land. The U.S. Forest Service and Bureau of Land Management dominate the management of these lands. Local economies have historically depended on ranching, recreation, government, mining, and some timber.

We conducted over 160 semi-structured household interviews for a parallel social assessment. Respondents in these interviews

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helped define numerous assumptions used in the economic models. Respondents defined the trade "hierarchy" used in the economic model. In such a hierarchy, some communities "trade up" to a central trade community from which money "leaks" to larger, outside trade centers. To accomplish this, we asked both personal interview and business interview respondents to describe the spatial pattern of their purchases. For example, they broke purchases down into local and non-local categories. We added further detail by asking which purchases were made in which local communities. This information was used to build the local trade hierarchy. In central Idaho, it is reasonable to assume that Salmon is a dominant trade area. The Tendoy/Leadore, Pahsimeroi, Northfork, and, to a lesser extent, Challis communities are connected to the trade center at Salmon. The Mackay area has sufficient trade with Challis to warrant inclusion in the trade hierarchy. The Stanley Basin, on the other hand, is in Custer County but has less trade in the 2 county area. Its primary economic trade with the rest of the county involves fuel, transportation services, and outfitters and guides.

Respondents also assisted in defining functional economic areas. We disaggregated the 2 counties into 7 functional economic areas closely resembling the Census areas from the 1990 Census of Population[1]. Figure 1 outlines these areas. Census areas are usually defined in rural areas by physical boundaries, political boundaries, or long distances between population centers. The functional areas described by respondents matched very well with the areas used in the Census.

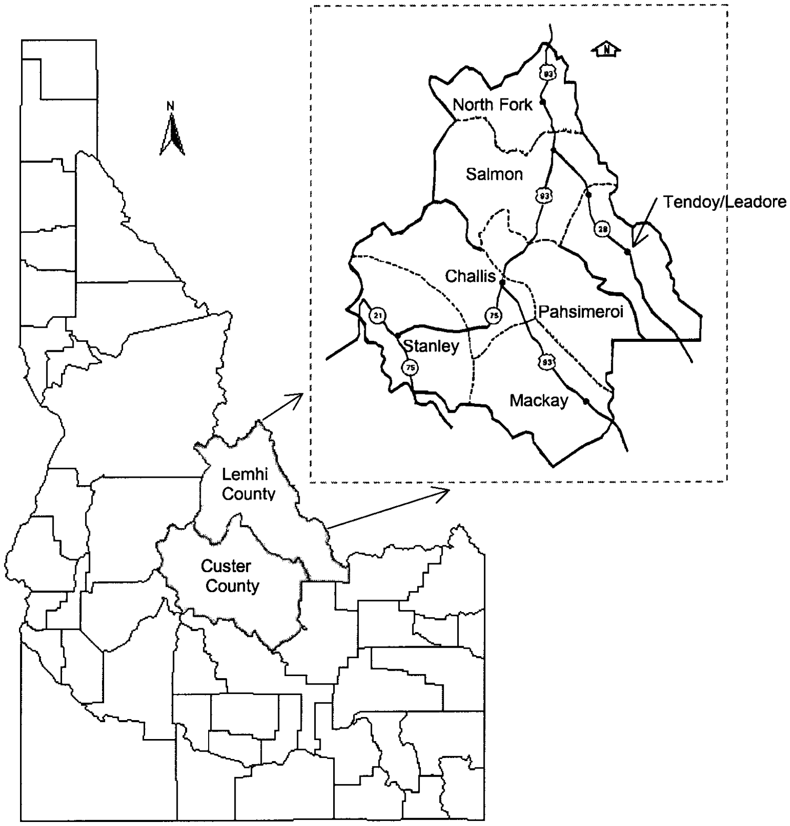

Fig. 1. Central Idaho study area.

The primary economic sector examined in this paper is agriculture and this is almost exclusively cow/calf ranching. [A small dairy sector around Salmon supplies milk to a small cheese plant there.] Ranch sector data is derived from actual ranch records of 15 enterprises in the 2 county area using the FINPACK program (FINPACK 1993). These 15 enterprises are not a sample. They represent all local ranches willing to provide the very detailed financial records necessary to accurately estimate and evaluate ranch costs and returns using FINPACK. These data are used to construct a detailed ranch sector in the I/O model. According to the 1992 Census of Agriculture 316 ranches in this area are commercially viable and 217 of these operations hold federal grazing permits. A small percentage of land is privately owned. Our interviews with local ranchers indicated that, in the short run, few if any private forage options exist for federal permit holders. Ranchers indicated that in the past they had more options than they do currently. When feasible, nearby ranches could be purchased for additional forage and federal AUMs. The current appreciation of ranch land for non-agricultural uses mitigates this strategy. Many respondents had focused their efforts in recent years on upgrading their agronomic and irrigation practices to raise forage yields on their private ground. As an option, this was seen as quickly reaching its technical limits. Purchasing hay or grazing forage outside the area was judged to be unrealistic even in the long run. In the end, we concluded that if federal AUMs are reduced, herd size must be reduced or management intensified on existing private forage while searching for other forage sources and opportunities[2].

For all other economic sectors, telephone books and local interviews were used to identify businesses in each community. We attempted to survey all known local businesses using drop off/pick up and personal interview methods. Respondents supplied information about their employment, sales, where they purchased inputs, and to whom they make sales, by sector. Over 250 businesses were surveyed. The data were used along with employment totals from state and federal sources to build the final model. Finally, we derived unearned income estimates from household income breakdowns for the respective Census areas. These estimates include Social Security payments, dividends, interest, rents, pensions, income support, Medicare, and similar payments. The base year for this model was 1991.

We derived model parameters from interviews with ranchers and businesses in each area. These interviews provided insights into trade patterns, economic exports, income sources, functional economic areas, and reactions to possible changes in the ranch economy. The accuracy and legitimacy of this model rests on these extensive interviews which allowed us to make the fewest assumptions possible.

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[1] For a technical description of this model and its theoretical basis, see Robison (1997).

[2] More intensive management of existing private forage on the part of federal permit holders might make up for some of the AUM reduction, but this factor is almost impossible to estimate and will not be evaluated here..

Table 1: Custer and Lehmi combined economy, and income summary, 1991.

	Earnings		Employment	
	($1,000's)		(Jobs)	
Agriculture	21,254	21.8%	1096	24.2%
Mining	27,887	28.6%	850	18.7%
Timber	8,543	8.8%	314	6.9%
Visitors	13,725	14.1%	1030	22.7%
Linked to RUI[1]	5,387	5.5%	228	5.0%
Government				
S & L Local	8,861	9.1%	377	8.3%
Federal	9,906	10.2%	562	12.4%
Other	2,032	2.1%	78	1.7%
Total Earnings	97,595	100.0%	4535	100.0%

Two–County Income Summary

	($1,000's)	%
Earnings Total	97,595	78.6%
RUI1	26,540	21.4%
Total	124,135	100.0%

[1] RUI is residents' unearned income. This is all unearned income such as dividends, transfer payments, rents, pensions, income support payments, etc. or income that is unrelated to employment. Earnings and income in this category represent secondary economic activity attributable to the expenditure of residents' unearned income.

Economy of Custer and Lemhi Counties

Table 1 displays the combined economy and income summary of Custer and Lemhi counties. The economy appears most dependent on agriculture, mining, government and visitors for its earnings and employment. It is important to note that about 21% of total income comes from residents unearned income (RUI), which in turn generates about 5% of the total economic activity. The low percent of economic activity related to RUI is derived from the its relation to economic activity. Unlike most sectors, unearned income does not generate direct employment or sales. It is spent as household expenditure, and therefore its impact is limited to a few sectors. Visitors account for about 14% of earnings, but almost 23% of the jobs in the 2 county area. Low wages and seasonal employment account for this disparity.

The economies of the 7 communities are presented in Tables 2, 3, and 4. Table 2 presents earnings and Table 3 presents employment, by sector, for each community. Table 4 presents a breakdown of earned and unearned income for each community. Salmon is the county seat of Lemhi County and the trade center for the 2 county region. The government accounts for over 24% of the earnings due to a BLM District office, a U.S. Forest Service supervisor's office, and state and local government including the school districts. Visitors account for almost a quarter of all jobs, but less than 20% of the earnings. Northfork is heavily reliant on visitors who account for 43% of earnings and 63% of employment. At the same time, over 50% of their income is unearned. This situation is not reflected in the local economy because Northfork has few services or retail establishments where local people can spend that income. They must drive to Salmon to buy most goods and services. Wholesale trade and fuel come to North Fork from Salmon to supply goods that are sold there. This is an example of how Salmon serves as a trade center.

The economy of Tendoy/Leadore is clearly dominated by agriculture. The same situation holds for the Pahsimeroi Valley. Over 85% of earnings in Tendoy/Leadore, and 96% of the earnings in the Pahsimeroi Valley are derived from ranching. These levels of dependence are extremely high. They also represent extreme departures from the local economy depicted at the 2 county level of aggregation. Note also that almost 44% of the income in the Pahsimeroi Valley comes from unearned income, income unrelated to earnings. While the earnings of people in the valley are dependent on ranching, almost half of the personal income has nothing to do with ranches. This is partially an artifact of Census aggregation techniques. The Patterson Census area includes a small subdivision on the Salmon River with a largely retired population. This accounts for the high proportion of unearned income. Again, people travel to Salmon or Challis for household purchases so the contribution of this income to their local economy is minimal. A high dependence on mining holds for Challis. Almost 69% of earnings in that area are derived from mining activities. These payrolls push the percentage of total income from earnings to well over 90%. The economy of the Stanley area is similar, but the dependence instead is on visitors. Finally, the economy of Mackay illustrates another situation. Ranching is extremely important to this area. At the same time, resident's unearned

Table 2. Earnings in 7 communities in Custer and Lemhi Counties, 1991.

	EARNINGS													
	Salmon		Northfork		Tendoy–Leadore		Pahsimeroi		Challis		Stanley		Mackay	
	($1000)	(%)	($1000)	(%)	($1000)	(%)	($1000)	(%)	($1000)	(%)	($1000)	(%)	($1000)	(%)
Agriculture	7,126	15.8	19	1.0	4,089	85.4	2823	96.5	3194	10.0			4003	49.8
Mining	5,660	12.5							22001	68.8			226	2.8
Timber	7,866	17.4	75	3.9					410	1.3			192	2.4
Visitors	8,886	19.7	838	43.7	93	1.9%	16	0.5	1587	5.0	2002	72.3	303	3.8
Linked to ROI	3,564	7.9	56	2.9	53	1.1%	24	0.8	729	2.3	22	0.8	939	11.7
Government														
S & L Local	5,495	12.2	216	11.3	305	6.4%	39	1.3	1644	5.1	197	7.1	965	12.0
Federal	5,635	12.5	709	36.9	245	5.1%	24	0.8	1656	5.2	497	17.9	1140	14.2
Other	935	2.1	6	0.3	3	0.1%			765	2.4	50	1.8	273	3.4
Earnings Total	45,167	100.0	1,919	100.0	4,788	100.0%	2926	100.0	31987	100.0	2769	100.0	8042	100.0

Table 3. Employment in 7 communities in Custer and Lemhi Counties, 1991.

	EARNINGS													
	Salmon		Northfork		Tendoy–Leadore		Pahsimeroi		Challis		Stanley		Mackay	
	(Jobs)	(%)	(Jobs)	(%)	(Jobs)	(%)	(Jobs)	(%)	(Jobs)	(%)	(Jobs)	(%)	(Jobs)	(%)
Agriculture	522	22.7	5	2.8	139	76.8	68	84.0	157	13.1			205	50.7
Mining	181	7.9							664	55.4			5	1.2
Timber	293	12.7	3	1.7					12	1.0			6	1.5
Visitors	572	24.8	112	63.6	11	6.1	7	8.6	143	11.9	151	79.1	34	8.4
Linked to ROI	150	6.5	4	2.3	3	1.7	2	2.5	32	2.7	1	0.5	36	8.9
Government														0.0
S & L Local	234	10.2	9	5.1	13	7.2	2	2.5	70	5.8	8	4.2	41	10.1
Federal	309	13.4	43	24.4	15	8.3	2	2.5	97	8.1	30	15.7	66	16.3
Other	42	1.8	0	0.0					24	2.0	1	0.5	11	2.7
Employment Total	2303	100.0	176	100.0	181	100.0	81	100.0	1199	100.0	191	100.0	404	100.0

income accounts for about 35% of the total income and generates enough secondary activity to account for well over 12% of the earnings. This situation is mostly due to the number of care facilities for the elderly located in Mackay. This draws unearned income in the form of Medicaid, Social Security and pensions into the economy, and a large portion of it is spent in these care facilities. Finally, employees of the Idaho National Engineering Laboratory near Idaho Falls also live in Mackay, accounting for a higher proportion of federal government earnings.

The economic structure of these 7 communities differs greatly from that of the 2 county aggregate area. Examined at the aggregate level, the economy of this area appears balanced, as does the economy of Salmon, its major trade center. However, extreme departures from this economic structure are the dependence of Tendoy/Leadore and the Pahsimeroi Valley on ranching, the role of mining in the economy of Challis, and the dependence of the Stanley Basin on visitors and tourism. The spatial distribution of economic change in this area is now examined with respect to the ranching sector.

Spatial Distribution of Economic Impacts

Significant changes to the ranching sector in Custer and Lemhi Counties will clearly affect these 7 communities in different ways. To illustrate this spatial distribution of effects, the input/output model is used to examine 2 scenarios, 1 real and 1 hypothetical. First, we examine the impact of the decline in cattle prices from 1991 to 1996. This serves as an example of the straightforward economic fluctuation of a cattle cycle that affects community economies. Second, we examine a hypothetical reduction in available AUM's on federal range. This serves as an example of a public policy impact that, while hypothetical, is commonly discussed and for which impacts are often estimated.

Reduced Cattle Prices: FINPACK data indicated that total revenue per cow in Custer and Lemhi counties averaged $508 in 1991. By 1996, this was reduced to $398 per cow, or a 21.7% drop in per cow revenue[3]. We do not expect ranchers to reduce herd size significantly in response to lower prices. Their proprietor's income is reduced and their options include postponing household purchases, or reducing the overall household draw from ranch revenues. We evaluate the reduced income by reducing household consumption. The implication is that herd size and associated costs remain fixed.

The total impact of this reduction in price on the 2 county area and the 7 communities is presented in Table 5. Sales, earnings and employment in the 2 county area each fall about 2%. The distribution of these impacts differs among communities. These differences depend, largely, on primary versus secondary impacts. North Fork has few ranches, and loses little. The Pahsimeroi Valley and Tendoy/Leadore experience different effects. The Pahsimeroi area has few establishments at which ranch households can spend money. Hence, the impacts presented in Table 5 are almost exclusively direct impacts. In terms of sales and earnings, the Mackay economy is hit hardest. Ranches in this area can trade for household goods in Mackay to a greater extent than the more ranch-dependent areas of Pahsimeroi and Tendoy/Leadore. Challis is dominated by mining and this dilutes the overall impact of falling cattle prices on the local economy. In addition, these areas trade with Salmon. Salmon therefore loses sales, earnings and jobs from direct impacts on its ranching sector. It also derives secondary impacts from lost regional trade. However, the overall impact represents a small percentage due to the relative size and diversity of the Salmon economy.

Reduced federal AUMs: The recovery of endangered fish species is an important issue in Custer and Lemhi Counties. Frequently, recovery plans in this area include proposals to reduce grazing near riparian fish habitat on both public and

Table 4. Community income summary for 7 communities in Custer and Lemhi Counties, 1991.

	Total Earnings		RUI		Total Income
	($1000)	(%)	($1000)	(%)	($1000)
Salmon	45,167	77.3	13,298	22.7	58,465
Northfork	1,919	49.6	1,952	50.4	3,871
Tendoy–Leadore	4,788	85.3	826	14.7	5,614
Pahsimeroi	2,926	56.3	2,273	43.7	5,199
Challis	31,987	90.9	3,207	9.1	35,194
Stanley	2,769	81.9	611	18.1	3,380
Mackay	8,042	64.8	4,373	35.2	12,415

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[3] Ranchers might use the futures market to reduce price risk. Our experience, however, is that this excellent option is rarely utilized.

Table 5. Impacts on sales, earnings and employment of drop in cattle prices, 1991 to 1996.

	CHANGE					
	Sales		Earnings		Employment	
	($1,000)	(%)	($1,000)	(%)	(Jobs)	(%)
CHALLIS	$(2,059)	–1.8	$(801)	–2.5	(39)	–3.2
Stanley	$ –	0.0	$ –	0.0	0	0.0
Mackay	$(1,225)	–4.7	$ (246)	–3.1	(9)	–2.3
Pahsimeroi	$(45)	–0.6	$ (18)	–0.6%	(1)	–1.6
SALMON	$ (1,837)	–1.5	$ (745)	–1.6%	(33)	–1.4
Tendoy–Leadore	$(280)	–2.5	$ (113)	–2.3	(6)	–3.4
North Fork	$ (1)	0.0	$ (0)	0.0	(0)	0.0
2 *County Change*	$ (5,447)	–1.9	$ (1,923)	–2.0	(89)	–2.0

private land. The National Marine Fisheries Service (NMFS) directs recovery efforts in this region for endangered and threatened salmon species. In the delineation of critical habitat, NMFS has suggested that salmon require a 25% reduction in grazing on federal public lands in this area (Huppert et al. 1992 p.3–82 [citing Haynes et al. 1992]). Other similar proposals to reduce grazing on public lands are common throughout the West. Thus, a common policy question is the economic impact such reductions will have on ranchers and rural communities. We model a 25% reduction in federal grazing and estimate how these impacts would be distributed across the 7 community area.

Table 6. Available AUMs, Custer and Lemhi Counties, 1991.[1]

	Custer[2]	Lemhi[2]	Total	Total
Federal AUMs				(%)
USFS			113,716	14.7
BLM			107,570	14.0
Total Federal AUMs			221,286	28.7
Private Pasture AUMs			243,700	31.6
Hay AUMs			306,067	39.7
Total Feed AUMs	305,322	465,731	771,053	100.0

[1] Source: Census of Agriculture (1992).

[2] These AUMs cannot be disaggregated. Ranchers have permits in both counties, the Challis National Forest is in both, and the county line splits the Pahsimeroi Valley.

The available AUMs, both private and federal, are presented in Table 6. Federal AUMs account for over one quarter of all AUMs in the 2 county area. Private pasture accounts for another third of the AUMs. Private land is very limited in these counties and rancher interviews indicate that virtually no additional private pasture is available to compensate for lost federal AUMs in the short run. To estimate the changes in sales, earnings and employment from a 25% reduction in all federal AUMs in the 2 counties, we estimate the corresponding reduction in the cow herd and the resulting drop in ranch revenue.

There were 221,286 federal AUMs in Custer and Lemhi Counties in 1991. A 25% reduction would be a loss of 55,322 AUMs. Data from FINPACK indicate that 13.1 AUMs are required per cow per year (7.9 pasture and 5.2 hay). With the absence of additional private pasture, a loss of 55,322 AUMs results in an estimated 2 county herd reduction of 4,223 cows (7.4%). Though not ideal, the most reasonable way to estimate the impact of this loss is to distribute the herd reduction proportionally across the seven areas defined in the model. Table 7 presents baseline and reduced cow herd numbers and cow revenues and reflects a 7.4% reduction in cow herd for each area. The economic impact of this reduction in AUMs and revenues is presented in Table 8. The impact on the overall economy is small, less than 2% of sales, earnings and employment. Even in those areas highly dependent on ranching, the losses in sales, earnings and employment are roughly in the 5% to 7% range. The impact on any single ranch operation of a loss in federal AUMs might be enormous, depending on the flexibility of its nonfederal forage base and other factors. Nonetheless, the overall impact on each community of a 25% loss of federal grazing ranges from negligible to just over 7% of economic activity, and the magnitude of the impact is a function of the economic dependence on ranching.

Ideally, the actual AUM reductions would be enumerated by ranch and aggregated in each community area. This would shift the spatial distribution of the cuts to an unknown degree, and result in a different spatial pattern of impacts. However, current discussions about endangered species recovery often include area-wide reductions in grazing and/or forage utilization and cross federal agency jurisdictions and county boundaries. The assumption that all areas will have a proportional AUM reduction is reasonable.

Conclusions

An input/output model of 7 communities in a 2 county area of central Idaho was described. This model incorporates intercommunity trade and the spatial detail of the local economies. The important result is the degree to which local economies differ from the aggregate 2 county economy. To illustrate this finding, the model was used to evaluate 2 changes in the local ranching industry: the fall in cattle prices from 1991 to 1996, and a 25% reduction in available federal grazing AUMs. The spatial distribution of those changes indicated that communities highly dependent

Table 7. Cow herd distribution and revenues before and after 25% reduction in federal AUMs, 1991.

	Baseline Cows	Baseline Revenues	Proportional Herd Reduction	Proportional Revenue Reduction
	(Number)	($1,000)	(Number)	($1,000)
Mackay	9,370	$ 4,760	696	$ (354)
Pahsimeroi	12,250	$ 6,223	910	$ (462)
Challis	8,500	$ 4,318	631	$ (321)
Tendoy/Leadore	14,545	$ 7,389	1,080	$ (549)
Northfork	75	$ 38	6	$ (3)
Salmon	12,120	$ 6,157	900	$ (457)
Stanley	0	$ –	0	$ –
Total	56,860	$ 28,885	4,223	$ (2,145)

Table 8. Impacts on sales, earnings and employment 25% reduction in federal AUM's, 1991.

	CHANGE					
	Sales		Earnings		Employment	
	($1,000)	(%)	($1,000)	(%)	Jobs	(%)
CHALLIS	–517	–0.5%	–194	–0.6%	10	–0.8%
Stanley	0	0.0%	0	0.0%	0	0.0%
Mackay	–676	–2.6%	–210	–2.6%	11	–2.7%
Pahsimeroi	–521	–7.3%	–214	–7.3%	5	–6.4%
SALMON	–1,000	–0.8%	–389	–0.9%	31	–1.4%
Tendoy–Leadore	–668	–6.0%	–273	–5.7%	9	–4.9%
North Fork	–3	–0.1%	–1	–0.1%	0	–0.2%
2 County Change	–3,385	–1.2%	–1,281	–1.3%	–66	–1.5%

on ranching experience greater overall economic impact than do communities with more diverse economies, or those highly dependent on other industries such as tourism or mining. This situation is not surprising yet it is overlooked in most public policy assessments.

There are larger, more normative policy implications that can be drawn from this research. First, if the impact of eliminating all public land grazing in Custer and Lemhi counties is evaluated at the level of the Idaho state economy, it is probably negligible. The impact of a 25% reduction in AUMs in those counties appeared to be negligible on the 2-county area as a whole, but did have differential impact on individual communities. Nonetheless, the decision to evaluate the impacts of a public policy at the state level implicitly chooses to ignore local impacts. Moreover, economic changes from different sources can produce cumulative impacts greater for some economies than others. The model presented here forces recognition that local impacts often differ greatly from aggregate impacts. The level of analysis in evaluating grazing policies is a vital issue in the overall public debate.

Second, changing cattle prices affect local economies differently than a reduction in AUMs. We assume that ranchers reduce household consumption when prices fall, but maintain production expenditures, at least in the short run. Reductions in AUMs require overall production in the area to be reduced in addition to contractions in household consumption. In the long run, a reduction in AUMs creates a demand for additional forage in an area where private land is both scarce and high priced. Thus, management flexibility greatly determines how well ranchers can respond to change. Over time, ranchers respond to fewer AUMs via management options and this produces a proportionally larger impact on local economies than a short-term price reduction. To illustrate this, a 21.7% drop in prices results in a 21.7% reduction in revenues, and reduces economic activity by about 2% [Table 5]. The loss of 25% of AUMs reduces herd size and associated revenues by about 7.4% [Table 7], reducing economic activity by about 1-1.5% [Table 8]. The overall impact of the AUM loss is proportionally greater than the impact of the price drop.

These findings have implications for modeling efforts addressing public land policy in general. As we show, the structure of local economies can be very different. Many of the policy options frequently offered to ease the economic transition of rural communities to less dependence on traditional industries fail to account for these very different local economies. Some argue that growth in the services and recreation sectors and in single proprietorships not dependent on local resources (so-called “lone eagles”) is the best future for the west (Power 1996, Rasker 1993). These sectors can be very important to rural communities, particularly recreation. However, their economic impact depends on the structure of the local economy. In this study, areas like Challis would benefit differently from an expanded recreation sector than would the Tendoy/Leadore area. A basic economic infrastructure exists to capture recreation dollars in Challis, but is almost negligible in Tendoy/Leadore. Moreover, the relationship between earnings and employment in this model reflects the low pay and seasonal nature of many jobs in the service and recreation sectors. These issues are often ignored when the economic future of rural communities in the west is discussed.

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Supplementation of yearling steers grazing Northern Great Plains rangelands

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Abstract

Growing yearling steers on summer rangelands as part of a cow-calf-yearling operation would allow producers to maximize forage utilization, and selling yearling steers when forage was in short supply would minimize potential genetic losses in the cow herd. A series of summer supplementation and intake studies were conducted from 1988–1992 to determine if weight gains of grazing yearling steers could be increased by supplemental energy (ground barley), phosphorus (P), or crude protein. Studies were conducted at 2 locations on pastures of approximately 51 ha each, which contained quite different mixtures of forage species. Forage P, crude protein and IVDOM levels were monitored throughout the grazing season. Supplementation results varied among years and between locations. There were significant ($P < 0.14$) location by treatment interactions in 1989 and 1990 because steers at the WEST location tended to respond more to supplementation than steers at the EAST location, but EAST location steers had the highest rates of gain. Providing supplements at gradually increasing rates produced results comparable to supplementing at a constant rate all summer. Supplemental crude protein showed no significant benefit, but crude protein levels in pasture forage were generally above steer requirements. Weight gains averaged over all 5 years were greater ($P < 0.05$) for steers supplemented with barley or barley and P, compared to unsupplemented control steers. The response to supplementation should be beneficial most years, but results may vary with the quantity and quality of available forage.

Key Words: Dry matter intake, forage crude protein, forage phosphorus, ground barley

Resumen

El desarrollar novillos en pastizales de verano como parte del sistema vaca-becerro-novillo podría permitir a los productores maximizar la utilización de forraje y vender los novillos cuando el forraje es escaso y minimizar las perdidas genéticas potenciales en el hato de vacas. De 1988 a 1992 se condujo una serie de estudios de consumo y suplementación de verano para determinar si las ganancias de peso de novillos en apacentamiento podrían ser incrementadas por la suplementación energética (cebada molida), de fósoforo (P) o de proteína cruda (PC). Los estudios se condujeron en 2 localidades en potreros de aproximadamente 51 ha cada uno, los cuales contenían mezclas de especies forrajeras muy diferentes. El contenido de fósforo, proteína cruda del forraje y su digestibilidad in vitro de la materia orgánica se monitorearon a través de la estación de apacentamiento. Los resultados de la suplementación variaron entre años y entre localidades. En 1989 y 1990, hubo interacciones significativas ($P < 0.14$) entre tratamiento y localidad, esto debido a que los novillos de la localidad OESTE tendieron a responder mejor a la suplementación que los novillos de la localidad ESTE, pero los novillos de la localidad ESTE tuvieron mayores tasas de ganancia de peso. El proveer el suplemento a tasas graduales de incremento produjeron resultados comparables que suplementar a una tasa constante durante todo el verano. La proteína cruda suplementaria no mostró beneficios significativos, pero los niveles de proteína cruda en el forraje del potreo generalmente fueron superiores a los requerimientos de los novillos. Las ganancias de peso, promediadas en los 5 años, fueron mayores ($P < 0.05$) para los novillos suplementados con cebada o con cebada y fósforo que las ganancias obtenidas por los novillos sin suplemento (control). La respuesta a la suplemetación debe ser benéfica en la mayoría de los años, pero los resultados pueden variar con la cantidad y calidad del forraje disponible.

Grazing yearling steers on Northern Great Plains native rangelands could improve the economic viability of a ranching operation. During dry years, steers could easily be sold without jeopardizing the investment in a high quality cow herd. When forage production was abundant, steers could be used to harvest the extra forage without increasing cow numbers. Enhancing the weight gains of grazing steers through appropriate supplementation may make this option even more viable. Chemical composition data for Northern Great Plains native forages reported by Karn (1992) suggest that phosphorus (P), crude protein, and energy are probably the nutrients which most limit animal productivity, especially during the latter part of the grazing season.

Although the recommended (NRC 1996) range of P for yearling steers is 0.15–0.24%, depending on steer weight and rate of gain, Call et al. (1978) reported that P supplementation was not beneficial to replacement heifers receiving a basal diet containing 0.14% P (as fed basis). However, Echevarria et al. (1987) reported that steers grazing grasses containing 0.16 to 0.19% P had improved weight gains when supplemented with dicalcium phosphate. Winter (1988) reported an immediate weight gain response in P supplemented steers grazing grasses containing 0.1 to 0.15% P during the wet but not the dry season.

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Table 1. Precipitation and mean monthly ambient air temperatures between April and September for 1988, 1989, 1990, 1991, and 1992, and the 80-year average.

	1988		1989		1990		1991		1992		80-year average	
	Temp.	Precip.	Temp.	Precip.	Temp.	Precip.	Temp.	Precip.	Temp.	Precip.	Temp.	Precip.
	(°C)	(mm)	(°C)	(mm)	(°C)	(mm)	(°C)	(mm)	(°C)	(mm)	(°C)	(mm)
Apr.	6.7	2.5	6.6	54.1	6.5	3.3	8.0	47.5	4.9	7.9	5.3	39.1
May	16.0	33.8	13.5	48.8	12.0	55.1	13.9	67.3	14.9	37.3	12.5	57.4
June	24.3	23.1	17.3	19.6	18.6	132.8	19.6	97.8	17.1	110.2	17.8	89.2
July	22.7	38.6	24.0	31.0	21.0	25.6	21.8	21.1	17.0	77.0	21.2	56.9
Aug.	20.8	82.0	20.9	32.8	21.9	48.5	22.9	22.3	17.6	36.6	20.4	50.0
Sep.	13.3	15.7	14.3	27.2	16.4	41.1	14.9	59.4	13.3	26.7	14.0	39.6

Denham (1975) found that supplementing steers grazing annual rye with 0.9 kg of corn daily over a 63-day period increased daily gains by 0.33 kg. Vadiveloo and Holmes (1979) reported that when herbage supply was limiting, weight gains of grazing steers were significantly increased by supplemental energy but not by protein, however, when herbage was adequate supplementation was not beneficial. Reyneke (1976) reported that strategic supplementation of grazing steers produced significant results 2 out of 3 years, with protein concentrate producing the greatest response and maize meal producing the least. Lusby et al.(1981) also reported that in the late summer and fall, steer weight gains were efficiently increased by supplemental protein but not by energy. The inconsistency of previous results, plus a lack of research on supplements for grazing steers in the Northern Great Plains, suggested a need for further research. Thus, the objective of the current research was to determine the effect of crude protein and energy supplementation, at either constant or variable rates, and P supplementation at a constant rate, on the performance of yearling steers summer grazing on native rangelands.

Materials and Methods

Study Site

Two pastures located near Mandan, N.D., were used in these studies and will be referred to as EAST and WEST. Each pasture contained approximately 51 ha and was primarily native rangeland, but the topography and species represented in each pasture was quite different. The WEST pasture was relatively flat and contained primarily western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love), needleandthread (*Stipa comata* Trin. and Rupr.), green needlegrass (*S. viridula* Trin.), blue grama (*Bouteloua gracilis* (H.B.K.) Griffiths), prairie junegrass [*Koeleria cristata* (Lam.) Beauv.], and upland sedges (*Carex* spp.). The EAST pasture was more rolling and contained a greater diversity of species, including the same species as the WEST pasture plus lead plant (*Amorpha canescens* Pursh), western snowberry (*Symphoricarpos occidentalis* Hook), buffaloberry [*Sherpherdia argentea* (Pursh) Nutt.], and the introduced cool-season grass species crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schultes] and smooth broomegrass *(Bromus inermis* Leyss).

Daily precipitation and ambient minimum and maximum air temperatures were recorded at a weather station located about 3.2 km north of the study site. Monthly precipitation totals and mean monthly temperatures (minimum and maximum) were calculated and compared to historic values (Table 1).

Supplementation

A series of supplementation trials were conducted with yearling steers (*Bos taurus*) grazing during the summer on the previously described pastures. Supplementation trials were conducted at the WEST pasture in 1988 and 1989, while both supplementation and intake trials were conducted at the EAST pasture. In 1990, 1991, and 1992 replicated studies were conducted at both locations. Trials were conducted from 26 May to 4 October 1988 (131 days); 30 May to 6 October 1989 (129 days); 5 June to 12 October 1990 (129 days); 31 May to 11 October 1991 (133 days); and 28 May to 8 October 1992 (133 days). Straight bred Hereford steers were used in all years, but in 1988, Hereford-Simmental crossbred steers also were used to compare the effect of breed type on supplementation response. Initial and final steer weights, as well as weights taken at 21-day intervals, were obtained following an overnight stand without feed or water.

1988

Supplementation treatments in 1988 were no supplement (control), ground barley, and ground barley plus P. There were 6 steers per treatment and 2 breed types for a total of 36 steers at the WEST location and 5 Hereford steers per treatment for a total of 15 steers at the EAST location. Supplement composition and amounts fed daily (as-fed basis), 6 days per week, are shown in Table 2.

1989

The control, barley, and barley + P treatments were also used in 1989, but there

Table 2. Barley (B), barley-phosphorus (BP), barley-soybean meal (BS), and barley-soybean meal-phosphorus (BSP), supplement ingredients, and the grams (as-fed basis) fed per steer per day during the summers of 1988, 1989, 1990, 1991, and 1992.[1]

Year/	B	BP		BS		BSP		
Month	Barley	Barley	MSP[2]	Barley	SBM[2]	Barley	SBM	MSP
	(g)							
1988[3]	908	908	23	--	--	--	--	--
1989[3]	908	908	23	--	--	--	--	--
1990[3]	908	908	23	454	454	454	454	23
1991–1992[4]								
Jun.	454	454	23	--	--	363	91	23
Jul.	681	681	23	--	--	454	227	23
Aug.	908	908	23	--	--	454	454	23
Sep.	1135	1135	23	--	--	681	454	23
Oct.	1498	1498	23	--	--	817	681	23
Mean	908	908	23	--	--	539	369	23

[1] Steers were fed 6 days per week.

[2] MSP=monosodium phosphate; SBM=soybean meal.

[3] Steers supplemented at a constant rate all summer.

[4] In 1991 and 1992, steers were supplemented at a variable rate; there were 24 feeding days at the June, July, August, and September rates respectively, and 18 feeding days at the October rate.

Table 3. Phosphorus, crude protein and metabolizable energy provided daily, 6 days per week in supplements fed to yearling steers grazing native rangelands in 1988, 1989, 1990, 1991, and 1992.[1,2]

Period of Use		Supplements								
1988-1990	1991-1992	B			BP			BSP		
		P	CP	ME	P	CP	ME	P	CP	ME
		(g)	(g)	(mcal)	(g)	(g)	(mcal)	(g)	(g)	(mcal)
Jun.-Oct.	Jun.	1.6	58	1.2	6.0	58	1.2	7.5	88	1.2
	Jul.	2.4	87	1.8	8.4	87	1.8	9.2	163	1.8
	Aug.	3.3	116	2.4	9.7	116	2.4	11.5	265	2.4
	Sep.	4.1	145	3.1	9.7	145	3.1	11.4	300	3.1
	Oct.	5.4	192	4.0	10.8	192	4.0	13.0	418	4.0

[1] B = ground barley; BP = ground barley and monosodium phosphate; BSP = ground barley, monosodium phosphate and soybean meal.

[2] The barley-soybean meal supplement used in 1990 had the same crude protein and metabolizable energy content with 6 grams less phosphorus than the August BSP supplement.

were 7 steers per treatment for a total of 21 steers at the WEST location and 6 steers per treatment for a total of 18 steers at the EAST location.

1990

In 1990, in addition to the control, barley, and barley + P treatments, supplements containing a 50-50 mixture of barley and soybean meal and a 50-50 mixture of barley and soybean meal plus P were also used. Supplements were isocaloric. There were 5 steers per treatment per location for a total of 50 steers.

1991 and 1992

In 1991 and 1992, only the control, barley, barley + P, and barley + soybean + P treatments were used, and there were 7 steers per treatment per location for a total of 56 steers used each year. Supplements in 1991 and 1992 were fed at gradually increasing rates from June through October in contrast to 1988, 1989, and 1990 when supplements were fed at a constant rate throughout the summer (Table 2). Supplement levels were increased to coincide with the usual decline in forage quality. Levels of P, crude protein, and metabolizable energy supplied by supplements are shown in Table 3.

Supplementation Procedure for all Years

In all treatments where P was supplemented, monosodium phosphate was used as the P source and it was fed at a rate of 6 g P steer^{-1} day^{-1}. Steers at each location were maintained together at all times except when corralled each morning between 0600 and 0800 hours, 6 days per week, separated into treatment groups and bunk fed their respective supplements by group. Non-supplemented steers were also corralled while supplemented steers were being fed. Trace mineralized salt containing 96-98.5% salt, 0.35% zinc, 0.34% iron, 0.20% manganese, 0.033% copper, 0.007% iodine, and 0.005% cobalt (Akzo Salt, Inc., Clarks Summit, Penn.) was available at all times.

Intake

Five intake trials were conducted at the EAST location each summer during 1988 and 1989, and 2 intake trials were conducted at each location during the summers of 1991 and 1992. Intake trials were initiated on 23 June, 14 July, 4 and 25 August and 15 September 1988; and 22 June, 13 July, 3 and 24 August and 14 September 1989. In 1991, trials were initiated on 26 June (early summer) and 28 August (late summer), and in 1992, trials were initiated on 15 July (early summer) and 9 September (late summer). Dry matter intake was estimated for unsupplemented (control) steers, steers fed ground barley, and steers fed ground barley + P in 1988 and 1989 and for control and barley + soybean + P treatment steers in 1991 and 1992. All steers at the EAST location were used in the 1988 and 1989 intake trials, and all steers on the control and barley + soybean + P treatments at both locations were used in 1991 and 1992 trials.

Fecal output was estimated using chromium as an external indicator. In 1988 and 1989, gelatin capsules containing chromic oxide were administered daily. In 1991 and 1992, chromium was delivered with an intra-ruminal continuous release device[1] (Adams et al. 1991) administered at the beginning of each trial. Five daily fecal collections were made following a 10-day adjustment period to insure that chromium had reached a consistent concentration in the digestive tract. During the first 2 trials in 1988, steers were dosed with 10 g chromic oxide per steer daily, which was midway between levels used by Rittenhouse et al. (1970) and Adams et al. (1986). From the third trial on and for all of the 1989 trials, chromic oxide was given at the rate of 8 g per steer daily (Rittenhouse et al. 1970). The continuous release device used in 1991 had mean release rates of either 1.57 or 1.74 g chromic oxide day^{-1} and the continuous release device used in 1992 had mean release rates of 1.48 g chromic oxide day^{-1} according to the manufacturer. Two unsupplemented steers in 1988 and 1989 and 3 unsupplemented steers in 1992 were fitted with fecal collection bags and dosed with chromic oxide during each trial in 1988 and 1989 or given a continuous release device at the beginning of each trial in 1992 to measure total fecal output for chromium recovery calculations. Daily fecal collections during each trial were composited on an equal wet volume basis across days for each steer, so that a single sample per steer per trial was saved for analysis.

Indigestible neutral detergent fiber (INDF) was determined on extrusa, supplement, and fecal samples as suggested by Ellis et al. (1984) and was used instead of lignin to calculate forage intake according to procedures outlined by Rittenhouse et al. (1970). Because supplements and forages are likely to have different digestibilities, the amount of fecal dry matter originating from supplements must be partitioned from the total fecal dry matter before forage intake can be calculated. Since the amount of supplement dry matter is known, the amount of an internal indicator such as lignin or indigestible NDF, which is presumed to be indigestible can be determined for supplements and feces. Then the amount of indicator originating from the supplement can be subtracted from the total amount of indicator in the feces. The remaining quantity of the indicator is presumed to originate from ingested forage. Forage intake can then be determined by dividing the weight of indicator in the feces originating from the forage by the concentration of the indicator in the forage. Once forage dry matter intake is determined, total dry matter intake is calculated by combining forage and supplement intake values.

Sampling Procedures

Forage samples were collected each year at both locations with 3 mature esophageally fistulated steers at approximately 3 week intervals throughout the grazing season. Fistulated steers were penned off feed overnight before each sampling date to ensure that they would

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[1] Captec chrome manufactured by Captec PTY, LTD., Laverton, Victoria, Australia.

Table 4. Mean (± SD) monthly phosphorus and crude protein concentrations in Northern Great Plains native pastures being grazed by yearling steers receiving energy, phosphorus and crude protein supplements in 1988, 1989, 1990, 1991, and 1992.[1,2,3]

		Phosphorus					Crude protein				
Year	Location	Jun.	Jul.	Aug.	Sep.	Location mean	Jun.	Jul.	Aug.	Sep.	Location mean
		(% of D.M.)					(% of D.M.)				
1988	E	0.235±0.018	0.204±0.011	0.277±0.046	0.179±0.022	0.213±0.041	12.5±0.6	11.3±0.9	16.4±1.9	10.7±3.2	12.2±2.8
	W	0.174±0.023	0.178±0.020	0.166±0.018	0.144±0.012	0.167±0.021	8.6±0.7	9.1±0.5	11.1±.0.6	8.2±0.1	9.4±1.4
1989	E	0.229±0.004	0.183±0.009	0.140±0.024	0.176±0.008	0.180±0.029	13.7±0.5	9.9±0.5	8.7±1.2	11.3±0.1	10.9±1.8
	W	0.195±0.023	0.133±0.007	0.151±0.009	0.234±0.003	0.178±0.038	11.4±1.8	11.6±0.5	9.0±0.8	12.1±0.7	10.8±1.7
1990	E	0.238±0.014	0.262±0.029	0.190±0.008	0.194±0.019	0.224±0.038	13.5±0.4	13.1±2.5	8.5±0.6	10.6±0.9	11.6±2.4
	W	0.243±0.004	0.202±0.035	0.172±0.004	0.166±0.010	0.192±0.035	14.2±0.5	16.2±4.4	9.3±0.1	10.0±1.0	12.7±3.9
1991	E	0.220±0.018	0.170±0.019	0.144±0.015	0.138±0.020	0.168±0.037	11.2±1.5	8.8±0.3	5.9±0.4	7.2±1.5	8.3±2.2
	W	0.209±0.029	0.175±0.017	0.135±0.009	0.129±0.020	0.162±0.038	13.8±1.6	9.3±0.4	6.0±0.3	6.2±0.9	8.8±3.3
1992	E	0.166±0.011	0.189±0.018	0.140±0.016	0.122±0.001	0.159±0.029	12.5±0.8	14.4±1.1	10.8±1.4	9.9±0.2	12.2±2.0
	W	0.122±0.004	0.138±0.011	0.112±0.006	0.091±0.013	0.119±0.021	13.3±0.6	12.3±2.0	9.0±0.8	7.5±0.7	10.7±0.3

[1] Samples were collected with unsupplemented esophageal fistula steers in 1988-1991 and by hand clipping in 1992.

[2] The EAST (E) location pasture was used for the intake trials in 1988 and 1989 and as a replicate pasture in 1990, 1991, and 1992.

[3] Monthly values are means of 3 to 6 sample collections.

graze the following morning. Grazing selectivity did not appear to be affected by this method. Individual animal collections were mixed, subsampled, freeze dried and analyzed for nitrogen (N), in vitro digestible organic matter (IVDOM) and INDF. Extrusa subsamples for P analysis were squeezed to remove saliva (Hoehne et al. 1967) and oven dried at 50° C. In 1992, because no squeezed extrusa samples were collected, samples were hand clipped to simulate grazing (Karn and Hofmann 1990) and analyzed for N and P. Hand clipped samples were freeze dried before grinding. All forage samples were ground to pass a 1 mm screen before chemical analyses.

Chemical Analyses

Nitrogen and P in forage were determined with a Quikchem 8000 continuous flow autoanalyzer (Lachat Instruments, Milwaukee, Wisc. 53218). Fecal samples from the intake trials were prepared for chromium analysis according to Williams et al. (1962), and chromium was determined with a Perkin Elmer P II inductive coupled plasma optical emission spectrophotometer (Perkin Elmer, Norwalk, Conn.). In vitro digestible organic matter was determined by the Tilley and Terry (1963) procedure as modified by Moore and Mott (1974). Indigestible neutral detergent fiber was determined by following a 6-day in vitro fermentation (Ellis et al. 1984) with neutral detergent fiber analysis of the fermentation residue (Goering and Van Soest 1970).

Statistical Analyses

Steer weight gain data were analyzed over locations by year using a randomized design, with locations considered as replications and treatment groups considered the experimental unit. Treatment and location were tested with the treatment x location interaction term. Although crossbred and Hereford steers responded similarly to supplements, only Hereford steer data were included in the analysis over both locations in 1988 so that data would be more nearly balanced. Treatment means for individual years were separated by the Student-Newman-Keuls' test. In a second analysis, treatments in common over the 5 years were analyzed as a mixed model according to a treatment by location factorial in a randomized block design. Least squares means were separated by a Tukeys test. Constant versus increasing supplementation levels were considered as nested within treatments (Milliken and Johnson 1984).

Intake data in 1988, 1989, 1991, and 1992 were analyzed as a completely randomized design, with the steer within treatment term used to test treatment in the 1988 and 1989 trials, and the steer within treatment by location term used to test treatment, location, and treatment x location in 1991 and 1992 trials. Least squares means were calculated for intake data using SAS (1985) GLM procedures in 1991 and 1992. Treatments were considered different at the 5% probability level unless otherwise stated.

Results and Discussion

According to the NRC (1996), the crude protein requirement of growing steers, of the weight used in these studies, ranges between 8 and 12% of the diet dry matter depending on steer weight and daily gains. Crude protein at both locations was generally within this range throughout the summer, except for 1991 (Table 4) which probably explains the lack of a significant response to supplemental protein in 1990 and 1992. Forage P levels during August and September at both locations were generally at or below the NRC (1996) recommended range of 0.15–0.24% P for yearling steers. Forage growth and hence forage quality, especially for cool-season grasses, is very closely related to seasonal precipitation patterns. In 1988, August precipitation (Table 1) was above normal which facilitated forage regrowth and resulted in unusually high August forage crude protein, P and IVDOM levels, especially at the EAST location (Tables 4 and 5).

Steer weight gain data were analyzed by year as well as over all years because there were apparent differences in treatment responses among years and between locations which reflected differences in topography and forage types between locations.

1988

In 1988 crossbred and straight-bred Herefords at the WEST location responded similarly to barley and barley + P treatments (data not shown), but only Hereford steer data were analyzed with weight gain data from the EAST location (Table 6) so that data would be more nearly balanced. There were no significant treatment differences; however, there was a location effect with steers at the EAST location having higher daily gains than steers at the WEST location (1.07 vs. 0.72 kg; $P < 0.05$). This was thought to be due to forage quality differences between pastures since P, crude protein, and IVDOM were all higher in forage from the EAST pasture (Tables 4 and 5).

1989

In 1989, daily gains (Table 6) were higher ($P < 0.15$) for steers receiving the

Table 5. Mean (± SD) monthly IVDOM of extrusa samples from Northern Great Plains native pastures being grazed by yearling steers receiving energy, phosphorus and crude protein supplements in 1988, 1989, 1990, 1991, and 1992.[1,2]

Year	Location	Jun.	Jul.	Aug.	Sep.	Loc. Mean
		(%)				
1988	E	70.4 ± 1.0	63.3 ± 2.0	67.0 ± 1.9	61.8 ± 0.4	64.6 ± 3.5
	W	59.2 ± 1.8	58.0 ± 1.5	59.9 ± 3.0	58.4 ± 1.1	59.1 ± 2.1
1989	E	74.3 ± 0.5	67.4 ± 2.1	63.8 ± 1.0	60.7 ± 1.2	65.7 ± 5.0
	W	70.5 ± 4.1	65.1 ± 4.1	62.8 ± 0.8	56.4 ± 1.6	64.1 ± 6.4
1990	E	69.5 ± 0.8	65.8 ± 3.7	61.8 ± 1.1	57.2 ± 3.1	62.9 ± 5.4
	W	63.6 ± 1.4	65.6 ± 3.7	63.6 ± 1.4	59.8 ± 1.7	63.0 ± 3.4
1991	E	67.4 ± 4.8	64.2 ± 1.4	61.5 ± 3.5	58.5 ± 1.8	62.9 ± 4.4
	W	69.0 ± 3.2	60.4 ± 2.1	63.4 ± 2.6	59.9 ± 1.8	63.2 ± 4.3
1992	E	68.4 ± 0.8	64.4 ± 1.1	60.7 ± 1.9	57.8 ± 2.2	62.7 ± 4.0
	W	65.9 ± 0.9	62.5 ± 1.9	57.1 ± 2.2	57.3 ± 0.6	60.4 ± 3.9

[1] The EAST (E) location pasture was used for intake trials in 1988 and 1989 and as a replicate pasture in 1990–1992.
[2] Monthly values are means of 3 to 6 sample collections.

barley + P supplement compared to the control treatment (1.10 vs 0.88 kg). There was also a significant ($P < 0.14$) location by treatment interaction. Daily gains of steers at the EAST location were again higher than at the WEST location (1.10 vs 0.91 kg; $P<0.07$).

1990

There were no significant treatment differences in 1990 ($P > 0.20$; Table 6); however, there was a significant treatment by location interaction ($P < 0.05$). Steers at the WEST location tended to benefit more from the barley + P supplement [(barley + P) - control = 0.26 kg] than steers at the EAST location [(barley + P) - control = 0.06 kg]. Steers at the EAST location continued to gain more than WEST location steers, but the difference was not as great as in previous years (1.10 vs 0.99 kg; $P<0.08$).

1991 and 1992

Because the barley + soybean treatment used in 1990 had shown little benefit, it was eliminated so that the number of steers per treatment could be increased from 5 to 7. Barley significantly ($P < 0.05$) improved weight gains compared to control steers in both years whereas the barley + P treatment increased weight gains compared to barley alone in 1992 but not in 1991 (Table 6). These results show the consistent benefit of feeding barley and the inconsistent benefit of feeding phosphorus. The barley + soybean + P treatment was not different from the barley treatment in 1991 or the barley + P treatment in 1992, suggesting that supplemental protein was not beneficial either year. Steers at the EAST location had higher gains than WEST location steers both years, but the difference was greatest in 1992 (1.15 vs 0.98 kg; $P < 0.05$).

1988–1992

When treatments common to all 5 years were analyzed together, steers supplemented with barley had higher ($P < 0.05$) gains than control steers, and steers receiving the barley + P treatment had higher gains than steers receiving only barley, indicating that both barley and phosphorus were beneficial.

Data for 1988–1990 were compared with 1991–1992 data to determine whether supplementation results were affected by feeding at a constant rate compared to a gradually increased rate. Weight gains were not affected ($P > 0.20$) by feeding method. However, feeding at a gradually increasing level would be more desirable because steers would more readily consume a small amount of feed in the early summer and increasing supplement levels would more nearly coincide with decreasing forage quality later in the summer.

In these studies the most consistent response was from barley (energy supplement), which agrees with results reported by Denham (1975) and Vadiveloo and Holmes (1979), but disagrees with Lusby et al. (1981) who reported a beneficial effect from protein but not from energy. Supplemental P produced inconsistent results among years but over all 5 years it significantly increased ADG compared to barley alone. Winks et al. (1977) in Australia also reported erratic results with P supplementation; in the wet season, P supplementation increased weight gains, but in the dry season it did not.

Steers at the rolling EAST location on the control, barley, and barley + P treatments had higher weight gains each year compared to steers at the flat WEST location. The consistent weight gain difference between locations may have been due to generally higher quality diets (Tables 4 and 5) at the EAST location. This may also help to explain why steers at the EAST location did not respond as well to supplements. Forage availability was not considered to be a limiting factor at either location during these studies.

Intake

During the summer of 1988, dry matter intake in early July was significantly lower than for other periods when expressed as kg/day, but intake was not significantly different among periods when expressed as a percent of body weight (Table 7). In 1989, dry matter intake as a percent of body weight and in kg/day generally declined throughout the season. Dry matter intakes expressed as a percent of body weight for control, barley, and barley + P supplement treatments were 2.7, 2.9 and 3.0%, respectively, in 1988 and 2.7, 2.6 and 2.8%, respectively, in 1989. However, treatments were not significantly different ($P > 0.05$) either year and there was no treatment by period interaction.

Intake trials were conducted in 1991 and 1992 at both the EAST and WEST locations to determine if the higher ADG of

Table 6. Average daily gains of yearling steers grazing native rangelands in the Northern Great Plains and supplemented with energy, phosphorus, and/or crude protein in 1988, 1989, 1990, 1991, and 1992.

		Treatments					
Year	Steers/ Treatment	C[1]	B[1]	BS[1]	BP[1]	BSP[1]	SE
		(kg)					
1988	11	0.80^{a}	0.90^{a}	--	0.93^{a}	--	0.05
1989	13	0.88^{b}	1.00^{ab}	--	1.10^{a}	--	0.05
1990	10	0.95^{a}	0.98^{a}	1.08^{a}	1.11^{a}	1.10^{a}	0.06
1991[2]	14	0.73^{c}	0.94^{ab}	--	0.89^{b}	0.98^{a}	0.01
1992[2]	14	0.88^{c}	1.05^{b}	--	1.17^{a}	1.15^{a}	0.02
		Combined analysis of treatments common to all years[2,3]					
	62	0.85^{c}	0.98^{b}	--	1.04^{a}	--	0.02

[1] C=Control, (no supplement); B=ground barley; BS=ground barley and soybean meal; BP=ground barley and monosodium phosphate; and BSP=ground barley, soybean meal and monosodium phosphate.
[2] In 1989, treatments with different letters differed significantly at ($P<.15$). In 1991, 1992, and over all 5 years, treatments with different letters differed significantly at ($P<0.05$).
[3] Least squares means.

Table 7. Daily dry matter intakes by period averaged across supplemental treatments in 1988 and 1989.[1, 2]

Trial	Period	1988 Dry Matter		1989 Dry Matter	
		(% B.W.)	(kg day^{-1})	(% B.W.)	(kg day^{-1})
1	Early Jul.	2.7a	9.6b	3.2a	12.4a
2	Late Jul.	3.0a	11.4a	2.8b	11.0ab
3	Mid Aug.	3.0a	11.9a	2.6b	11.1ab
4	Early Sep.	3.0a	12.6a	2.6b	11.6ab
5	Late Sep.	2.8a	12.4a	2.3c	10.6b
	SE	0.10	0.44	0.08	0.45

[1] Means are averages of 15 values in 1988 and 18 values in 1989.

Table 8. Dry matter intakes for control (C) and supplemented (BSP) steers for early and late summer in 1991 and 1992.[1,2,3]

	Dry Matter							
Period	C	BSP	Period mean	SE	C	BSP	Period mean	SE
	(% of B.W.)				(kg day^{-1})			
				1991				
Early Summer	2.2	2.2	2.2a	0.08	8.5	8.1	8.3a	0.33
Late Summer	1.8	2.2	2.0a	0.08	7.6	9.6	8.6a	0.33
Treatment Mean	2.0a	2.2a			8.0a	8.9a		
SE	0.09	0.09			0.37	0.37		
				1992				
Early Summer	2.3	2.5	2.4a	0.11	8.8	10.0	9.4a	0.49
Late Summer	2.3	2.6	2.5a	0.12	10.0	12.2	11.1b	0.51
Treatment Mean	2.3a	2.6b			9.4a	11.1b		
SE	0.09	0.09			0.54	0.53		

[1] Dry matter intake was not significantly different between locations either year.

[2] Within a year, least squares treatment means with different letters differ ($P<0.07$).

[3] Within a year, least squares period means with different letters differ ($P<0.05$).

steers at the EAST location could be due to higher dry matter intakes. Trials conducted in early and late summer of each year indicated that dry matter intake did not differ ($P > 0.05$) between locations (data not shown). In 1991 dry matter intake was not different between early and late summer trials (Table 8). However, in 1992 dry matter intake in kilograms per steer per day was higher in late summer. Dry matter intake tended to be numerically higher for supplemented steers in the 1991 late summer trial and was significantly higher ($P < 0.07$) for supplemented steers over both trials in 1992 (Table 8).

Conclusions

Average daily gains and the inconsistent response to supplementation between years and locations suggests that the nutrient content and dry matter intake of grazed forage in these studies were quite high. Ground barley was usually beneficial, whereas P was beneficial in some years and locations, but crude protein showed little benefit. Over all 5 years, ground barley and ground barley plus P increased ADG by 0.13 and 0.19 kg, respectively, above unsupplemented steers. In most years, feeding a supplement containing a combination of ground barley and P should be beneficial, but the response to supplements will vary according to the quantity and quality of available forage. Feeding gradually increasing levels of supplement during the summer would probably be a more desirable supplementation approach because steers would more readily consume small amounts of supplement early in the summer and larger amounts of supplement in late summer. This supplementation pattern would also help to compensate for expected declines in forage nutritive quality.

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Spotted knapweed and grass response to herbicide treatments

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Abstract

Picloram at 0.28 kg ai ha^{-1}, clopyralid plus 2,4-D at 0.21 kg ai ha^{-1} plus 1.12 kg ai ha^{-1}, or dicamba plus 2,4-D at 0.56 kg ai ha^{-1} plus 1.12 kg ai ha^{-1} were applied to spotted knapweed (*Centaurea maculosa* Lam.) at the spring-rosette, bolt, bud, flower, or fall-rosette growth stages in 1991 on 2 sites in Montana. Treatments (3 herbicide treatments, 5 growth stages) were applied in a randomized-complete-block design and replicated 3 times at each site. Effects of herbicides on mature and seedling spotted knapweed density depended upon spotted knapweed growth stage at the time of application and the number of years after application. Picloram consistently reduced mature spotted knapweed density to low levels (<5 plants m^{-2}), regardless of growth stage, and its effect persisted through 1994. Clopyralid plus 2,4-D applied at the bolt or bud stage reduced spotted knapweed densities similar to that of picloram (95%) at the Avon site, while providing about 50% reduction in density 3 years after application at Missoula. This treatment may provide an alternative to picloram in environmentally sensitive areas. Dicamba plus 2,4-D was most effective when applied during the bud and bolt growth stages, and least effective when applied during the spring- and fall-rosette stages. In most situations, picloram and clopyralid plus 2,4-D provided greater control of spotted knapweed than dicamba plus 2,4-D. Herbicide treatments increased perennial grass biomass from 173 kg ha^{-1} in the nontreated controls to 494, 880, and 1,309 kg ha^{-1} for dicamba plus 2,4-D, clopyralid plus 2,4-D and picloram, respectively.

Key Words: Pasture and rangeland weed control, clopyralid, dicamba, picloram, 2,4-D, *Centaurea maculosa*

Spotted knapweed (*Centaurea maculosa* Lam.), a short-lived perennial weed, was introduced to the Pacific Northwest from Eurasia about 1900 (Roché and Talbott 1986). Since its introduction, spotted knapweed has aggressively invaded rangeland and open canopy forest sites in the northern intermountain region (Lacey et al. 1992, Losensky 1987, Roché et al. 1986). More than 2.8 million ha in Montana and adjoining states and Canadian provinces are infested with spotted knapweed (Lacey 1989). This weed can form dense infestations that reduce vigor and diversity of native plants (Forcella and Harvey 1983, Tyser and Key 1988).

Resumen

En 1991, en dos sitios de Montana, se aplicaron los herbicidas picloram (0.28 kg ia ha^{-1}), clopiralid mas 2,4-D (0.21 kg ia ha^{-1}mas 1.12 kg ia ha^{-1}) y dicamba mas 2.4-D (0.56 kg ia ha-1 mas 1.12 kg ia ha^{-1}) a "Spotted knapweed" (*Centaurea maculosa* Lam.) en las etapas de desarrollo: roseta de primavera, aparición de tallos florales, yemas, flores, floración y roseta de otoño. Los tratamientos (3 herbicidas y 5 etapas de desarrollo) se aplicaron bajo un diseño experimental de Bloques completos al azar con 3 repeticiones en cada sitio. Los efectos de los herbicidas en la densidad de plantas maduras y plántulas de "Spotted knapweed" dependieron de la etapa de desarrollo en que se encontraba el "Spotted knapweed" al momento de la aplicación y del número de años después de la aplicación. El picloram redujo a niveles consistentemente bajos (<5 plantas m^{-2}) la densidad de plantas maduras de "Spotted knapweed', esto sin importar la etapa de desarrollo en la que se encontraban y el efecto persistió hasta 1994. En el sitio Avon, el clopiralid mas 2,4-D aplicado en las etapas de aparición de tallos florales o yemas redujo la densidad de "Spotted knapweed" en forma similar que el picloram (95%), en tanto que en el sitio de Missoula, después de 3 años de la aplicación, la redujo en 50%. Este tratamiento puede proveer una alternativa al picloram en áreas ambientalmente sensitivas. El dicamba mas 2,4-D fue mas efectivo cuando se aplico durante las etapas de aparición de yema y tallos florales y menos efectivo cuando se aplico durante los estados de roseta de primavera y otoño. En la mayoría de los casos picloram y clopiralid mas 2,4-D controlaron mejor el "Spotted knapweed" que dicamba mas 2,4-D. Los tratamientos de herbicidas incrementaron la biomasa de pastos perennes de 173 kg ha^{-1} en las áreas sin tratamiento a 494, 880, y 1,309 kg ha^{-1} cuando se aplico dicamba mas 2,4-D, clopiralid mas 2,4-D y picloram respectivamente.

Spotted knapweed reduces forage production from 60 to 90%, which causes economic losses to the livestock industry and impairs wildlife populations (Watson and Renney 1974, Bucher 1984, Bedunah and Carpenter 1989). Spotted knapweed costs the livestock industry $11 million each year in direct costs, and could cost the industry $155 million if allowed to spread to its potential ecological range in Montana (Hirsh and Leitch 1996).

Integrating biological, cultural, and chemical control methods will be necessary to effectively manage large infestations of spotted knapweed (Cuda et al. 1989, Sheley et al. 1996). At this time, biological control with insects, pathogens, and grazing animals

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Table 1. Average seasonal precipitation (cm) during the 4–year study (1991 to 1994) and long–term precipitation at a recording station located 6.4 km from the Missoula study site (Missoula WSO) and 24.1 km from the Avon study site (Ovando).

	1991		1992		1993		1994		4-yr Mean		Long term Average
Months	Msla[b]	Avon	Msla	Avon	Msla	Avon	Msla	Avon	Msla	Avon	Msla
						(cm)					
Jan–Mar	5.8	3.1	7.7	2.8	5.5	3.3	3.4	2.0	5.6	2.8	7.6
Apr–Jun	13.9	11.0	11.4	9.5	13.3	12.1	15.8	17.1	13.6	12.4	8.7
Jul–Sep	3.0	4.7	7.8	7.2	9.4	18.7	3.9	3.0	6.0	8.4	8.1
Oct–Dec	7.4	6.4	5.8	4.9	7.3	3.3	6.4	6.1	6.7	5.2	6.8
Total	30.1	24.9	32.7	24.1	35.5	37.4	29.5	28.2	31.9	28.8	31.2

[a] No long term data available for Avon study site.
[b] Msla=Missoula study site.

has shown limited success in reducing spotted knapweed density (Story 1992, Lacey et al. 1994, Olson et al. 1997). Mechanical treatments are restricted by soil type and terrain on many rangeland sites. Therefore, herbicides are a necessary component of most successful integrated weed management projects.

Previous studies of other perennial weeds, such as leafy spurge (*Euphorbia esula* L.) and Russian knapweed (*Acroptilon repens* L.) indicate that herbicide efficacy depends upon the growth stage at the time of application (Lym and Messersmith 1983, Whitson et al. 1993). Studies focusing on the effect of application timing on spotted knapweed control are limited. Whitson et al. (1986) reported that spotted knapweed could be controlled easily with either spring or fall herbicide applications. In another study, spotted knapweed control was similar 2 months after application when herbicides were applied at the bud or flower stage (Lym and Messersmith 1986). Early spring treatments using picloram, clopyralid plus 2,4-D, and dicamba plus 2,4-D are commonly recommended to control spotted knapweed and increase forage production (Harris and Cranston 1979, Lacey et al. 1992, Lacey 1985, Fay et al. 1995).

No long-term studies report the optimum timing of herbicide application to maximize spotted knapweed control and subsequent forage production. Specific objectives of this study were to evaluate spotted knapweed control using picloram, clopyralid plus 2,4-D, and dicamba plus 2,4-D, and to determine the optimum growth stage at which to apply herbicides to maximize spotted knapweed control and grass production.

Materials and Methods

Study Sites

This study was conducted near Missoula and Avon, Mont., from 1991 through 1994. The Avon site was located on native rangeland with a long-term grazing history of light to moderate use (0–50% utilization, annually). The area had not been grazed for 8 years prior to the study. The Missoula site was seeded with crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] during the 1940s and had not been grazed by livestock since the 1930s. Although neither site was grazed by domestic livestock during the study, some use by wildlife was noted.

The Avon site was located on a nearly level floodplain at 1455 m elevation. Soil was a Typic Haploboroll with a gravelly loam texture, 3.9% organic matter, and pH 5.8. The Missoula site was located on foothills at 975 m elevation with a northwest aspect. Soil was a Typic Argiboroll with a gravelly loam texture, 4.8% organic matter, and pH 6.2. Average seasonal precipitation during the 4-year study at both sites, and long-term precipitation near Missoula are presented in Table 1.

Rough fescue (*Festuca scabrella* Torr.), bluebunch wheatgrass [*Pseudoroegneria spicatum* (Prush) Love], prairie junegrass (*Koeleria cristata* (L.) Pers.), and Idaho fescue (*Festuca idahoensis* Elmer) were dominant grasses at Avon. Crested wheatgrass was the most abundant grass at the Missoula location. Spotted knapweed was the dominant forb at both locations, averaging 36 mature plants m^{-2} at each site.

Procedures

Herbicides were applied using a CO_2 backpack sprayer equipped with a 3.1-m, 6-nozzle spray boom, calibrated to deliver 168 liters ha^{-1}. Plot size was 3.1 by 9.1 m. Picloram was applied at 0.28 kg active ingredients (ai) ha^{-1}, clopyralid plus 2,4-D at 0.21 kg ai ha^{-1} plus 1.12 kg ai ha^{-1}, and dicamba plus 2,4-D at 0.56 kg ai ha^{-1} plus 1.12 kg ai ha^{-1}. Applications were made when spotted knapweed was at the spring-rosette, bolt, bud, flower, or fall-rosette growth stage during 1991 (Table 2). Treatments (3 herbicide treatments, 5 growth stages) were applied in a randomized--complete-block design and replicated 3 times at each site.

Sampling

Spotted knapweed density was determined in 3 randomly located 0.25-m^2 quadrants per plot during flowering in 1992, 1993, and 1994. Spotted knapweed

Table 2. Five phenological stages of spotted knapweed and dates of herbicide application at 2 study sites in western Montana.

Spotted knapweed growth stage	Growth stage description	Herbicide application date Missoula	 Avon
Rosette	plants 50–150 mm diamter	12 May 1991	17 May 1991
Bolt	85% of plants @125–230 mm bolt 15% of plants @ 50–125 mm bolt	7 June 1991	11 June 1991
Bud	75% of plants @ mid–bud stage 25% of plants @ early-bud stage	25 June 1991	3 July 1991
Flower	mid–flower stage; 90% of plants flowering	1 Aug. 1991	3 Aug. 1991
Fall regrowth	basal rosettes expanded to 50–150 mm diameter	12 Sept. 1991	12 Sept. 1991

plants were categorized as seedlings (defined as those that germinated during the current growing season and had 1 to 5 leaves) or mature plants (defined as those that had been growing for more than a season and had more than 5 leaves). Above-ground perennial grass biomass was harvested at peak standing crop during the third growing season following application. Plant material was clipped to a height of 1 cm within the 0.25-m^2 quadrats after spotted knapweed density had been determined. Samples were dried in a ventilated, heated (45°C) room to a constant weight (168 hours) and weighed. Perennial grasses were not separated by species during sampling because the objective was to determine overall response of perennial grasses to herbicide treatments.

Table 3. Mean squares generated from analysis of variance of spotted knapweed density data.

		Mean square			
		Missoula		Avon	
Source of variation	Df	Mature	Seedlings	Mature	Seedlings
Rep	2	525	178326	48	20267
Herb	3	26868**	4038920**	10638**	1490652**
Stage	4	3091**	485239**	302**	38005**
Herb * Stage	12	2080**	193600**	272**	21639**
Error A	38	3040	63215	50**	11806
Year	2	2002**	1022605**	1275**	72193**
Year * Herb	6	401*	67794**	360**	33598**
Year * Stage	8	151	20457	28	7502
Year * Herb * Stage	24	1090	33743**	69**	7625
Error B	80	30	15764	22	7072

[a] *, ** significant at the 5% and 1% levels of probability, respectively.

Analysis

All data were pooled and analyzed using analyses of variance. Site differences were detected; therefore, each site was analyzed separately. The model used for determining treatment differences in spotted knapweed density was a split-plot in time with herbicide treatment, growth stage, and herbicide treatment by growth stage tested using replication by herbicide treatment by growth stage as the error term. Year, year by herbicide treatment, year by growth stage, year by herbicide treatment by growth stage were analyzed as wholeplots. Biomass data were analyzed as a randomized-complete-block design. Herbicide treatment and growth stage at time of application were main effects. Herbicide by growth stage interaction was included in the model. All other sources of variation were pooled into the error term. Mean separations were made using Fisher's protected LSD's at P=0.05 (Peterson 1985).

Results

Mature Spotted Knapweed Density

At Missoula, analysis of variance indicated that the effect of herbicide treatments on mature spotted knapweed density depended upon the growth stage at which the herbicides were applied (Table 3). Applied at the spring-rosette stage, picloram and clopyralid plus 2,4-D reduced the number of mature spotted knapweed plants similarly for 3 years following treatment (Fig. 1). Dicamba plus 2,4-D reduced spotted knapweed density to about 50% compared to the control, but knapweed density was about 4 times greater than in plots sprayed with either picloram or clopyralid plus 2,4-D. Treatments applied at the bolt growth stage yielded similar densities to those applied at the spring-rosette growth stage, except that dicamba plus 2,4-D reduced spotted knapweed density to about 5 plants m^{-2}. This was similar to results of the clopyralid plus 2,4-D and picloram treatments. All herbicide treatments reduced mature spotted knapweed plant density similarly when applied at the bud growth stage. Picloram applied at the flower and fall-rosette growth stage yielded lowest spotted knapweed density at those stages. Clopyralid plus 2,4-D and dicamba plus 2,4-D yielded similar mature spotted knapweed densities at these growth stages. All herbicide treatments reduced spotted knapweed density below that of the control, regardless of growth stage at the time of application.

At Missoula, analysis of variance also indicated that the effect of herbicides on the density of mature spotted knapweed depended upon the year after application (Table 3). Picloram and clopyralid plus 2,4-D yielded the lowest mature spotted knapweed density in 1992 (Fig. 2). Dicamba plus 2,4-D reduced spotted knapweed density 3 times lower than that of

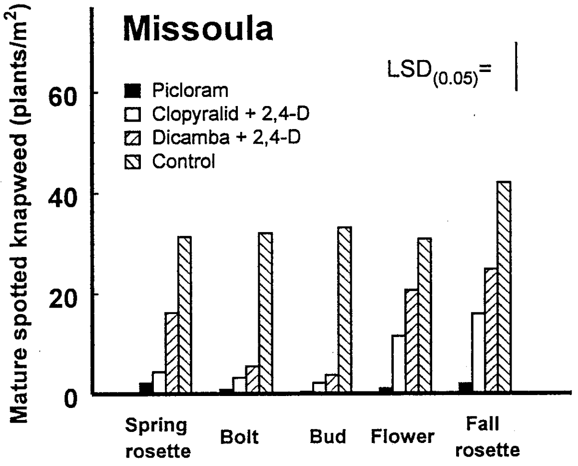

Fig. 1. Effect of herbicides applied at 5 growth stages on mature spotted knapweed at Missoula.

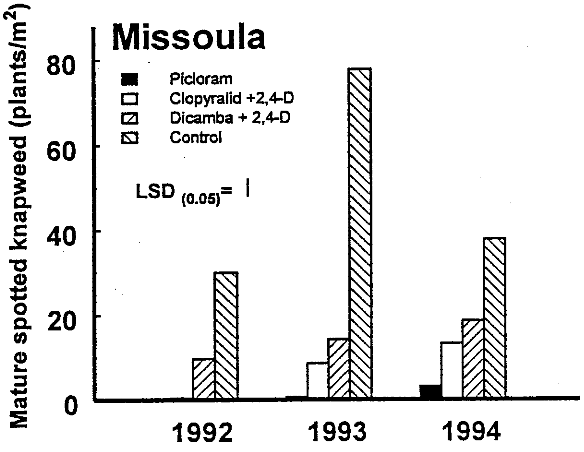

Fig. 2. Effect of herbicides each year following application on mature spotted knapweed at Missoula.

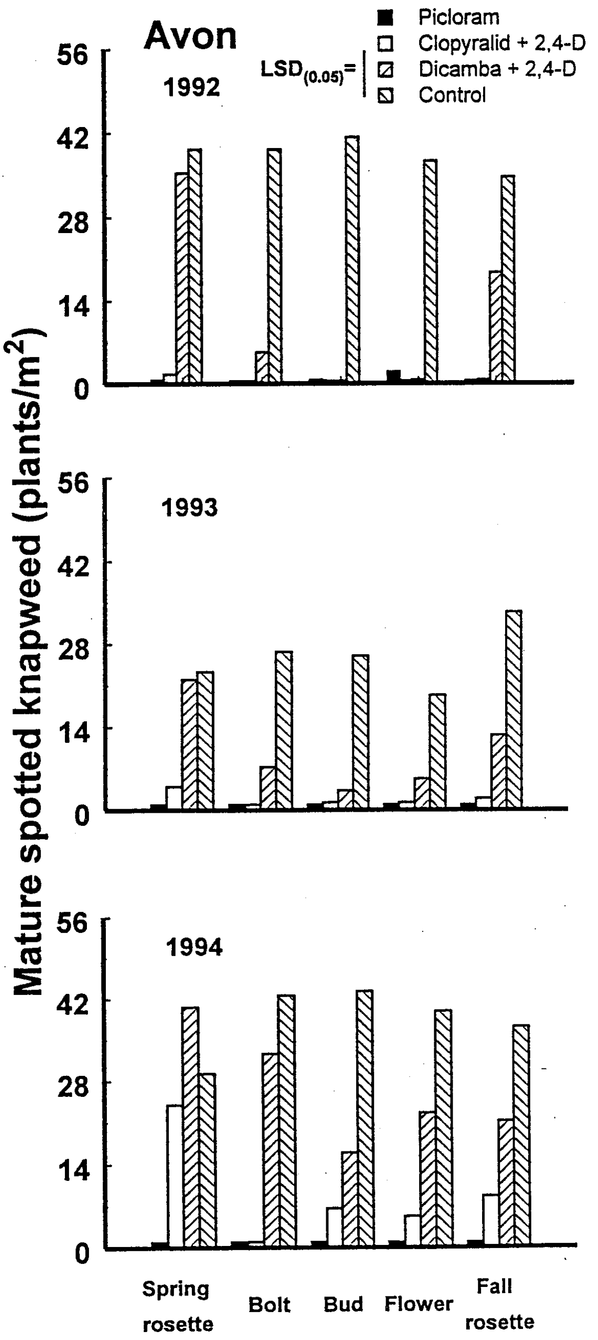

Fig. 3. Effect of herbicides applied at 5 growth stages on mature spotted knapweed in 1992, 1993, and 1994 at Avon. Comparisons can be made within or among bargraphs.

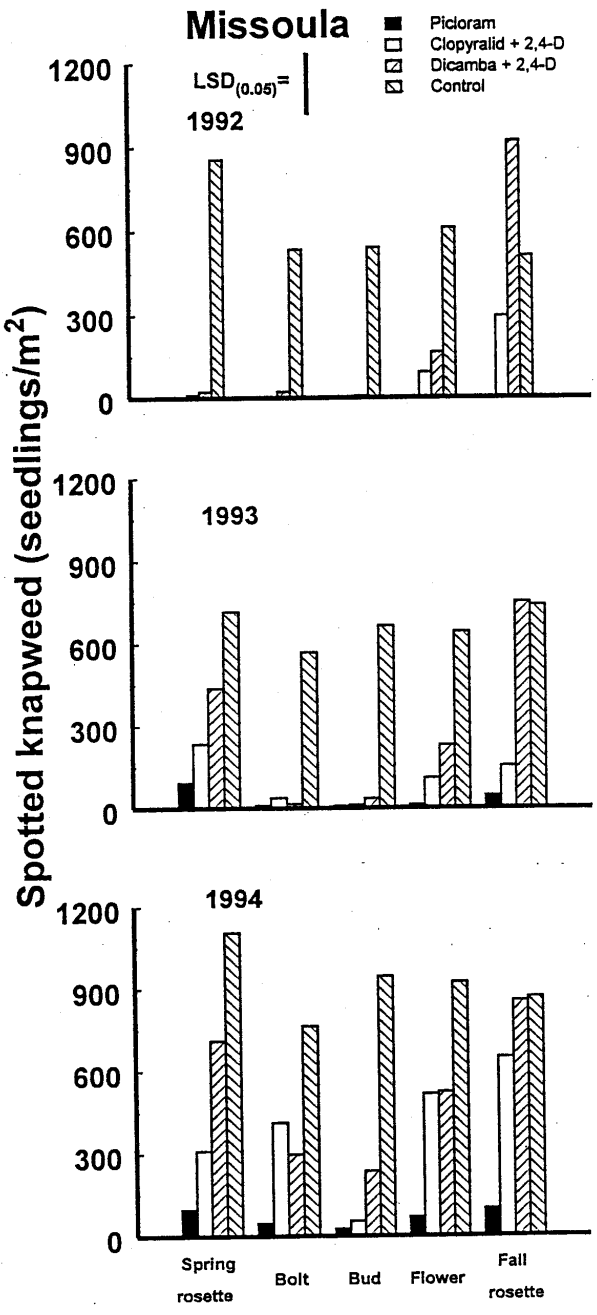

Fig. 4. Effect of herbicides applied at 5 growth stages on spotted knapweed seedlings in 1992, 1993, and 1994. Comparisons can be made within or among bargraphs.

the control that year. In 1993 and 1994, picloram yielded the lowest spotted knapweed density. Spotted knapweed density in plots treated with clopyralid plus 2,4-D was about 8.5 and 13 plants m^{-2}, while its density in plots treated with dicamba plus 2,4-D was about 14 and 19 plants m^{-2} in 1993 and 1994, respectively. All herbicide treatments reduced spotted knapweed density below that of the control, through the third year after application. At Avon, effect of the herbicide treatments on mature spotted knapweed density depended on the weeds growth stage and the number of years after application (Table 3). During each year and growth stage, picloram yielded nearly complete reduction of spotted knapweed density (Fig. 3). In 1992 and 1993, clopyralid plus 2,4-D reduced spotted knapweed density similarly to that of picloram at all growth stages. By 1994, only the bolting stage application of clopyralid plus 2,4-D remained as effective as picloram. This herbicide treatment was least effective when applied during the spring-rosette growth stage and moderately effective at the bud, flower, and fall-rosette growth stages by end of the study. In 1992, dicamba plus 2,4-D yielded nearly complete reduction of mature spotted knapweed density when applied at the bud and flower growth stages at Avon (Fig. 3). After treatment at these growth stages, spotted knapweed density increased as years after application increased. Among the dicamba plus 2,4-D treatments, the bud stage application yielded the lowest mature spotted knapweed density in 1994. Application of dicamba plus 2,4-D at the bolt growth stage reduced spotted knapweed density to about 4 plant m^{-2} in 1992, but the weed rapidly reestablished after this treatment. Dicamba plus 2,4-D applied at the fall-rosette growth stage reduced spotted knapweed density from about 35 to 20, 12, and 24 plants m^{-2} in 1992, 1993, and 1994, respectively. Of the herbicide treatments, dicamba plus 2,4-D applied at the spring-rosette growth stage was the least effective in reducing mature spotted knapweed density.

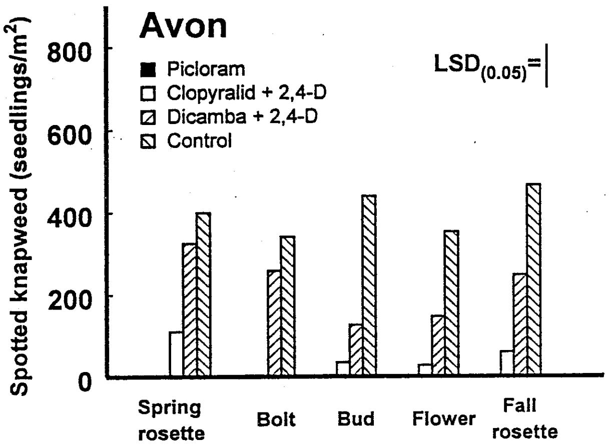

Fig. 5. Effect of herbicides applied at 5 growth stages on spotted knapweed seedlings at Avon.

Spotted Knapweed Seedling Density

At Missoula, effect of herbicide treatment on seedling spotted knapweed density depended upon growth stage and the time elapsed since application (Table 3). In 1992, picloram, clopyralid plus 2,4-D, and dicamba plus 2,4-D applied at the spring-rosette, bolt, bud, or flower growth stage provided similar seedling density reduction (Fig. 4). Picloram eliminated spotted knapweed seedlings for a full year when applied at the fall-rosette growth stage. Clopyralid plus 2,4-D and dicamba plus 2,4-D applied during the fall-rosette growth stage had seedling densities of 225 and 900 plant m^{-2}, respectively, in 1992. In 1993, all 3 herbicide treatments provided similar density reduction, with the exception of dicamba plus 2,4-D applied at the spring-and fall-rosette growth stage. Dicamba plus 2,4-D applied in the spring-rosette growth stage yielded about 450 plants m^{-2}, which was similar to that of clopyralid plus 2,4-D applied at the same stage that year. Dicamba plus 2,4-D applied at the fall-rosette growth stage yielded seedling densities similar to that of the control in 1993. By 1994, picloram and clopyralid plus 2,4-D yielded lowest seedling spotted knapweed density when applied at the spring-rosette growth stage. Dicamba plus 2,4-D reduced seedling densities of spotted knapweed by about 400 plant m^{-2} below that of the control applied at this growth stage. Applied at the bolt growth stage, picloram yielded the lowest number of spotted knapweed seedlings in 1994. Clopyralid plus 2,4-D and dicamba plus 2,4-D reduced spotted knapweed seedling density by about 50% at that time. In 1994, all 3 herbicide treatments yielded similar densities when applied at the bud growth stage. Applied at the flower and fall-rosette growth stages, picloram yielded the lowest seedling densities. Clopyralid plus 2,4-D applied at the flower growth stage reduced seedling spotted knapweed densities by about 50% of the control, but the herbicides effect was removed by 1994 when applied at the fall-rosette growth stage.

At Avon, analysis of variance indicated that the effect of herbicide treatments on spotted knapweed seedling density depended upon growth stage at which the herbicides were applied (Table 3). Picloram applied at any growth stage and clopyralid plus 2,4-D applied at bolt, bud, flower, and fall-rosette growth stages provided lowest spotted knapweed seedling density (Fig. 5). Clopyralid plus 2,4-D applied at the rosette growth stage lowered spotted knapweed seedling density to about 110 plants m^{-2}. Dicamba plus 2,4-D did not reduce spotted knapweed seedling densities when applied at the spring-rosette or bolt growth stage. At all other growth stages, dicamba plus 2,4-D yielded densities ranging from 120 to 250 seedling m^{-2}.

At Avon, analysis of variance also indicated the effect of herbicide treatment on spotted knapweed seedling density depended upon the year after application (Table 3). Picloram (0 seedlings m^{-2})and clopyralid plus 2,4-D (50 seedlings m^{-2}) yielded lowest spotted knapweed seedling density all three years after application (Fig. 6). Dicamba plus 2,4-D yielded 239, 265, and 159 seedling spotted knapweed plants m^{-2} in 1992, 1993, and 1994, respectively. All herbicide treatments reduced seedling spotted knapweed density below that of the control at this site.

Grass biomass

At the Missoula site, the effect of herbicide treatment on grass biomass 3 years after application depended upon the growth stage of spotted knapweed at the time of application (Table 4). Applied at the spring-rosette growth stage, picloram and clopyralid plus 2,4-D yielded greatest grass biomass, while dicamba plus 2,4-D yielded least grass biomass (Fig. 7). Applied at the bolt growth stage, picloram yielded highest grass biomass. Clopyralid plus 2,4-D (610 kg ha^{-1}) and dicamba plus 2,4-D (590 kg ha^{-1}) yielded similar grass biomass at that growth stage. Picloram and clopyralid plus 2,4-D yielded highest bio-

Table. 4. Means squares generated from analysis of variance of biomass data.

		Mean square	
Source	Df	Missoula Biomass	Avon Biomass
Rep	2	4077739.0	548844.2
Herb	3	3999166.9**[a]	5139628.9*
Stage	4	565234.1 **	216856.2
Herb * Stage	12	148020.1**	132272.3
Error	38	68109.9	98702.0

[a],** significant at the 5% and 1% levels of probability, respectively.

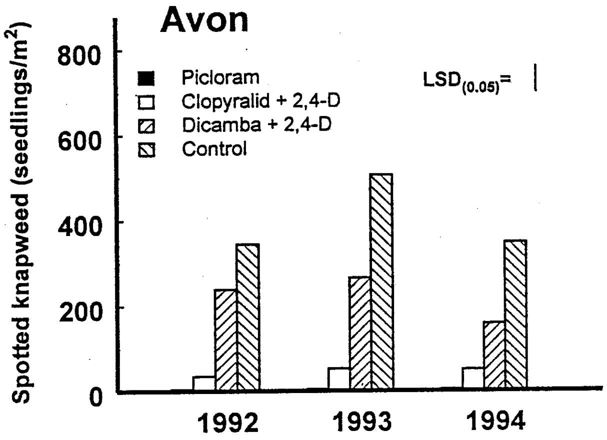

Fig. 6. Effect of herbicides each year following application on spotted knapweed seedlings at Avon.

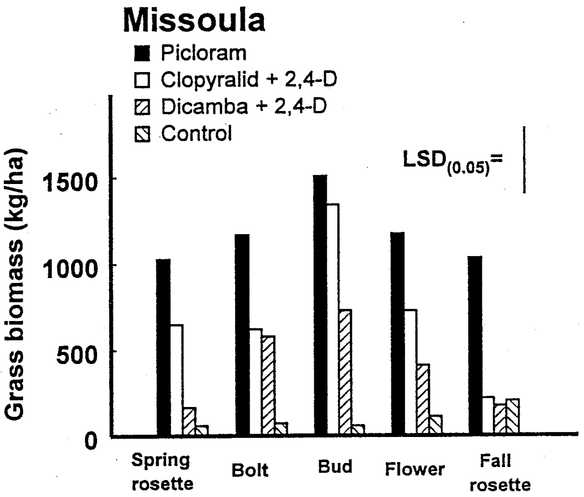

Fig. 7. Effect of herbicides applied at 5 growth stages on perennial grass biomass at Missoula.

mass, but was similar to picloram applied at the bolt and flower growth stages. Dicamba plus 2,4-D applied at the bud growth stage yielded about 750 kg/ha^{-1} of grass, which was about 10 times that of the control. Picloram and clopyralid plus 2,4-D yielded highest grass biomass when applied at the flower growth stage; however, clopyralid plus 2,4-D yielded grass biomass similar to that of dicamba plus 2,4-D at this growth stage. Dicamba plus 2,4-D did not increase grass yields over those of the control. Applied at the fall-rosette growth stage, picloram yielded highest grass biomass. All other herbicide treatments were similar to the control when applied at this stage.

Herbicide treatments affected grass biomass at Avon and was not dependent upon growth stage (Table 4). Picloram, clopyralid plus 2,4-D, and dicamba plus 2,4-D yielded 1600, 1175, and 620 kg ha^{-1} of grass biomass, respectively (Fig. 8). All herbicide treatments produced greater biomass than that of the control.

Discussion

Picloram provides consistent and effective control of spotted knapweed. Davis (1990) found that picloram applied at 0.07, 0.11, 0.14, 0.22, 0.25, and 0.28 kg ai ha^{-1} during the bud growth stage provided 100% control for 3 to 5 years. In this 4-year study, we found that the efficacy and persistence of spotted knapweed control using picloram at 0.28 kg ai ha^{-1} was independent of the weeds growth stage and the time of application. Based on our study, we concluded that spotted knapweed reestablishes from its seedbank, rather than regrowth from mature plants. Spotted knapweed seeds remain dormant, but viable in the soil for over 8 years (Davis et al. 1993).

In many situations, land managers apply picloram when they notice the flowering plants. Unfortunately, this may be the least effective method of determining timing of herbicide applications. In this case, knapweed plants continue to produce seeds after picloram has been applied, but before the plants die. This replenishes the seedbank and results in continuous, periodic picloram applications, which are probably not cost effective (Griffith and Lacey 1991). Applying picloram before flowers appear may prevent spotted knapweed seed rain and reduce the seedbank. Over a long period (>10 years), spotted knapweed density may be reduced to occasional plants or patches, which can be retreated by spot spraying. An alternative method for determining timing of repeated application would be to identify threshold levels of spotted knapweed that would optimize the value of the application based of the response of the desired plant community.

Clopyralid plus 2,4-D (0.21 kg ai ha^{-1} plus 1.12 kg ai ha^{-1}) applied at the bolt or bud stage provided control of spotted knapweed similar to picloram (about 95% control) at Avon and about 50% control 3 years after application at Missoula. Fay (1990) found clopyralid plus 2,4-D at similar rates provided nearly 100% control of spotted knapweed 1 year following application on 2 sites in Montana. Clopyralid has a shorter soil residue period and adsorbs to soil particles more tightly than picloram (Fay et al. 1991). In addition, clopyralid plus 2,4-D may maintain greater species diversity than picloram (Rice et al. 1992). Therefore, clopyralid plus 2,4-D may provide an alternative to picloram in environmentally sensitive areas.

Dicamba is more effective in controlling spotted knapweed than 2,4-D because it provides 2 to 3 years of control depending on the level of plant competition following treatment (Fay et al. 1989). In another study, dicamba at 2.2 kg ai ha^{-1} provided excellent control when applied in the rosette growth stage (Lacey et al. 1986). In our study, dicamba plus 2,4-D (0.56 plus 1.12 kg ai ha^{-1}) was most effective when applied during bolt and bud growth stages, and least effective during the spring-and fall-rosette growth stage. However, clopyralid plus 2,4-D provided greater control

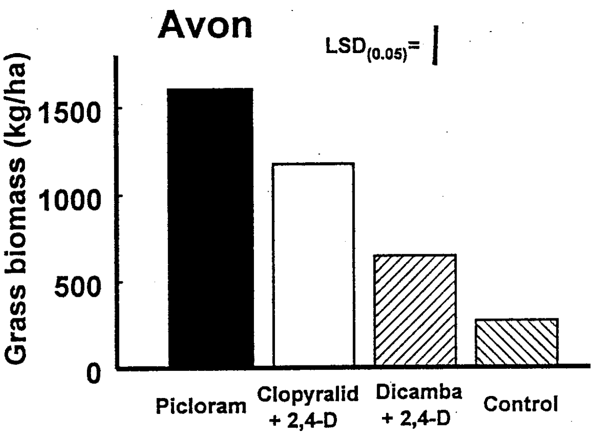

Fig. 8. Effect of herbicides on grass biomass at Avon.

than dicamba plus 2,4-D at those stages. Dicamba plus 2,4-D is currently recommended for controlling spotted knapweed on small ranchettes (about 44 ha) because the combination provides good control, but is not persistent enough to limit landowners' options in the future (Fay et al. 1995). This study suggests that clopyralid plus 2,4-D may provide more effective and longer-term spotted knapweed control without greatly limiting future land management options.

Although picloram persists in the soil and affects weeds for 12 to 30 months (Hamaker et al. 1967, Lacey 1985), extended control is enhanced by competition from residual perennial grasses that are released from competition by the herbicide application (Renney and Hughes 1969). In most cases, picloram yielded highest grass biomass 3 years after treatment, which may help explain the persistence of control of spotted knapweed using this herbicide. Picloram increased grass biomass by 1,000 to 1,550 kg ha^{-1}. These results were similar to those found by Davis (1990) and Sheley and Jacobs (1997). Long-term herbicidal control of spotted knapweed using picloram can be cost-effective on cattle ranches with highly productive rangeland and a residual (suppressed) grass understory (Griffith and Lacey 1991). However, future research should focus on incorporating picloram and other herbicides into effective and sustainable integrated weed management strategies.

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Residual nitrogen effects on soil, forage, and steer gain

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Abstract

Nitrogen fertilization is a common practice on introduced grass pastures established on marginal farmland in the Southern Great Plains. The efficiency of N fertilizer use on pastures and concern about nitrate movement into substrata prompted this study of residual N effects following fertilization. The study was conducted on Old World bluestem (*Bothriochloa ischaemum* L.) pastures on Pratt soil (sandy, mixed thermic Psammentic Haplustalfs) in western Oklahoma where the 57-year average annual precipitation is 566 mm yr^{-1}. Herbage production and steer gains were quantified over 3 summer grazing seasons on paddocks fertilized annually with 0, 34, 68, or 102 kg N ha^{-1} yr^{-1} during the preceding 5 years. Peak standing ungrazed herbage yields were 2- to 4-fold greater in paddocks fertilized the preceding 5 years and were linearly related to the total N applied the previous 5 years. Steer weight gain responded linearly to N with an average of 0.63 kg gain over 3 years per kg N applied over the preceding 5 years. No differences ($P > 0.05$) in soil nitrate concentrations to a depth of 2.8 m were measured among the N rate treatments. Overall, substantial effects of residual N were measured in both herbage mass and steer weight gain for 3 years following 5 years of N fertilization.

Key Words: Southern Plains, marginal farmland, grass fertilization, Old World bluestem, *Bothriochloa ischaemum*, forage quality

Resumen

La fertilización nitrogenada es una práctica común en las praderas de pastos introducidos establecidas en las tierras agrícolas marginales de las Grandes Planicies del Sudeste. La eficiencia del uso de fertilizante nitrogenado en praderas y la preocupación acerca del movimiento de los nitratos hacia el substrato motivo la realización de este estudio de los efectos del nitrógeno residual seguido de la fertilización. Este estudio se condujo en praderas de "Old World Bluestem" (*Bothriocloa aschaemum* L.) en suelo Pratt (sandy, mixed thermic, Psemmentic Haplustalfs) localizadas en el oeste de Oklahoma, en donde el promedio de precipitación de 57 años es de 566 mm yr^{-1}. La producción de forraje y las ganancias de los novillos se cuantificaron en 3 estaciones de apacentamiento en verano en potreros que habían fertilizado anualmente durante 5 años con 0, 34, 68 o 128 kg ha-1 yr^{-1} de nitrógeno. Los rendimientos máximos de producción del forraje sin apacentar fue de 2 a 4 veces mayor en los potreros fertilizados durante los 5 años previos y estuvieron linealmente relacionados con la cantidad total de nitrógeno aplicado en los 5 años. Las ganancias de peso de los novillos respondieron linealmente a la aplicación de nitrógeno con un promedio en 3 años 0.63 kg de ganancia por kg de nitrógeno aplicado en los 5 años anteriores. No se encontraron diferencias ($P > 0.05$) entre tratamientos de nitrógeno con respecto en las concentraciones de nitratos medidas hasta una profundidad de 2.8 m. En general, se midieron efectos substanciales del nitrógeno residual tanto en la producción de forraje como las ganancias de peso de los novillos durante 3 los tres años posteriores a 5 años de fertilización nitrogenada.

Nitrogen (N) fertilization of introduced grass pastures is a common practice in western Oklahoma and adjacent areas in Texas (Dahl and Cotter 1984, Berg and Sims 1995). These pastures are usually established on marginal farmland that are deficient in plant-available N as a result of up to 100 years of cultivation and subsequent erosion (Haas et al. 1957). Management of N fertilized pastures requires a balance among production, profit, and environmental quality (Bock and Hergert 1991).

A single application of 68 kg N ha^{-1} yr^{-1} in April to WW Spar Old World bluestem (*Bothriochloa ischaemum* L.) pastures in western Oklahoma generally resulted in maximum forage mass and steer weight gain (Berg and Sims 1995). However, fertilizer N-use efficiency in steer weight gain was greater for a lower N application rate of 34 kg N ha^{-1} yr^{-1}. Fertilizer N-use efficiency averaged 3.3 kg steer weight gain per kg N applied with the first 34 kg N ha^{-1} yr^{-1} increment, 1.0 kg for the second 34 kg N ha^{-1} yr^{-1} increment (total of 68 kg N ha^{-1} yr^{-1}) and was negligible for the third 34 kg N ha^{-1} yr^{-1} increment (total of 102 kg N ha^{-1} yr^{-1}).

This study is a continuation of an earlier N rate study reported by Berg and Sims (1995). The objectives of the present study were to determine the residual N effects after 5 years of pasture fertilization on: 1) concentrations of nitrate, ammonium, total N and organic C in the soil; and 2) herbage mass, forage nutritive value, and steer weight gain in the ensuing 3 years without fertilization.

Materials and Methods

This study was conducted on the Southern Plains Experimental Range near Fort Supply (99° 23'W, 36° 27'N) in western Oklahoma. Soils are predominately a deep loamy sand (Pratt series-sandy,

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mixed, thermic Psammentic Haplustalfs). Prior to cultivation, the land supported a sand sagebrush (*Artemisia filifolia* Torr.)-mixed grass prairie with sand bluestem (*Andropogon hallii* Hack.), sand dropseed (*Sporobolus cryptandrus* (Torr.) Gray), blue grama (*Bouteloua gracilis* (H.B.K.)Lag.), switchgrass (*Panicum virgatum* L.), and little bluestem (*Schizachyrium scoparium* (Michx.) Nash) as dominant grasses (Berg 1994).

The study area was farmed for about 40 years before 'WW-Spar' Old World bluestem was established in the early 1980's. The bluestem pasture was fertilized with 68 kg N ha^{-1} yr^{-1} and grazed in 1986 and 1987. In 1988 the pasture was divided into 16 paddocks and ammonium nitrate treatments of 0, 34, 68, and 102 kg N ha^{-1} yr^{-1} were broadcast applied in April of each year in a randomized complete block design with 4 replications. The N treatments were repeated for 5 years between 1988 and 1992 (Berg and Sims 1995). Incremental N rates were obtained by repeat applications of fertilizer, on the same day, with a drop spreader calibrated for the 34 kg N ha^{-1} yr^{-1} rate. Thus, the total amount of N applied over the 5-year period was 0, 170, 340, and 510 kg N ha^{-1} for the respective annual N treatments. Paddocks were 1.2 ha for the control (no N) and 0.8 ha for each N-fertilized treatment.

Paddocks were grazed 4 of the 5 years N fertilizer was applied (Berg and Sims 1995). A low temperature of –20 °C on 22 December 1989, following a dry fall (4 mm precipitation October through December 1989) resulted in extensive winterkill of WW-Spar Old World bluestem. To allow forage recovery, the bluestem pastures were not grazed during the 1990 growing season.

Soil sampling was designed to test differences among N-rate treatments following 5 years of N fertilization. Samples were taken in the spring of 1988 prior to N fertilization and again in the spring of 1993, approximately 1 year following the last application of N fertilizer. Two groups of soil samples were taken; the first was to characterize fertility in the surface 15 cm of soil, the second was to determine nitrate (NO$_3$) and ammonium (NH$_4$) movement and accumulation to a depth of 2.8 m. Prior to soil sampling in 1988 and 1993, forage aftermath was burned in March. For the soil fertility sampling, because of soil heterogeneity within paddocks caused by topography and erosion, 3 representative 6 x 10 m areas within each paddock were permanently marked and sampled in 1988 and resampled in 1993. Twenty-eight random 2-cm diameter cores were taken to a depth of 15 cm in each 6 x 10 m sampling area, composited by 5 cm increments, and air dried. Soil samples were passed through a 2 mm sieve to remove roots and foreign material prior to storage or analysis. Thus, 9 soil samples, composited from 28 subsamples, were collected in 1988 and again in 1993 for analyses from each paddock (3 areas x 3 depths). Data were averaged from the 3 areas (subsamples) per paddock for later statistical analyses. Nitrate was determined by 1 M KCl extraction and Cd reduction (Gelderman and Fixen 1988), extractable ammonium by 1 M KCl extraction and the indophenol blue method (Keeny and Nelson 1982), total N by a Kjeldahl procedure (Bremner and Breitenbeck 1983), and organic C by the Mebius method (Nelson and Sommers 1982). Soil samples were air dried and stored in a cool, dry area and all analyses made in 1994.

Nitrate and ammonium concentrations to a depth of 2.8 m were determined in 4-cm diameter soil cores taken at increments of 0-0.4, 0.4-1.2, 1.2-2.0., and 2.0-2.8 m. One core was taken per paddock in 1988, the location marked, and another core taken in 1993 within 0.5 m of the original location. Samples were air dried and nitrate and ammonium determined by methods given above.

Precipitation measured at the Southern Plains Experimental Range headquarters, about 1.5 km from the research site, was 459 mm in 1993, 480 mm in 1994, and 457 mm in 1995 (Table 1). The 57 year mean is 566 mm yr^{-1}. January through June precipitation was 257 mm in 1993, 201 mm in 1994, and 338 mm in 1995; the 57 year January through June precipitation mean is 290 mm. Average annual precipitation for the previous 5 years, beginning in 1988 was 503, 679, 560, 409, and 503 mm, respectively.

Peak standing herbage mass was harvested within five, 1.25 x 4 m exclosures within each paddock on 15 July 1993, 28 June 1994, and 1 July 1995. The exclosures were moved annually. Herbage was cut at a 7-cm height with a Hegge sickle bar plot harvester on 1.25 X 4 m areas within each exclosure, collected as one sample, and weighed. Herbage mass in each paddock was also cut at a 7-cm height with a Hegge sickle bar plot harvester by randomly sampling five, 1.25 x 4 m areas within each paddock at the time steers were placed in the paddocks, 3 weeks later, and when the steers were moved. Herbage subsamples, of approximately 300 g size, were collected and dried at 57°C to determine dry matter content. These dried samples were ground to pass a 1-mm screen and analyzed for N (Bremner and Breitenbeck 1983) and in vitro dry matter digestibility (Tilley and Terry 1963 as modified by White et al. 1981). Nitrogen concentration was multiplied by 6.25 to estimate crude protein.

In this monoculture pasture, herbage mass sampled to a stubble height of 7 cm was considered to approximate the available forage mass for the grazing animal. Thus, herbage allowance was calculated as the average herbage mass in each paddock within each sampling interval divided by the number of steers and steer weight (kg) in the paddock over that period.

Yearling steers were placed in the paddocks in June when grass height was visually estimated to be between 15 and 20 cm. Steers were grazing similar Old World bluestem forage prior to the beginning of this summer grazing study. Steers grazed Old World bluestem in this study at or near peak nutritive value and when grass growth rates were generally high until mid July or early August. Steers, crosses of Hereford or Angus with Simmental, Limousin, or Brahman, were implanted with 200 mg progesterone and 20 mg

Table 1. Monthly precipitation (mm) during the years of the study (1993–1995) compared to the 57-year mean at the Southern Plains Experimental Range, 1940–1989, Ft. Supply, Okla.

Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
							(mm)						
1993	36	36	40	56	78	11	59	86	22	10	17	10	459
1994	12	17	28	74	55	15	78	48	28	64	26	34	480
1995	15	4	103	28	115	73	53	13	36	0	1	18	457
Mean	21	19	57	53	83	33	63	49	29	25	15	21	465
56-year	14	24	40	46	90	76	71	64	52	42	28	21	566

estradiol benzoate in May. Initial weights of the 56 steers used each year averaged 298 ± 3 (SE) kg in 1993, 232 ± 3 kg in 1994, and 257 ± 3 kg in 1995. Steers were weighed on the morning they were placed in the paddocks, and the day after they were removed. All steer weights followed an 18 hour fast without feed or water.

The number of steers used during the first 3 weeks was based on experience from the earlier 5-year N fertilization study by Berg and Sims (1995) and from previous studies at the Southern Plains Experimental Range (Sims and Dewald 1982). Steer numbers were adjusted slightly for the second grazing interval in an attempt to maintain similar amounts of forage mass per steer in each paddock. Because of variation in herbage growth, the subsequent grazing level was not always precise. Thus, care must be exercised in interpreting average daily weight gain and gain ha^{-1}. Steer weight gain per paddock was the experimental unit used in the statistical analysis (SAS Institute 1985).

Cattle were removed and the pastures allowed to regrow before fall dormancy. Number of continuous grazing days was 35, 33, and 42 days in 1993, 1994, and 1995, respectively. Aftermath was burned in March 1993, but mowed and dropped in place in March of 1994 and 1995.

Residual N fertilizer use efficiency was calculated for each year (1993–95) by subtracting steer weight gain ha^{-1}yr^{-1} on the unfertilized paddocks from steer weight gain ha^{-1}yr^{-1} on paddocks N fertilized over the 1988–1992 period and then dividing by the total amount of N applied over the 1988–1992 period.

For the soil analyses our major interest was 5 years differences (deltas between 1988 and1993) as affected by N treatments; therefore, the delta values were used in statistical analyses. Soil sampling design was a randomized complete block with rate of N as the treatment variable. Observations were made at incremental depths vertically within treatments. The analysis of variance (AOV) model was a randomized complete block with a block effect, N rate effect and depths analyzed as a repeated factor, which allowed for adjustment for correlation between depths when testing for depths and the depth x N rate interaction effects. The significance levels for N rates were determined by F tests and significance levels for depth and the depth x N rate interaction were determined by Kendall's Tau. Analysis of variance was conducted for steer weight gain ha^{-1} as affected by N rates over years and for each year; treatment effects were also partitioned into linear, quadratic, cubic, and residual components by year. Peak standing herbage mass for each year (1988–1994) was analyzed using a repeated measure, 2-way AOV with correction for correlation between successive years. The AOV was conducted for average daily steer gain (ADG) and forage nutritive components. Duncan's new multiple range test ($P < 0.05$) was used to separate treatment effects on steer ADG. Statistical analyses was conducted using SAS Institute (1985) procedures.

Results and Discussion

Soil N and C

In the soil fertility analyses of the surface 15 cm, nitrate was low with no significant change ($P > 0.05$) following 5 years of pasture fertilization compared to non-fertilization (Table 2). Ammonium concentration increased ($P < 0.01$) with increased N application, however, overall ammonium concentrations were lower in 1993 than in 1988. Extractable mineral N (nitrate and ammonium) has been commonly used as a routine soil test for plant-available N in cultivated soils (Dahnke and Johnson 1990). However, peak herbage standing mass (Fig. 1) indicated that substantially more N was available to plants in paddocks receiving higher N rates in the preceding 5 years. Thus, routine agricultural soil tests for extractable nitrate and ammonium appear to be of little to no value in predicting N availability to plants in these and similar pastures. An exception to this might be when excessive fertilizer N is applied. Soil incubation tests (Dahnke and Johnson 1990) however, may be useful for quantifying N which becomes available from mineralization of organic N in pastures.

Table 2. Soil nitrate, ammonium, total N, and organic C concentrations to 15 cm soil depth before (1988) and after (1993) 5 years of N fertilization and grazing of an Old World bluestem at the Southern Plains Experiemental Range, Ft. Supply, Okla.

Component	Total N (kg ha^{-1}) applied (1988–1993)							
Depth	0		170		340		510	
cm	1988	1993	1988	1993	1988	1993	1988	1993
Nitrate	(mg N kg^{-1})[1]							
0–5	0.3 ± 0.5[2]	0.6 ± .07	0.4 ± .05	0.8 ± .16	0.05 ± .05	0.9 ± .09	0.5 ± .20	0.9 ± .07
5–10	0.3 ± .04	0.5 ± .01	0.3 ± .07	0.5 ± .07	0.3 ± .02	0.6 ± .03	0.4 ± .20	0.6 ± .08
10–15	0.1 ± .01	0.3 ± .09	0.2 ± .04	0.5 ± .03	0.1 ± .02	0.4 ± .0.4	0.3 ± 1.4	0.4 ± .06
Ammonium	(mg N kg^{-1})[3]							
0–5	6.7 ± .7	3.5 ± .5	9.8 ± 2.1	4.8 ± .8	7.0 ± .8	4.6 ± .3	7.4 ± .4	5.1 ± .6
5–10	5.9 ± .6	1.8 ± .1	6.3 ± .8	1.9 ± .5	5.7 ± .5	2.6 ± .2	5.0 ± .8	2.9 ± .4
10–15	3.8. ± .2	2.1 ± .3	4.4 ± .4	2.0 ± .3	3.1 ± .1	2.2 ± .1	2.9 ± .5	2.0 ± .1
Total N (	g N kg^{-1})[4]							
0–5	0.77 ± .09	0.87 ± .09	0.93 ± .17	1.03 ± .19	0.73 ± .05	0.92 ± .05	0.81 ± .10	0.86 ± .07
5–10	0.58 ± .03	0.58 ± .05	0.63 ± .06	0.63 ± .07	0.57 ± .03	0.58 ± .05	0.52 ± .03	0.52 ± .03
10–15	0.50 ± .03	0.46 ± .04	0.52 ± .06	0.54 ± .06	0.46 ± .04	0.52 ± .03	0.44 ± .03	0.44 ± .03
Organic	C (g C kg^{-1})[5]							
0–5	7.9 ± .9	9.1 ± .8	9.5 ± 2.0	12.2 ± 2.6	7.5 ± .6	10.9 ± .5	8.4 ± 1.2	10.4 ± .9
5–10	5.5 ± .4	5.8 ± .7	5.8 ± 0.8	4.4 ± 1.8	5.4 ± .3	6.0 ± .4	5.1 ± .5	4.7 ± .2
10–15	4.6 ± .4	4.6 ± .3	4.7 ± 0.6	5.2 ± 0.7	4.3 ± .3	5.0 ± .5	4.1 ± .3	4.3 ± 2

[1] P > F for differences in nitrate levels between years for N treatments = 0.85, soil depths = 0.09, and N X soild depths = 0.98.

[2] Standard error (s.e.), n = 4.

[3] P > F for differences in ammonium levels between years for N treatments = 0.01, soil depths = 0.01, and for N X soil depths = 0.87.

[4] P > F for differences in total N levels between years for N treatments = 0.13, soil depths = 0.01, and for N X soil depths = 0.68.

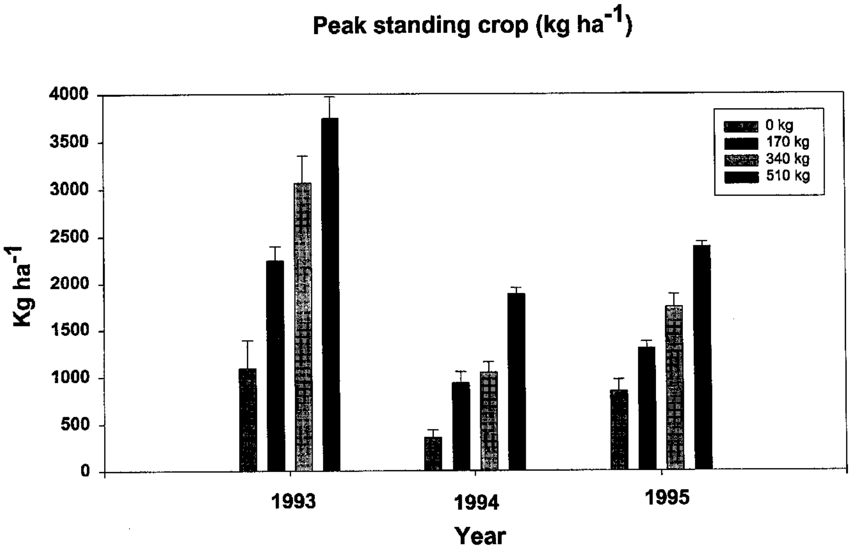

Fig. 1. Peak standing herbage mass (kg ha^{-1} ± s.e.) in 1993, 1994, and 1995 in exclosures within paddocks. Paddocks were fertilized with a total of 0, 170, 340, and 510 kg N ha^{-1} during the previous 5 years at the Southern Plains Experimental Range, Ft. Supply, Okla.

Total soil N and organic C concentrations increased in the surface 5 cm in all treatments over the 1988–1993 period. However, our major interest was whether or not there was a greater change in total N and organic C in the N-fertilized paddocks than in the unfertilized paddocks. Thus, we calculated the change from 1988 to 1993 in total N and organic C for each N treatment and subjected the data to AOV. No significant change was measurable in total N ($P = 0.13$), but organic C increased ($P = 0.03$) with increased N application (Table 2).

The potential for movement of mineral N into substrata and eventually into groundwater has been a concern with N fertilization of pastures. There was more ($P < 0.05$) extractable nitrate in all treatments to a depth of 2.8 m in 1993 than in 1988 (Table 3). However, most levels of extractable nitrate, about 1 mg N kg^{-1} soil (1 ppm extractable nitrate N), were low. Higher nitrate concentrations were found at depths of 1.2 to 2.8 m in some soil samples from the higher N rate treatments; however, this was not consistent among replications and thus N treatments x depths interaction was not significant ($P > 0.05$). We believe that more intensive sampling is needed to quantify nitrate movement than the single adjacent soil cores we took per paddock in 1988 and 1993.

Herbage dynamics

Peak standing herbage yields from exclosures within paddocks that were N fertilized the preceding 5 years were 2- to 4-fold greater than yields from exclosures within paddocks that had not been fertilized (Fig. 1). There were significant differences ($P < 0.01$) in peak standing herbage yields between the N levels and years when residual N effects were measured. These differences were, however, not independent ($P < 0.05$) because the relative difference in herbage mass and amount of N applied during the previous 5 years was not the same in all years, particularly in 1994 (Fig. 1). The increase was linearly related to total N applied with r^2 values of 0.82 in 1993, 0.85 in 1994, and 0.90 in 1995. This linear relationship indicated that N was a limiting factor in herbage mass yields on all residual N treatments each year the residual effect was measured. In contrast, yields of herbage mass during the 5 years that N was applied was curvilinearly related as increasing N fertilizer increments produced smaller increases in herbage mass (Berg and Sims 1995). Precipitation during the growing season for 1993, 1994, and 1995 was 185, 172, and 339 mm, respectively (Table 1). The dynamics of peak standing herbage is a function of available N levels in the soil and recent precipitation. The separate effects on these 2 factors cannot be partitioned in this study. However, the relative responses from the N fertilizer treatments were consistent across all 3 years.

Available herbage mass per 100 kg steer^{-1} weight averaged 60 ± 3 kg across all treatments, grazing periods, and years (Table 4). There were no significant differences in the amounts of herbage mass per 100 kg steer^{-1} between treatments within each period. Over the 3 years, herbage allowance averaged 139 ± 15, 170 ± 20, 133 ± 14, and 172 ± 16 kg forage steer^{-1} for the 0, 170, 340, and 510 kg total N ha^{-1} applied, respectively. There were

Table 3. Soil nitrate, ammonium concentrations to 2.8 msoil depth before (1988) and after (1993) 5 years of N fertilization and grazing of an Old World bluestem at the Southern Plains Experimental Range, Ft. Supply, Okla.

Component	Total N (kg ha^{-1}) applied (1988–1993)							
Depth	0		170		340		510	
m	1988	1993	1988	1993	1988	1993	1988	1993
Nitrate				(mg N kg^{-1})[1]				
0–0.4	0.3 ± 0.1[2]	0.7 ± .0.1	0.3 ± 0.1	0.9 ± 0.1	0.3 ± 0.1	1.0 ± 0.2	0.3 ± 0.1	1.0 ± 0.1
.0.4–1.2	0.4 ± 0.1	0.7 ± 0.1	0.3 ± .07	05. ± .07	0.3 ± .02	0.6 ± .03	0.4 ± .20	0.6 ± .08
1.2–2.0	0.3 ± 0.1	0.7 ± 0.1	0.5 ± 0.2	1.1 ± 0.4	0.3 ± 0.1	1.0 ± 0.4	0.3 ± 0.1	0.5 ± 0.4
2.0–2.8	0.6 ± 0.1	0.8 ± 0.1	0.9 ± 0.3	1.4 ± 0.2	0.9 ± 0.3	2.9 ± 1.5	0.3 ± 1.6	3.0 ± 2.0
Ammonium				(mg N kg^{-1})[3]				
0–0.4	5.2 ± 0.4	2.4 ± 0.3	4.7 ± 0.5	2.5 ± 0.2	5.2 ± 0.3	2.6 ± 0.1	5.1 ± 0.9	2.7 ± 0.3
0.4–1.2	1.9 ± 0.1	2.0 ± 0.4	2.3 ± 0.3	2.0 ± 0.4	2.0 ± 0.4	1.5 ± 0.2	2.3 ± 0.3	1.8 ± 0.6
1.2–2.0	1.6 ± 0.1	1.2 ± 0.2	2.3 ± 0.6	1.9 ± 0.3	1.5 ± 0.3	1.0 ± 0.2	1.8 ± 0.5	3.0 ± 1.2
2.0–2.8	1.6 ± 0.1	1.5 ± 0.2	2.3 ± 0.6	2.1 ± 0.6	1.4 ± 0.2	1.9 ± 0.2	1.1 ± 0.2	.1.5 ± 0.2

[1] P > F for differences in nitrate levels between years for N treatments = 0.21, soil depths = 0.25, and N X soild depths = 0.27.

[2] Standard error (s.e.), n = 4.

[3] P > F for differences in ammonium levels between years for N treatments = 0.52, soil depths = 0.01, and for N X soil depths = 0.31.

Table 4. Stocking density and available herbage per 100 kg yearling steer^{-1} (kg ± se) for 2 summer grazing periods to determine residual N effects over 3 years following 5 years of N fertilization with 0, 170, 340, and 570 kg N ha^{-1} at the Southern Plains Experimental Range, Ft. Supply, Okla.

Year	Grazing Interval	Total N (kg ha^{-1}) applied from 1988 to 1992							
		0		170		340		510	
		(Steer ha^{-1})	(kg herbage per 100 kg steer)	(Steer ha^{-1})	(kg herbage per 100 kg steer)	(Steer ha^{-1})	(kg herbage per 100 kg steer)	(Steer ha^{-1})	(kg herbage per 100 kg steer)
1993	7 June–29 June	2.5	24 ± 6	3.7	45 ± 14	4.9	36 ± 10	4.9	46 ± 9
	30 June–12 July	2.3	43 ± 9	3.1	84 ± 28	4.3	54 ± 14	4.9	63 ± 16
1994	8 June–27 June	2.5	61 ± 4	3.7	79 ± 11	4.9	70 ± 9	4.9	91 ± 6
	28 June–11 July	2.5	56 ± 5	3.4	93 ± 11	4.9	74 ± 11	5.3	107 ± 6
1995	20 June–11 July	2.5	57 ± 6	3.7	54 ± 9	4.9	48 ± 6	4.9	76 ± 22
	12 July–1 Aug.	2.5	61 ± 14	3.7	51 ± 9	4.1	37 ± 6	4.9	44 ± 12

significant differences in herbage mass, however, between the early and late grazing periods for treatments within years ($P < 0.01$) and between years ($P < 0.01$). Averages for the early (June) and late (July) summer grazing periods were 57 ± 4 and 64 ± 3 kg 100 kg steer^{-1}, respectively. There were significant year effects ($P < 0.01$) for both the June and July periods; treatment effect was significant ($P < 0.05$) only for the June grazing period. The treatment means for the June period were 48 ± 7, 59 ± 11, 51 ± 25, and 71 ± 38 kg 100 kg steer^{-1} for the 0, 170, 340, and 510 kg total N ha^{-1} applied , respectively. Although, there were no significant differences in herbage mass steer^{-1} between treatments within a grazing period, care is still needed in interpretation of the impacts on steer weight gains.

Forage crude protein concentration was considerably higher ($P < 0.05$) on 7 June 1993, compared to 1994 and 1995, in paddocks that had received higher N rates in the preceding 5 years (Table 5). In contrast, on 7 June 1994 and on 19 June 1995 crude protein concentrations were relatively low and similar in all treatments. This may have resulted from sampling all herbage material above a 7 cm height rather than selectively grazed material. Crude protein was low in 1993 and 1994 on all treatments at the end of seasonal grazing. In contrast, crude protein was relatively high at the end of seasonal grazing in 1995. We believe this is a reflection of increased soil N mineralization following favorable March through July 1995 precipitation (Table 1). When these pastures were fertilized during the previous 5 years, mid-summer crude protein levels averaged 5.3, 6.3, 7.2, and 8.8 percent for the 0, 34, 68, and 102 kg N ha^{-1} treatments, respectively (Berg and Sims 1995). Thus, forage crude protein level is an early sign that N is limiting plant production.

In vitro dry matter digestibility (IVDMD) was higher ($P < 0.01$) in June 1993 and 1994 on treatments that had received the higher N rates (Table 5). By the time steers were removed in mid July 1993 and 1994, IVDMD was lower ($P < 0.05$) on treatments that had received the higher N rates. This lower IVDMD was a reflection of a higher proportion of stems and mature seed heads in paddocks that had received the higher N rates. In contrast, few Old World bluestem plants produced seedheads in the 0 N treatment. We have observed a similar absence of Old World bluestem heading in 5 to 10 year old Old World bluestem Conservation Reserve Program (CRP) plantings on N-deficient farmland. During the years of fertilization, IVDMD in early summer averaged 70 to 72 percent and 59 to 61 percent during the mid-July period (Berg and Sims 1995).

Steer gains

Steer average daily gain (ADG) in 1993 was greater ($P < 0.01$) on the higher N treatments (Table 6), probably a reflection of higher crude protein concentration in forage (Table 5). Conversely, steer ADG in 1994 was relatively low on all treatments, again a reflection of low crude protein concentrations in forage. Steer ADG during 1995 averaged 0.89 kg steer^{-1} day^{-1}, apparently a reflection of higher forage protein concentrations later in the grazing season (Table 5).

Weight gains of steers during 1993–1995 increased linearly with increasing N rates applied during the preceding 5 years (Fig. 2). Over the 3 years, steer weight gain averaged 0.63 kg per kg N applied during the preceding 5 years. The value can also be calculated by averaging residual N-use efficiency over 3 years for each N application rate from values of 0.59 ± 0.29 (se) kg steer weight gain per total kg N applied for the 170 kg N application, 0.68 ± 0.06 kg gain per kg N for the 340 kg N application, and 0.63 ± 0.06 kg gain per kg N for the 510 kg N application. Total steer weight gain averaged over the 3 residual grazing years was 185 kg ha^{-1} for the 0 N application, 285 kg ha^{-1} for the 170 kg N ha^{-1} application, 416

Table 5. Crude protein and in vitro dry matter digestibility of Old World bluestems at the beginning and end of seasonal grazing of paddocks fertilized annually for the total N applied (kg N ha^{-1}) during the preceding 5 years at the Southern Plains Experimental Range, Ft. Supply, Okla.

Forage component	Date	Total N applied (kg N ha^{-1}) 0	170	340	510
Crude protein		- - - - - - - - - - - - - - - - -	(%)	- - - - - - - - - - - - - - - - - -	
	7 June 1993	8.7^{c}	9.6^{c}	10.9^{b}	12.1^{a}
	15 July 1993	5.0^{a}	4.8^{a}	4.6^{a}	5.2^{a}
	7 June 1994	7.3^{a}	7.1^{a}	7.6^{a}	7.6^{a}
	14 July 1994	6.1^{a}	5.7^{a}	4.8^{b}	4.7^{b}
	19 June 1995	7.6^{a}	7.8^{a}	7.6^{a}	7.7^{a}
	1 Aug. 1995	6.6^{b}	7.1^{b}	7.9^{a}	6.8^{b}
In vitro dry matter digestibility					
	7 June 1993	65.7^{c}	67.0^{bc}	68.4^{ab}	69.0^{a}
	15 July 1993	56.6^{a}	54.2^{a}	52.8^{b}	51.1^{c}
	7 June 1994	62.1^{b}	63.5^{a}	64.2^{a}	64.0^{a}
	14 July 1994	57.5^{a}	57.3a	52.9^{b}	51.3^{b}
	19 June 1995	61.0^{a}	62.1^{a}	62.7^{a}	60.1^{a}
	1 Aug. 1995	56.6^{a}	57.4^{a}	54.3^{a}	52.9^{a}

[1] Values within a date followed by a common superscript are not significantly different ($P > 0.05$).

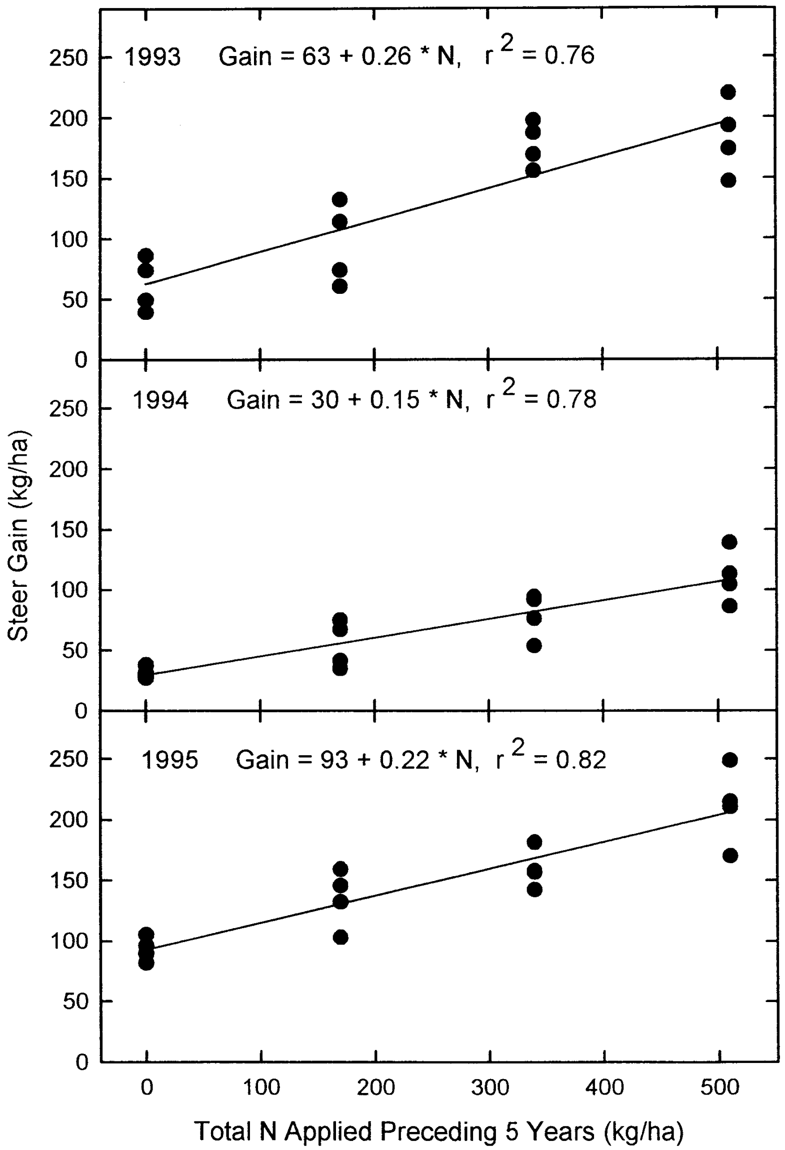

Fig. 2. Steer weight gain over 3 years as related to the total amount of N applied the preceding 5 years at the Southern Plains Experimental Range, Ft. Supply, Okla.

kg ha^{-1} for the 340 kg N ha^{-1} application, and 505 kg ha^{-1} for the 510 kg N ha^{-1} application. We speculate that the residual N effect will be present, but diminish, over the next several years.

The residual N-use efficiency averaging 0.63 kg steer weight gain per kg N applied the preceding 5 years was additive to the fertilizer N-use efficiency previously reported (Berg and Sims 1995). A rigorous summation of fertilizer N-use efficiency during the years N was applied plus the residual effect was not appropriate since the study was N fertilized for 5 years and only grazed for 4 of these years. However, at the 34 kg N ha^{-1} yr^{-1} rate, N-use efficiency averaged 3.3 kg steer weight gain per kg N applied over 4 years the paddocks were N fertilized and grazed (Berg and Sims 1995) and the residual N effect reported here was an additional 0.59 kg steer weight gain per kg N applied. Thus, the summation suggests a N-use efficiency of about 3.9 kg steer weight gain per kg N applied for the most efficient N application rate of 34 kg N ha^{-1} yr^{-1}.

Conclusions and management implications

Annual N flux in rangeland is small in relation to the total N in soil, vegetation, and litter (Berg et al. 1997). The major N inputs in rangeland ecosystems are believed to be from atmospheric deposition and protein supplements fed to cattle. Primary outputs are ammonia volatilized from plant and animal wastes and livestock products sold (Woodmansee 1978, Lauenroth and Milchunas 1991). On native sandhills rangeland, 50 years of moderate grazing by cattle had no measurable effect on C and N concentrations in the surface 5 cm of the sandy soil or total N uptake by plants as compared with nongrazed areas (Berg et al. 1997). Fluxes of N in improved pastures would differ from those in rangeland in the amounts of N fertilizer applied and in the magnitude and distribution of livestock wastes distributed, protein supplements used, and products sold. An increase in total N averaging 5 to 8 kg ha^{-1} yr^{-1} over a 20 to 22 year period was found in N-fertilized pastures as compared to adjacent unfertilized pastures in western Oklahoma (Berg 1988).

Nitrogen fertilization can result in soil acidification. Soil pH in the surface 5 cm was reduced from 6.7 to 5.3 by 20 years of N fertilization of improved pastures on loamy sand soils in Oklahoma (Berg 1986). In Kansas, 20 years of 67 kg N fertilization ha^{-1} yr^{-1} decreased the surface pH of a silt loam soil under grass from 5.9 to 5.1 (Owensby et al. 1969). Generally, rangeland and grassland soils are not tillable and mixing lime to correct acidification may be difficult (Owensby and Launchbaugh 1971). Acidification of dryland grain-growing soils is an emerging problem in western North America (Mahler and Harder 1984, McCoy and Webster 1977, Westerman 1981). Plant species and selections within species vary in their sensitivity to acid soils. Foy (1984) found tall warm-season grasses were tolerant to pH of 4.5 to 5.0 while many legumes may be sensitive to acid soil at soil pH of 5.5 to 6.0.

This study indicated that substantial residual N effects can be expected in forage and beef production for several years after 5 years of N application to Old World bluestem pastures established on marginal farmland in the Southern Plains. The 3-year residual N effect resulted in steer weight gain of about 0.6 kg per kg N applied the preceding 5 years. At a custom grazing rate of about \$0.55 kg^{-1} stocker weight gain, this represents an additional return of about \$0.32 per kg of N applied. Economic returns appeared to favor the 34 kg ha^{-1} yr^{-1} pasture fertilization rate. At a cost of \$0.88 kg^{-1} N applied, the return was \$1.80 in steer weight gain (at the custom grazing rate) the year of application plus a potential \$0.30 in steer weight gain from the residual N effect. At higher N rates the return per unit of N applied is lower.

Table 6. Average daily steer weight gains (kg steer^{-1} day^{-1}) and preliminary economic analysis of residual N effects on steer weight gains (kg steer^{-1} day^{-1} and kg ha^{-1}) over 3 summer grazing periods on Old World bluestem paddocks fertlized annually at 4 rates of N applied (kg N ha^{-1}) during the preceding 5 years at the Southern Plains Experimental Range, Ft. Supply, Okla.

	N fertilization rate (kg N kg^{-1})			
Annual	0	34	68	102
Total 5-year	0	170	340	510
Average daily steer weight gains (kg steer^{-1} day^{-1})				
7 June–15 July 1993	0.67^{b1}	0.80^{b}	1.08^{a}	1.09^{a}
7 June–14 July 1994	0.38^{b}	0.45^{b}	0.47^{b}	0.65^{a}
19 June–1 Aug. 1995	0.89^{a}	0.85^{a}	0.83^{a}	1.00^{a}
Total steer gain				
• 3-year gain (kg ha^{-1})	185	285	416	505
• Total N cost ($0.66 kg^{-1} N)	0	$112.20	$224.40	$336.60
Economic component:				
• N-use (kg gain kg N^{-1})	Baseline	0.59	0.68	0.63
• Additional gain (kg ha^{-1})	–	100	231	320
Comparison based on steer ownership				
• Value of gain ($1.10 kg^{-1})	–	$110.00	$254.10	$352.00
• Total sales ($1.10 kg^{-1})	$203.50	$313.50	$457.60	$555.50
• Sales less N costs	$203.50	$201.30	$233.20	$218.90
Comparison based on custom grazing rates:				
• Custom rates ($0.55 kg^{-1})	$101.75	$156.75	$228.80	$277.75
• Return (Custom rate–N)	$101.75	$44.55	$4.40	–$58.85

[1] Steer weight gains within a year followed by a common superscript are not significantly different ($P > 0.05$).

Preliminary economic returns to the resources used and to management have been estimated for both yearling stocker ownership and custom grazing rates (Table 6). Assuming all other costs are proportional, the 68 kg N ha rate yielded $233.20 per ha for the 3 years of grazing pastures that were fertilized during the previous 5 years. The returns of all 4 fertilizer rates ranged between $203 and $233. Using a custom grazing rate of $0.55 kg^{-1}, returns to fertilizer applied ranged from a low of -$58.85 to a high of $101.75 for the 3 year period. In this case, the unfertilized control had the highest return, followed by the 34 and 68 kg N ha^{-1} at $44.55 and $4.40, respectively. The 102 kg N ha^{-1} rate lost an estimated $58.85 for the 3 years that residual N effects were measured. Additional economic analyses are needed to evaluate net returns for the 5 years of N fertilization plus the 3 years of residual N effects reported here.

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Technical note: Estimating aboveground plant biomass using a photographic technique

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Abstract

We present a non-destructive, photographic method to estimate biomass in semiarid grasslands. Though the method needs to be calibrated, it allows for a dramatic increase in the number of samples compared with the clipping method. The method is based on a relationship between the percentage of "green pixels" in a digital image and green biomass. We identified "green pixels" as those satisfying the following condition: $G/B > 1$ and $G/R > 1$, where G, B and R are the intensities of a particular pixel in the green, blue, and red bands respectively. The percentage of green pixels of the image and green grass biomass showed a correlation of 0.87 ($n = 36$, $p < 0.001$) when data were pooled from 3 sample dates. The relationship was slightly curvilinear and a log transformation of green biomass yielded a better correlation ($r = 0.91$, $n = 36$, $p < 0.001$). The percentage of green pixels showed a lower correlation with total green biomass than with grass biomass ($r = 0.59$ for the linear model and 0.73 for the log transformed model). The relationship between the percentage of green pixels and either green grass or total green biomass changed during the growing season. Both the slope and the Y-intercept of the model differed significantly among dates. Correlation coefficients for different dates ranged between 0.76 and 0.95.

Resumen

En este trabajo presentamos un método fotográfico no destructivo para estimar biomasa en pastizales semiáridos. A pesar de que necesita ser calibrado, este método permite un aumento dramático en el número de muestras, en comparación con el mEtodo de cortes. Este método está basado en la relación entre el porcentaje de "pixeles verdes" y la biomasa verde en una imagen digital. Identificamos "pixeles verdes" como aquellos que satisfac°an la siguiente condición: $G/B >1$ and $G/R >1$, donde G, B y R son las intensidades de un pixel particular en las bandas del verde, azul y rojo, respectivamente. El porcentaje de pixeles verdes en la imagen y la biomasa verde de los pastos mostró una correlación de 0.87 ($n= 36$, $p < 0.001$) al agrupar los datos de 3 fechas de medición. La relación era ligeramente curvilínea y una transformación log de la biomasa verde arrojó una mejor correlación ($r = 0.91$, $n = 36$, $p < 0.001$). El porcentaje de pixeles verdes mostró una menor correlación con la biomasa verde total que con la biomasa de pastos ($r = 0.59$ para el modelo lineal y 0.73 para el modelo transformado log). La relación entre el porcentaje de pixeles verdes y la biomasa verde de pastos o la biomasa verde total cambió durante la estación de crecimiento. Tanto la pendiente como la ordenada al origen del modelo difirieron significativamente entre fechas. Los coeficientes de correlación para las diferentes fechas oscilaron entre 0.76 y 0.95.

Key Words: ANPP estimation, non-destructive methods, semiarid grassland

Aboveground net primary production (ANPP) is a key attribute of grassland ecosystems. Aboveground net primary production data are relevant for both theoretical studies and applied research. Many functional and structural ecosystem traits are tightly related to aboveground net primary production, i.e. secondary production (McNaughton et al. 1989), root biomass and soil organic carbon (Sala et al. 1997). Aboveground net primary production can be used as an integrative attribute of ecosystem function (McNaughton et al. 1989). Aboveground net primary production is an important variable in natural resource management because it determines forage availability for both wild and domestic herbivores. Oesterheld et al. (1992) found a strong connection between stocking density and ANPP for South American rangelands.

Despite its importance, ANPP estimates for grasslands are scarce. Only a few experimental sites carry out regular long-term measurements of aboveground net primary production (see for example, Fernández et al. 1991, Briggs and Knapp 1995, Lauenroth and Sala 1992 and the ORNL DAAC at http://www-ecot.ornl.gov/npp/npp-home.html for some examples). The reason behind the lack of extensive ANPP databases is quite simple: it is time consuming and therefore expensive to estimate.

Net primary production is the rate of carbon accumulation in plants in an ecosystem, and it is generally calculated annually. However, ANPP estimates are not based on this rate, but on the changes in biomass through time (Lauenroth et al. 1986). Biomass is estimated a number of different ways including harvesting (Sims et al. 1978, Sala et al. 1981), visual estimates (Waite 1994), capacitance meter (Fletcher and Robinson 1956, Winkworth et al. 1962, Murphy et al. 1995), and spectral data (Tucker 1977) to name the most common methods. Photo keys

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have been also used to estimate biomass, however the overall accuracy of the method is low (Catchpole and Wheeler 1992). Double sampling techniques have been widely used to estimate biomass (Ahmed et al. 1983, Catchpole and Wheeler 1992). This approach involves the development of a regression equation between biomass and a variable easy to measure. The variables more commonly used were ground cover, sward height, total blade length per tiller and point contacts (Pasto et al. 1957, t'Mannetje 1976, Williamson et al. 1987).

Estimates of aboveground net primary production derived from changes in biomass are subject to under and over estimation errors (Lauenroth et al. 1986, Sala et al. 1988), both related to the number of biomass samples (in time or space) used to calculate ANPP. To increase both the availability of aboveground net primary production data and their accuracy, we need to be able to work with large sample sizes. Additionally, many studies need non-destructive methods because of small plot sizes or restricted areas. In this paper we present a non-destructive, photographic method to estimate biomass in grasslands. Biomass estimates are important in itself but also provide the basis to estimate ANPP (Lauenroth et al. 1986). Even though the method needs to be calibrated, it allows for a dramatic increase in the number of samples per operator compared to the clipping method. The method is based on a relationship between the percentage of green pixels in a digital image and green biomass.

Methods

This research was conducted at the Central Plains Experimental Range (CPER) in northcentral Colorado, North America (40° 49'N Lat, 104° 46' W Long). The CPER is administered by the USDA Agricultural Research Service (ARS) and is a National Science Foundation funded Long Term Ecological Research site. Mean annual precipitation is 321 mm (SD = 98 mm). Average annual temperature is 8.6° C (SD = 0.6° C). The climate of the CPER is typical of mid-continental semiarid sites in the temperate zone except for the large influence of the Rocky Mountains 60 km to the west. Maxima in precipitation and temperature occur in June, July, and August and minima occur in December, January, and February.

The vegetation is typical of the northern portion of the shortgrass steppe (Lauenroth and Milchunas 1992). The dominant species is the perennial bunchgrass *Bouteloua gracilis* H.B.K. Lag. Important associated species include *Buchlöe dactyloides* (Nutt.) Engelm, *Opuntia polyacantha* Haw, *Sphaeralcea coccinea* (Pursh) Rydb, and *Carex eleocharis* Bailey. All nomenclature follows The Great Plains Flora Association (1986).

We took photographs on 3 dates during the growing season (21 May, 10 June, 26 June 1996) of 0.25 m^2 circular plots using a 35 mm single lens reflex camera (PENTAX PZ10) with a 28-70 mm zoom lens. The camera was mounted on a tripod facing down 1.4 m above the ground with an angle lower than 10 degrees from the vertical. We used color slide film (200 ASA) (Kodachrome). Pictures were taken between 11:00 and 15:00 on clear days. The slides were digitized as TARGA files (TGA) at a resolution that yielded an average size for an individual pixel of approximately 0.25 mm^2 (ground area) (Fig. 1).

Aboveground biomass was harvested from each plot after the picture was taken. Plants were clipped at the soil surface and biomass was sorted into live and dead and by the following categories: grasses, forbs, lichens, and cactus. After sorting, the material was oven-dried at 50° C and weighed.

The estimates of green biomass from the images were based on the separation of the image into the 3 colors: red, green and blue. These primary colors are additive because their combination produces white. An image consists of 3 layers or matrices. Each layer is assigned to 1 additive color. Each pixel of each band has a particular intensity. In an 8-bit image, the intensity will range from 0 to 255 (2^8). A pixel with an intensity of 255 on each of the 3 bands will be white. For a black pixel the intensity in each of the 3 bands will be 0.

We identified "green pixels" as those satisfying the following condition:

$$G/B > 1 \text{ and } G/R > 1 \qquad \textbf{(1)}$$

where G, B and R are the intensities of a particular pixel in the green, blue and red bands respectively. We calculated the number and proportion of green pixels for the whole image. G_PIX is a DOS-based C-program that processes a pixel by pixel list of the input file (*.TGA) (a free copy of the program (G_PIX.EXE) is available at http://www.ifeva.edu.ar/pictures).

We performed simple correlation and regression analyses to investigate the strength of the relationship between the percentage of green pixels of the image and green grass biomass and total green biomass. We cropped the portion of the picture corresponding to the 0.25 m^2 quadrat using Adobe Photoshop 3.0 (Adobe Systems Incorporated 1994).

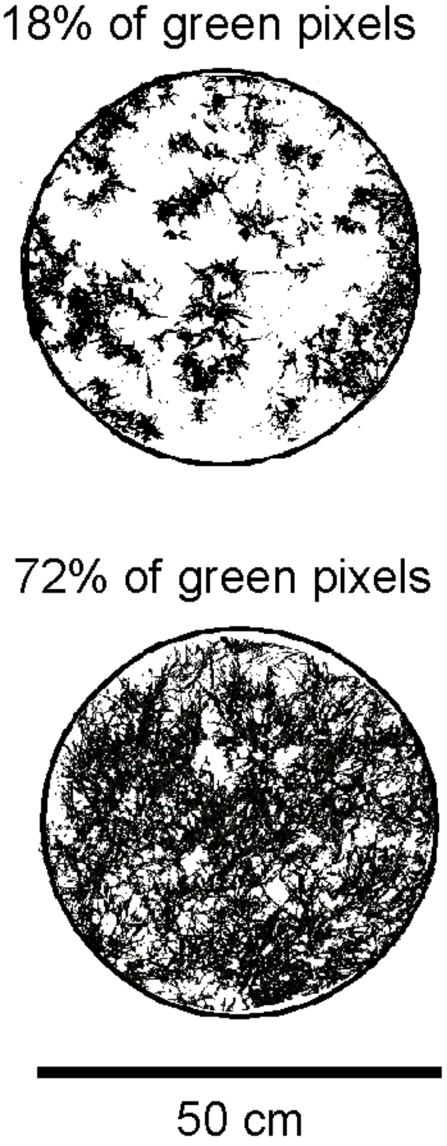

Fig. 1. Pictures that show contrasting biomass and percentage of green pixels in the shortgrass steppe. The circle corresponds to the area sampled in the calibration experiment (0.25 m^2). Green pixels appear as black and everything else as white.

Results and Discussion

The percentage of green pixels and green grass biomass showed a correlation of 0.87 (n = 36, $p < 0.001$) when data were pooled from all 3 sample dates (Fig. 2). The relationship was slightly curvilinear and a log transformation of green biomass yielded a better correlation r = 0.91, n = 36, $p < 0.001$) (Fig. 2). The percentage of green pixels showed a lower correlation with total green biomass than with green grass biomass r = 0.59 for the linear model and 0.73 for the log transformed model).

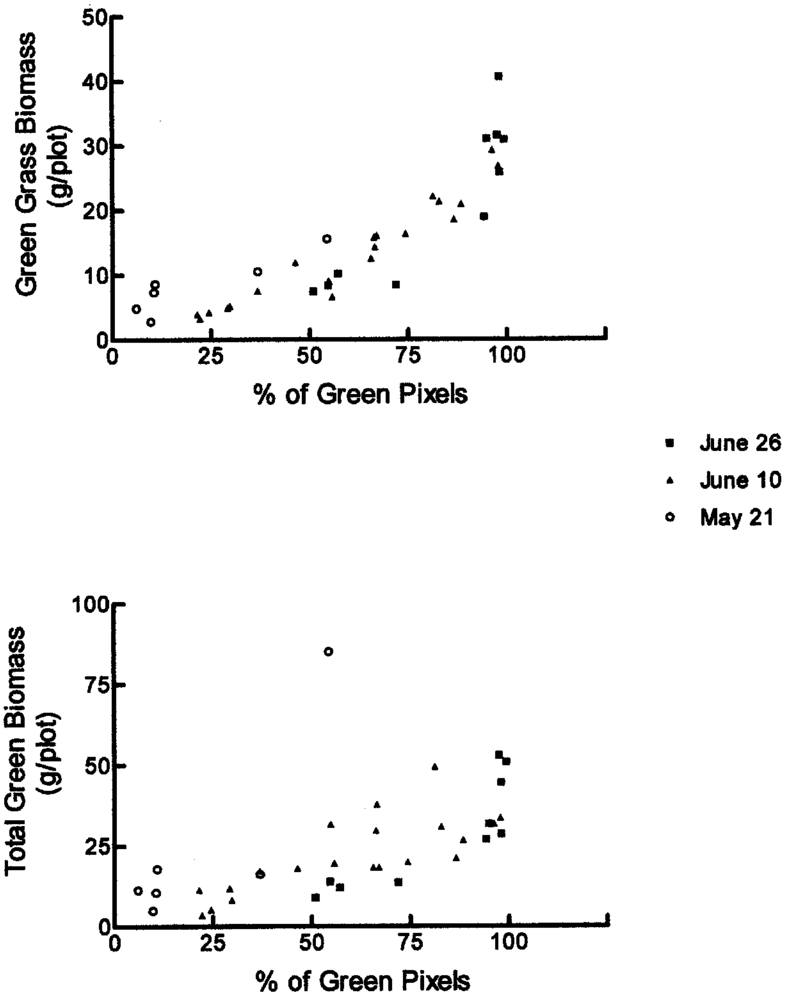

Fig. 2. Relationship between the percentage of green pixels and green grass biomass (GGB = 1.43 + 0.35 ln (%GP), r = 0.91, p < 0.001) (the upper panel) and total green biomass (TGB = 1.94 + 0.017 ln (%GP), r = 0.73, p < 0.001) (the lower panel). Open circles correspond to 21 May, triangles to 10 June and squares to June 26 sample dates.

The relationship between the percentage of green pixels and either green grass or total green biomass changed during the growing season (Table 1 and Fig. 2). Both the slope and the Y-intercept of the regression model differed significantly among dates (Table 1). However, the differences of slopes and Y-intercepts were more marked for the relationship involving total green biomass than for green grass biomass. Changes in the relative contribution of different plant functional types (forbs, succulents, lichens, and grasses) and modifications of the canopy structure may account for the greater differences in the relationship between the percentage of green pixels and total green biomass compared to grass biomass.

Our results showed that digital images and an algorithm based on color theory can provide good estimates of plant biomass in semiarid grasslands. The method of counting green pixels is a variation of the point-quadrat method (Greig-Smith 1983). In this method plant cover, leaf area index, or biomass is calculated from the proportion of hits on green tissues over the total number of observations. By counting the number of green pixels we are dramatically increasing the total number of observations. The area sampled in this study (0.25 m^2) included more than 70,000 pixels (it varies approx. 1% among pictures). As with the point-quadrat method, counting green pixels on a picture is a non-destructive method. That makes it especially useful for long-term studies of ANPP, plant cover or plant biomass.

This method also offers an interesting alternative for studying patch dynamics in arid and semiarid systems. Pictures allow one to track the dynamics of bare soil patches through time, recruitment of seedlings or the spread of clonal plants. The method proposed will be a useful tool for grassland and shrubland ecologists and managers. A picture represents a more objective alternative to assess plant cover or plant biomass than visual estimates. The use of digital cameras will speed up the process of assessing structural attributes of grassland and shrubland ecosystems. Pictures can be downloaded to the hard disk of a notebook computer from a digital camera directly in the field. G_PIX can calculate the percentage green pixels for a group of pictures and store the results in an ASCII file. Clearly multiple layers of leaves or complex canopies would reduce the accuracy of this approach. The shortgrass steppe presents a canopy structure near ideal to apply this method. For nonpostrate vegetation camera angles different from vertical may provide better estimates of green biomass.

Table 1. Correlation coefficients (r), slope, Y–intercepts, F–value and number of observations (n) for the linear models fit to the data of percentage of green pixels and green grass biomass (g/plot) (A) and total green biomass (g/plot) (B).

A) GREEN GRASS BIOMASS

Date	Y–intercept	Slope	r	F	n	
21 May	3.91	0.21	0.90	17.5	6	**
10 June	–4.04	0.38	0.95	17.9	20	**
26 June	–21.3	0.52	0.88	28.6	10	**

**p< 0.01

B) TOTAL GREEN BIOMASS

Date	Y–intercept	Slope	r	F	n	
21 May	–3.54	1.30	0.86	10.7	6	**
10 June	1.42	0.35	0.76	25.1	20	**
26 June	–27.47	0.68	0.86	21.8	10	**

**p<0.01

The method requires, however, a proper calibration based on double sampling, harvesting biomass, and taking pictures. Our results suggest that our calibration was not stable throughout the growing season, mainly for total green biomass, and therefore requires a calibration at each sample date and vegetation type. The high correlation suggests that a small number of samples would be necessary to describe the relationship. Despite this requirement this method has a very high probability of improving the process of collecting aboveground biomass data in semiarid grasslands and shrublands.

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Technical Note: A comparison of methods to determine plant successional stages

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Abstract

Twenty-six, 0.04 ha macroplots were sampled on 9 range sites in southwestern Montana to compare successional scores and condition classifications of range condition analysis and United States Forest Service (USFS) Ecodata and Ecopac (Strata) analysis methods. Range condition scores (0–100%) and range condition classes (poor, fair, good, excellent) were derived from the traditional Soil Conservation Service range condition analysis method, with the exception that only major decreaser and increaser graminoids and shrubs were individually clipped and bagged. Ecological status scores (1–100%) and ecological condition classes (low, mid, high, very high) were determined with United States Forest Service Ecodata methods. Range condition score means were greater ($p < 0.02$) than ecological status score means (48% vs 41%). Standing crop biomass affected differences ($p < 0.001$) between range condition scores and ecological status scores. Lower producing sites had greater range condition scores than ecological status scores and higher producing sites had greater ecological status scores than range condition scores. Range condition classes and ecological condition classes were not independent ($p < 0.02$). Differences between the 2 methods were attributable to the use of species composition by weight for the range condition analysis and the use of percent canopy cover by Ecodata methods. Rangeland managers trying to determine successional status should realize that range condition analysis and Ecodata methods produce similar condition classes but different condition scores.

Key Words: Range condition, seral stages, plant communities, succession

Resumen

Se muestrearon 26 macroparcelas (0.04 ha) en 9 sitios de pastizal del Sudoeste de Montana para comparar las calificaciones sucesionales y las clasificaciones de condición del análisis de condición del pastizal y de los métodos de análisis Ecodata y Ecopac ("Strata") del Servicio Forestal de los Estados Unidos (USFS).Las calificaciones de condición del pastizal (0-100%) y las clases de condición del pastizal (pobre, regular, bueno y excelente) se derivaron del método tradicional de análisis de condición del pastizal del Servicio de Conservación de Suelos, con la excepción de que solo las principales especies de gramíneas y arbustos decresores e incresores se cortaron y empaquetaron individualmente. Las calificaciones del estado ecológico (1-100%) y las clases de condición ecológica (bajo, medio, alto y muy alto) se determinaron con los métodos Ecodata del Servicio Forestal de los Estados Unidos. Las medias de las calificaciones de la condición del pastizal fueron mayores ($p < 0.02$) que las medias de la calificación del estado ecológico (48% vs 41%). La biomasa de la cosecha en pie afecto las diferencias ($p < 0.001$) entre las calificaciones de la condición del pastizal y las calificaciones del estado ecológico. En los sitos de baja producción las calificaciones de condición de pastizal fueron mayores que las del estado ecológico, en sitos con alta producción las calificaciones del estado ecológico fueron mayores que las de la condición del pastizal. Las clases de condición del pastizal y las de condición ecológica no fueron independientes ($p < 0.02$). Las diferencias entre los 2 métodos se atribuyeron al uso de la composición de especies por peso para el caso de la condición de pastizal y al uso del porcentaje de cobertura de copa en los métodos Ecodata. Los manejadores el pastizal que intentan determinar el estado sucesional deberán reconocer que el análisis de condición del pastizal y los métodos Ecodata producen clases de condición similares pero diferentes calificaciones de condición.

Range condition analysis was developed to monitor forage productivity and to evaluate grazing effects on plant communities. Methods developed by the Soil Conservation Service (SCS) have been the standard to determine range condition and trends in the western United States for many years (Svejcar and Brown 1991). Changes in land management policy began in the 1960s after societal awareness identified a need for increased conservation and improvement of the environment leading to the adoption of ecological guidelines for ecosystem management by the U.S. Forest Service (USFS) (Robertson 1992).

Traditional methods employed by SCS to determine range condition scores and range condition classes were based on plant species composition by dry weight. These values were compared to "climax" for a given range site. Range condition scores (0–100%) were determined according to the similarity of current vegetation compared to climax vegetation. Vegetation was further categorized into poor (0–25%), fair (26–50%), good (51–75%) and excellent (76-100%) condition classes to correspond with low, mid, high and very high seral stages. This method presents problems because climax vegetation is difficult to determine and secondary plant successional patterns may vary greatly on similar sites. Limitations of these methods have

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prompted federal agencies to develop other seral stage assessment methods which are more ecologically based.

There appears to be a trend by agencies towards more qualitative or observational methods to assess "range health" or "proper functioning condition". These methods do not yield any quantitative data for determining changes in plant communities over time. Therefore, some agencies have attempted to use quantitative methods to assess seral stages, which are based on different critera for determining potential natural plant communities.

In 1987, the Northern Region of the USFS began development of Ecodata and Ecopac as a standardized approach for environmental analysis and plant community classification (USDA 1987). The Northern Region proposed to inventory and classify vegetation based on Ecodata sampling methods and manage 3 million ha of public grazing allotments based on a determination of ecological status (RISC 1983).

The Strata program categorizes current vegetation and compares it to potential natural communities based on canopy cover. The degree of similarity between current vegetation and potential natural community is determined by Sorensen's quotient of similarity (Sorensen 1948). This quotient is determined by plant species occupancy in sampled communities compared to reference plant communities. An ecological status score is given from 1 to 100 and the seral stage is classified into 1 of 4 ecological condition classes (low, mid, high, very high) in 25% increments (USDA 1987).

The relationship of Ecodata sampling methods to standard range condition analysis methods has not been established and a lack of continuity exists in information gathered with different methods. A comparison of the Ecodata method to the standard range condition analysis would provide managers a basis for understanding Ecodata's relationship between ecological condition classes and range condition classes. The purpose of this study was to compare successional scores and condition classes derived from range condition analysis and Ecodata sampling methods on a variety of range sites. The objectives were to: 1) compare range condition scores and ecological status scores; 2) compare range condition classes and ecological condition classes; and 3) to determine those environmental parameters that may influence the differences between the range condition and ecological status scores. To our knowledge, similar published comparisons between these methods do not exist.

Methods

Study Area

The study was conducted on the Flying D Ranch, (45° N, 111° W), 16 km southwest of Bozeman, Mont., in Gallatin and Madison counties (USDA 1989). The 60,700 hectare ranch is characterized by intermontane valleys at 1,280–2,300 m elevations. The majority of the ranch receives 38–48 cm of annual precipitation an average annual temperature of 4.4° C and a 75 day frost-free period (USDA 1989).

Soils were classified as Argie, Pachie, Calcic or Lithic Cryoborolls (USDA 1989). Bridger, Earcree, Hanson, Orofino-Poin, and Poin-Sebud soil series with sandy, silty, and clay loam textures dominated the study area and were frequently modified by gravel, cobble, or stone fragments (USDA 1989, 1994). Potential natural communities varied with range site and average forage production values ranged from 300 to 1,200 kg/ha^{-1} (USDA 1989). Dominant plant species across range sites included big sagebrush (*Artemesia tridentata* [Nutt.]), bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love), Idaho fescue (*Festuca idahoensis* [Elmer]), lupine (*Lupinus* L), needle-and-thread (*Stipa comata* [Trin. and Rupr.]), prairie Junegrass (*Koeleria macrantha* [Ledeb.] J.A. Schultes), western needlegrass (*Stipa occidentalis*) Thurb. ex S. Wats.), and western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Love) (Ross and Hunter 1976).

Site Descriptions and Locations

Twenty-six, 11.3 m radius (0.04 ha) permanent Ecodata macroplots were established on the ranch as part of a baseline range condition inventory in 1990. Sampling was concentrated in grassland and shrub steppe rangeland to evaluate a variety of range sites (Westech 1991). Ecodata macroplots were established in major range sites and location was based on vegetation composition, soils, and precipitation information. Site selection in riparian corridors was minimal due to significant modification of lowland vegetation by livestock grazing and apparent poor condition. Upland areas were sampled more intensively to determine the extent of fair to excellent condition range sites and a number of range sites were sampled at several locations. Range condition and ecological status were compared on range sites/habitat types that had species composition data available for similarity analysis. Macroplots were established in a representative, homogenous range site/habitat type and permanently located with a 1.6-cm diameter capped rebar pin. Exact site locations and landmark descriptions are reported in Westech (1991).

Sampling

Plots were sampled in August 1990 according to the Ecodata ocular method, using the Ecodata ocular method, as outlined in Chapter 4 of the Ecosystem Classification Handbook (USDA 1987). Environmental features of the macroplot were noted and potential natural community and habitat type were determined with classification systems developed by Hansen et al. (1988), Mueggler and Stewart (1980), and Pfister et al. (1977). Range site was determined using SCS soil survey maps (USDA 1989). Site characteristics described included: soil type, plot position on the landscape, parent material, aspect, elevation, percent slope, and ground cover characteristics. Vegetation structure and production for the macroplot were recorded. Identification of dominant species (height x canopy cover) by vertical layer and estimation of total percent vegetative cover by life-form were determined.

Annual standing crop biomass was determined by clipping vegetation. Plant species identified as major decreaser graminoids, major increaser graminoids, or shrubs were individually clipped and bagged (USDA 1981). Other perennial forb species, annual/biennial forbs, minor decreaser graminoids, minor increaser graminoids, or annual graminoids were grouped into 1 separate class. Actual production was determined from 3 randomly placed, 0.5 x 1.0 m microplots within an Ecodata macroplot. Current year aboveground herbaceous biomass for each class of vegetation was clipped to ground level and bagged. Production samples were oven-dried at 70° C until constant weight was achieved (48–96 hours). Biomass (kg ha^{-1}) for each vegetation class, from each microplot, were used in determining mean macroplot production.

Ocular Plant Species Data Form 4 (USDA 1987) was used to record characteristics of the macroplot vegetation. Species life-form, percent canopy cover class, and mean height to the nearest foot were defined. Plants were identified by genus and species using Dorn (1984), Great Plains Flora Association (1986), Hitchcock et al. (1955–1969), and Hitchcock and Cronquist (1973). The USFS species list (USDA 1987) was used as standard nomenclature for entry into the plant composition database.

Determination of Range Condition and Classification

Range condition calculations were based on clipped forage weights of each vegetation class. Relative percent composition, for each vegetation class in each plot, was determined by dividing the dry weight of the class by total plot production. Existing relative percent compositions were then compared to the climax community species percent composition listed in the USDA SCS range site technical guides (1977). Actual amounts, not in excess of that shown in the guide, were totaled for all vegetation classes to arrive at the numerical range condition scores, a relative ecological rating of floristic similarity to climax community, for the plot (USDA 1981). The plot was then classified into 1 of 4 range condition classes determined by 25% increments of the range condition scores (USDA 1976).

Determination of Ecological Status and Condition

Data from each of the 26 macroplots was entered into the Ecodata general form and plant composition data bases (Data General System 1985). The data bases were linked to the Ecodata analysis package (Ecopac) through the Utility system and checked for errors (USDA 1987). The Plotid program was used to group the Ecodata macroplots and create text files for input into the plant community analysis program, Strata. A species synthesis table (species abundance by plot and strata) and constancy-average table (species canopy cover) was generated to select plants common to the 26 macroplots and the 159 plots sampled by Mueggler and Stewart (1980). Plant species composition of Mueggler and Stewart (1980) plots was based on forty, 0.2 x 0.5 m microplots per 20 x 20 m (0.04 ha) macroplot. The number of species common to both plots was limited to 88 to reduce noise in the similarity analysis (Gauch 1982). The Mueggler and Stewart (1980) plots were grouped into potential natural communities. The Ecopac subroutine, Strata, characterized differences, based solely on the estimated species percent canopy cover, between the existing 26 macroplots and the potential natural communities (habitat type strata) of Mueggler and Stewart (1980). The species composition of each study macroplot was compared to all 5 habitat types (potential natural communities) by plot-to-strata similarity analysis. The potential natural communities were *Pseudoroegneria spicata/Poa sandbergii* (Psespi/Poasan), *Artemisia tridentata/-Festuca idahoensis* (Arttri/Fesida), *Festuca idahoensis/Elymus caninus/-Geranium viscosissimum* phase (Fesida/-ElyCan/Gervis), *Festuca idahoensis/-Pascopyrum smithii* (Fesida/Passmi), and *Festuca idahoensis/Pseudoroegneria spicata* (Fesida/Psespi). The numerical macroplot ecological status score was calculated as degrees of floristic similarity to potential natural communities using Sorensen's (1948) coefficient K = 100 (2c/a+b), where c is the sum of percent canopy cover of a single species in two opposing plots, a is the canopy cover of all species in a plot (ie macroplot), and b is the canopy cover of all species in the other plot (ie Mueggler and Stewart's potential natural community plot). The plot was then classified into 1 of 4 ecological condition classes as determined by 25% increments of the ecological status scores (USDA 1992).

Statistical Procedures

Differences between the mean range condition scores and ecological status scores were compared using a non-parametric, two-tailed Wilcoxon's signed rank test (Steel and Torrie 1980). This was considered to be a more conservative approach than either the paired t-test or analysis of variance since the two sampling methods were employed at the same location, on the same day. The Wilcoxon's signed rank test only assumes data can be ranked and there are very few ties when ranking values. No other assumptions of independent sampling or normally distributed differences are necessary. There was only one tied rank in the data, therefore this was considered a valid statistical test. Plot was considered the experimental unit for this and all subsequent analyses. A paired t-test (SAS 1988) was used to compare differences of range condition scores and ecological status scores within similar range sites grouped across precipitation zones.

Range condition classes were poor, fair, good, and excellent and ecological condition classes were low, moderate, high, and very high. The 4 condition classes, for both methods, represented successional score percentage breaks of 0–25, 26–50, 51–75, and 76–100. Analyses of range condition classes and ecological condition classes were based on 21 of the 26 plots. A 2 x 2 contingency table was used to meet the criteria of having a minimum expected cell count of 5 (McClave and Dietrich 1985). Five plots were excluded because they represented single occurrences in the columns of the contingency table which render the statistical inference invalid for those columns. Class scores were transformed into numerical form (1–4). To determine the degree of independence between range condition classes and ecological condition classes, Chi-Square analysis (MSUStat 1994) was conducted with the 2-way contingency table. Association groups were determined according to the probability of such associations occurring by chance.

The difference between range condition scores and ecological status scores for each of the 26 plots was determined. Regression analysis (SAS 1988) was used to determine the influences of aspect, elevation, precipitation, production, range site, and slope on differences between range condition scores and ecological status scores. Range sites were grouped irrespective of precipitation zone. All statistical comparisons were evaluated at $p < 0.05$.

Results

Five hundred fifty-two vascular plant taxa were identified in the survey of the 9 range sites. Forage production values ranged from 139 kg ha^{-1} on the very shallow 38–48 cm precipitation range site, to 4,708 kg ha^{-1} on the silty 50+ cm precipitation range site (Westech 1991). Range condition scores varied from 15% on a silty 50+ cm precipitation range site to 78% on the silty 25–26 cm precipitation range site. Poor range condition classes occurred on 4% of the plots, fair condition on 54% of the plots, 35% of the plots were found to be in good condition, and 8% were in excellent condition. Ecological status scores varied from 13% on the Fesida/Passmi habitat type to 57% on the Psespi/Poasan/Sticom habitat type. Low ecological condition classes occurred on 12% of the plots, 62% of the plots were moderate, and 27% were classified as high ecological condition.

There was a 15% difference ($p<0.02$) between the range condition scores mean (48%) and the mean ecological status scores (41.3%). There were no differences ($p>0.05$) between range condition scores and ecological status scores within range sites (Table 1) with 1 exception. This occurred on the very shallow sites (n= 2),

Table 1. Comparison of mean range condition scores (RCS) and ecological status scores (ESS) for 24 macroplots in the same range sites (grouped across precipitation zones) in southwest Montana.

Range Site	n	RCS	ESS	P-Value
		(%)	(%)	
Silty	13	49	37	0.54
Shallow	7	47	44	0.78
Very Shallow	2	57	27	0.02
Overflow	2	24	27	0.82

where productivity was lower than other range sites.

Categorizing vegetation into mid or fair ecological condition and high or good range condition classes resulted in 16 of 21 plots being placed in the same seral categories. Chi-Square analyses revealed that range condition and ecological condition methods used to categorize condition classes or seral stages were not independent ($p < 0.02$).

Regression analysis indicated that aspect, elevation, habitat type, and precipitation did not affect differences between range condition scores and ecological status scores (Table 2). Production (Fig. 1) and range site ($p < 0.001$ and $p < 0.04$) were the only variables that affected the differences between range condition scores and ecological status scores. The equations of linear relationship between ecological status scores minus range condition scores and all other variables are provided in Table 2. Lower producing sites had greater range condition scores than ecological status scores and higher producing sites had greater ecological status scores than range condition scores (Fig. 1).

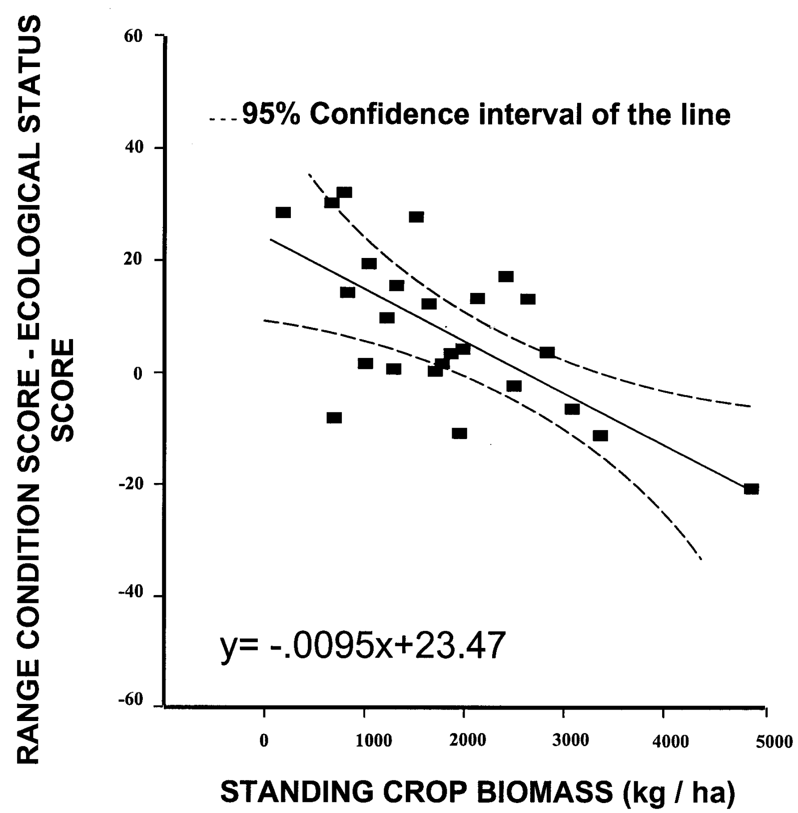

Fig. 1. Standing crop biomass effects on range condition score minus ecological status score on 26 macroplots in southwest Montana.

Discussion

Differences between range condition scores and ecological status scores were probably related to different assessment methods. Relative percent species composition by weight used in the range condition analysis method favors plants that produce more biomass, while the Ecodata system emphasizes canopy cover. Payne (1974) found that the average correlation of cover and weight was 0.62 for all grass species and provided evidence that correlations between weight and cover could vary from R = 0.98 to R = 0.14 depending on the individual plant species. Therefore, differences between ecological status scores and range condition scores could be due to variable correlations between plant weight and canopy cover.

Percent canopy cover estimates used with the Ecodata method are placed in cover class ranges, assigned a standard class midpoint, and assigned a class code. For example, in the canopy cover range of 1 - < 5%, the midpoint is 3.0%, and in the range of 35–45%, the midpoint is 40.0% (the median). The assigned midpoint may be biased by extremely low or high estimates (Daubenmire 1968). The experience of the investigator may affect the estimate. Plots with very low foliage cover are likely to be underestimated, and plots with greater foliar cover are likely to be overestimated (Meuller-Dombois and Ellenberg 1974). This may partially explain why ecological status scores are lower on sites with lower production and higher on sites with greater production.

Table 2. Simple linear equations and statistics for the effect of seven variables on the differences between range condition score and ecological status score in southwestern Montana.

Source	Equation	R	P-Value
Aspect	y = - 0.03x + 13.02	0.24	0.21
Elevation	y = - 0.003x + 12.87	0.1	0.83
Range Sites	y = 5.01x + -2.28	0.4	0.04
Habitat Type	y = - 0.24x + 8.09	0.1	0.78
Precipitation	y = - 0.61x + 33.49	0.17	0.38
Standing Crop Biomass	y = -0.0095x + 23.47	0.32	0.001
Slope	y = 0.31x + 0.39	0.67	0.11

Differences in the scores were probably not attributed to different concepts of climax or potential natural communities classification. Range site and habitat type have been found to classify the land unit and potential vegetation in essentially the same fashion (Hironaka 1989). Both the range site and habitat type concepts are based on soil characteristics unique to a site and on the differences in expected climax plant composition and production on the same site.

Mueggler and Stewart (1980) sampled 0.04 ha macroplots near-pristine areas and areas subject to mild grazing disturbance to determine climax plant communities. Our study used the same size macroplots as Mueggler and Stewart (1980), therefore it is unlikely that differences between the 2 methods were the result of plot size influences.

Range managers often rely on condition classes for management purposes. There were no differences in range condition classes and ecological condition classes. It appears that these classifications could be used interchangeably.

Conclusions

In this study, the mean of the ecological status scores, as determined by USFS Ecodata, was lower ($p < 0.02$) than the mean of the range condition scores, as determined by the SCS range condition analysis method. When conducting range inventories, Ecodata methods may indicate a decline in vegetation resources when the results are compared to range condition analysis methods. Differences between ecological status scores and range condition scores were probably due to variable correlations between plant weight and cover. Resulting condition classification from both Ecodata and range condition analysis methods were the same. These findings indicate that categorization of vegetative seral stages are comparable and that both methods are based on similar comparisons to climax or potential natural plant communities.

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Carbon exchange rates in grazed and ungrazed pastures of Wyoming

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Abstract

The influence of cattle grazing on carbon cycling in the mixed grass prairie was investigated by measuring the CO_2 exchange rate in pastures with a 13 year history of heavy or light grazing and an ungrazed exclosure at the High Plains Grasslands Research Station near Cheyenne, Wyo. In 1995, 1996 and 1997 a closed system chamber, which covered 1 m^2 of ground, was used every 3 weeks from April to October to measure midday CO_2 exchange rate. Green vegetation index (similar to leaf area index), soil respiration rate, species composition, soil water content, soil temperature, and air temperature were also measured to relate to CO_2 exchange rates of the 3 grazing treatments. Treatment differences varied among years, but overall early season (mid April to mid June) CO_2 exchange rates in the grazed pastures were higher (up to 2.5 X) than in the exclosure. Higher early season CO_2 exchange rates were associated with earlier spring green-up in grazed pastures, measured as higher green vegetation index. As the growing season progressed, green vegetation index increased in all pastures, but more so in the ungrazed exclosure, resulting in occasionally higher (up to 2 X) CO_2 exchange rate compared with grazed pastures late in the season. Seasonal treatment differences were not associated with soil temperature, soil respiration rate, or air temperature, nor was there a substantial change in species composition due to grazing. We hypothesize that early spring green-up and higher early season CO_2 exchange rate in grazed pastures may be due to better light penetration and a warmer microclimate near the soil surface because of less litter and standing dead compared to the ungrazed pastures. When all the measurements were averaged over the entire season, there was no difference in CO_2 exchange rate between heavily grazed, lightly grazed and ungrazed pastures in this ecosystem.

Resumen

En la Estación Experimental High Plains, cercana a Chayenne, Wyo., se investigo la influencia del apacentamiento de ganado en el reciclaje de carbón en pastizales mixtos. La determinación se efectuó mediante la medición de la tasa intercambio de CO_2 en potreros con un historial de 13 años de apacentamiento fuerte o ligero y en potreros excluidos al apacentamiento. Durante el período de Abril a Octubre de 1995, 1996 y 1997 se utilizó un sistema de cámara cerrada (el cual cubría un $1m^2$) a intervalos de 3 semanas para medir la tasa de intercambio de CO_2 al mediodía. También se midieron el índice de vegetación verde (similar al índice de área foliar), la tasa de respiración del suelo, la composición botánica, el contenido de agua del suelo y la temperatura del suelo y aire para relacionarlos con las tasas de intercambio de CO_2 de los 3 tratamientos de apacentamiento. Las diferencias entre tratamientos difirieron entre años, pero en general a inicios de la estación (Abril a Junio) las tasas de intercambio de CO_2 de los potreros apacentados fueron mayores (hasta 2.5 veces) que las tasas de los potreros excluidos. Las altas tasas de intercambio de CO_2 de inicios de estación se asociaron con altos índices de vegetación verde. Conforme la estación de crecimiento avanzó, el índice de vegetación verde aumento en todos los potreros, pero este incremento fue mayor en los potreros sin apacentamiento resultando en tasas de intercambio de CO_2 ocasionalmente altas (hasta 2 veces) en comparación con los potreros apacentados a fines de la estación. Las diferencias estacionales de los tratamientos no se asociaron con la temperatura el suelo, la tasa de respiración del suelo o la temperatura del aire, ni tampoco hubo un cambio substancial en la composición de especies vegetales debido al apacentamiento. Nosotros hipotetizamos que el rebrote temprano de primavera y las tasas altas de intercambio de CO_2 a inicios de estación de los potreros apacentados puede deberse a una mejor penetración de la luz y a un microclíma más cálido cerca de la superficie del suelo, esto porque hay menos mantillo y vegetación muerta en pie en comparación con los potreros sin apacentar. Cuando todas las mediciones se promediaron en toda la estación completa no hubo diferencias en la tasa de intercambio de CO_2 entre los potreros con apacentamiento fuerte, ligero y sin apacentamiento.

Key Words: Grazing, productivity, photosynthesis, soil respiration, species composition.

Domestic livestock grazing on rangelands has received much attention recently, as there is often disagreement on the impacts of grazing on ecosystem sustainability. The challenge is managing these important lands to provide food and products for society, while protecting this natural resource base. As human population increases, so do the demands on rangelands, making it even more important to understand the effects of management strategies on rangelands.

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Many of the world's rangelands have historically been grazed by large mammals, and there is convincing evidence that grasses co-evolved with grazers (Stebbins 1981). As many as 20 million bison existed on the Great Plains of North America before European settlement (Shaw 1995). Therefore, grazing by large mammals is the natural condition of the Great Plains (Milchunas et al. 1988).

The effect of grazing on primary productivity and the carbon cycle are important factors in the long-term sustainability of these ecosystems. However, the information of how animal grazing impacts primary productivity and carbon cycling is limited and inconsistent. For instance, depending on the particular study and rangeland investigated, one can find examples of negative, neutral or positive effects of grazing on above-ground net primary productivity (Milchunas and Lauenroth 1993, Sims and Singh 1978b). McNaughton (1979) maintains that an optimal level of grazing will maximize annual net primary productivity in most rangeland ecosystems, so presumably most of the negative effects of grazing may be examples of over-grazing for a particular ecosystem. Bremer et al. (1998) reported that grazing reduced annual soil respiration by up to 18% in the tallgrass prairie, indicating that grazing may have a large effect on the carbon cycle of this ecosystem.

Over time, soils will integrate long-term above and below-ground ecosystem processes (Manley et al. 1995, Berg et al 1997). Therefore, soil carbon can be a good relative indicator of the effect of grazing on many aspects of the carbon cycle. However, as with plant productivity, there are reports that grazing increases (Smoliak et al. 1972, Ruess and McNaughton 1987, Schuman et al. 1999), decreases (Bauer et al. 1987, Dormaar and Willms 1998) or does not affect soil carbon (Berg et al. 1997, Milchunas and Lauenroth 1993). Changes in species composition and accompanying changes in rooting patterns resulting from grazing can sometimes explain changes in soil carbon (Smoliak et al. 1972).

An important topic that has not been addressed in the evaluation of how grazing impacts rangeland primary productivity is the photosynthetic response of plant communities to grazing. Many studies have investigated the influence of grazing or simulated grazing on the photosynthesis of individual plants or leaves (Wallace 1990, Painter and Detling 1981). Clipping increases tillering in some grass species and typically stimulates photosynthesis in remaining leaves (Painter and Detling 1981, Detling et al. 1979). However, it is difficult to extrapolate results from single plant or leaf studies to the community level, where species interactions and competition may have a greater impact. Morgan and Brown (1983) reported a positive relation between leaf area index and canopy photosynthesis in mowed Bermudagrass swards. However, there have been few reports of photosynthesis measured on an actively grazed native plant community (McNaughton et al. 1996).

In the mixed grass prairie of southeastern Wyoming, Manley et al. (1995) and Schuman et al. (1999) measured soil carbon of pastures grazed for 12 years vs. ungrazed exclosures. They found greater soil carbon in the upper 30 cm of soil of grazed pastures compared with ungrazed pastures. Although minor changes in species composition resulted from grazing, this did not help explain the differences in soil carbon.

As a first step towards a more systems oriented approach to understanding the effects of cattle grazing on the carbon cycle in the mixed grass prairie, we investigated how grazing treatments of the same pastures examined by Manley et al. (1995) affected plant community photosynthesis. We hypothesized that the result of grazing on plant community CO_2 exchange rate would depend on how grazing affected the photosynthetic surface area of the canopy. We expected that treatment differences in CO_2 exchange rate could be explained by corresponding differences in green vegetative surface area of the pasture.

Materials and Methods

The study site is near Cheyenne Wyo., USA, at the USDA-ARS High Plains Grasslands Research Station (lat. 41° 11' N, long. 104° 54' W). The region is a northern mixed-grass prairie with elevations averaging 1,930 m, mean annual precipitation averaging 38.4 cm and an average of 127 frost free days. Mean air temperatures are 17.5°C in summer and –2.5°C in winter, with maximum July temperatures averaging 27°C. The major cool-season grasses are western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love) and needle-and-thread grass (*Stipa comata* Trin and Rupr.), and the major warm season grass is blue grama (*Bouteoloua gracilis* (H.B.K.) Lag. Ex Steud.). The soils are a mixed, mesic, Aridic Argiustolls with the soil series being an Ascalon sandy loam (Schuman et al. 1999).

The study was conducted on pastures grazed since 1982 at a continuous season-long (early June to mid-October) light stocking rate (21.6 steer-days ha^{-1}), continuous season-long heavy stocking rate (62.7 steer-days ha^{-1}) and an ungrazed, 0.5 ha exclosure. The continuous heavy and continuous light stocking rate amounted to about 50% and 10% utilization of the annual production. The heavily and lightly grazed pastures share a fence and the exclosure is in the continuous light pasture. Before the initiation of these grazing treatments, the site had not been grazed by domestic livestock for 40 years (for more detail see Hart et al. 1988). The high labor requirements to perform these measurements permitted only 1 pasture of each grazing treatment being sampled to evaluate CO_2 exchange rates. Initial soil sampling at the start of grazing trials showed that these pastures had the same soil type, thereby reducing experimental variability. The plant communities within each pasture were quite homogenous.

Metal, angle-iron frames that enclose 1 m^2 of ground were driven into the soil along a transect established in 1982. The frames were level with the soil surface and had no apparent effect on cattle activity. Five frames per pasture (pseudo-replications), spaced 5 m apart, were installed along the transect for a total of 15. Canopy CO_2 exchange rate was measured with a 40 (height) x 100 x 100 cm 'Lexan' (Regal Plastics, Littleton, Colo.[1]) chamber, which had a closed-cell foam gasket on the base, which formed a seal with the metal frames. Air in the chamber was circulated by small fans, and a sample was pumped to a portable infrared gas analyzer (Analytical Development Co. model LCA-2, Hoddesdon, UK). The CO_2 exchange rate is then estimated from the rate of CO_2 depletion within the chamber. Measurements were performed rapidly (about 2 minutes) to minimize changes to the microclimate caused by the chamber (Angell and Svejcar 1999). CO_2 exchange rate measurements were performed from about 1000 to 1300 hours (mountain standard time) approximately every 3 weeks during the growing seasons of 1995, 1996 and 1997. Diurnal measurements made during 1995 showed that maximum daily CO_2 exchange rate

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[1] Mention of a trademark or manufacturer by the USDA does not imply its approval to the exclusion of other products or manufacturers that may also be suitable.

occurred at this time of day (also see Detling et al. 1978). The sequence of measurement among pastures was varied each date to reduce differences related to time of day. In 1995, we measured CO2 exchange rate on only 6 dates due to inclement weather during the spring (measurement requires cloud free conditions).

On each measurement date the point frame method was used to determine the relative photosynthetic surface area and species composition within each sample frame (Warren-Wilson 1963). Though the point frame method has limitations when used to determine leaf area index and for detecting less abundant species (Hazlett 1992, D. G. Milchunas pers. comm.) we considered it the best method of nondestructively determining photosynthetic surface area and species composition on plots which were repeatedly sampled. Green leaves, stems, and sheaths were recorded by the point frame since all 3 are significant contributors to photosynthesis (Caldwell et al. 1981). Total number of green tissue "hits" as 100 points were passed through the canopy of each 1 m^2 plot (500 points per pasture) were recorded to get a "green vegetation index". The hits were identified by species for determination of community composition. Soil water content was estimated from 0–30 cm soil cores and converted to a volumetric basis by multiplying by the soil bulk density (Schuman et al. 1999). Air temperature and light intensity (Analytical Development Co. model PLC(N), Hoddesdon, UK) were also determined at the time of each CO_2 exchange rate measurement. Seasonal precipitation and air temperature were obtained from a weather station near the site.

Soil respiration rate and soil temperature (2.5 cm depth) were measured (PP Systems model SRC, Hertfordshire, UK.) on 5 small plots (82 cm^2) next to each of the 1 m^2 plots at the same time as the CO_2 exchange rate measurements. Plastic rings were inserted about 2.5 cm into the ground and all above-ground vegetation was clipped from within the ring. These small plots rested for 2 weeks before soil respiration rate was measured to avoid CO_2 fluctuations associated with soil disturbance. All above-ground vegetation was clipped prior to each measurement. These rings were moved twice during each season. In 1995 the soil respiration measuring equipment was not available until the later part of the season. Therefore, soil respiration rate was only measured on the last 2 sampling dates. The CO_2 exchange rate, calculated on a ground surface area basis, was corrected for soil respiration by adding the soil respiration rate (when available) to the chamber CO_2 exchange rate. Therefore, CO_2 exchange rate comprises plant canopy photosynthesis and respiration only.

Statistical analysis such as analysis of variance are not appropriate for this experiment since we only have 1 true experimental unit per treatment. Data from the five, 1 m^2 plots in each pasture are presented here as means + standard errors.

Results

Spring (May and June) of 1995 had greater than average precipitation, and May temperatures were cooler than long term averages (Fig. 1). Precipitation and temperature were more similar to long-term averages in 1996, while precipitation was higher than normal during the late summer of 1997. Soil water content varied greatly depending upon the season, but the ungrazed pasture tended to have higher soil water content than either of the grazed pastures (Fig. 2). This was believed to be the result of the greater accumulation of litter and standing dead in the exclosure (Schuman et al. 1999), which acts as a mulch, particularly in the spring time after water has been stored during the winter (Bremer et al. 1998). Although it is not apparent in Figure 1, due to greater than normal early June and late July precipitation, in 1997 a significant drought occurred from mid June to late July (see Fig. 2).

On the first measurement date in 1995 (16 May), CO_2 exchange rate was higher in both of the grazed pastures compared to the exclosure (Fig. 3A). Poor weather prevented sampling again for almost 4 weeks. On the next sampling date (13 June) the grazed plots again had higher CO_2 exchange rates than the exclosure, although treatment differences were very small. The same trend suggests that there was a period of several weeks when the CO_2 exchange rate was higher in the grazed vs. exclosed pastures. In contrast, CO_2 exchange rate was typically lower in the grazed pastures in autumn. Seasonal trends in CO_2 exchange rate among the grazing strategies were similar to trends in green vegetation index (Fig. 3B). Green vegetation index was higher in the grazed pastures on the first 2 measurement dates and was lower in the grazed pastures later in the season (green vegetation index was not measured on 14 September 1995). On the 2 dates that we measured soil respiration rate, the exclosure had the lowest res-

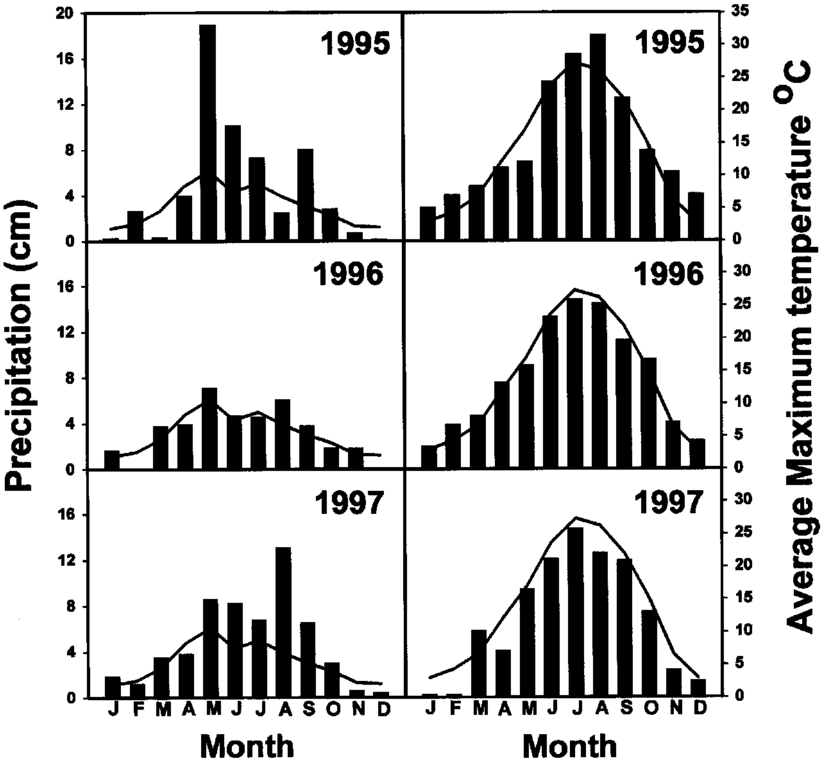

Fig. 1. Monthly total precipitation and average monthly maximum air temperatures of a mixed grass prairie site in Wyoming. The lines are long–term averages.

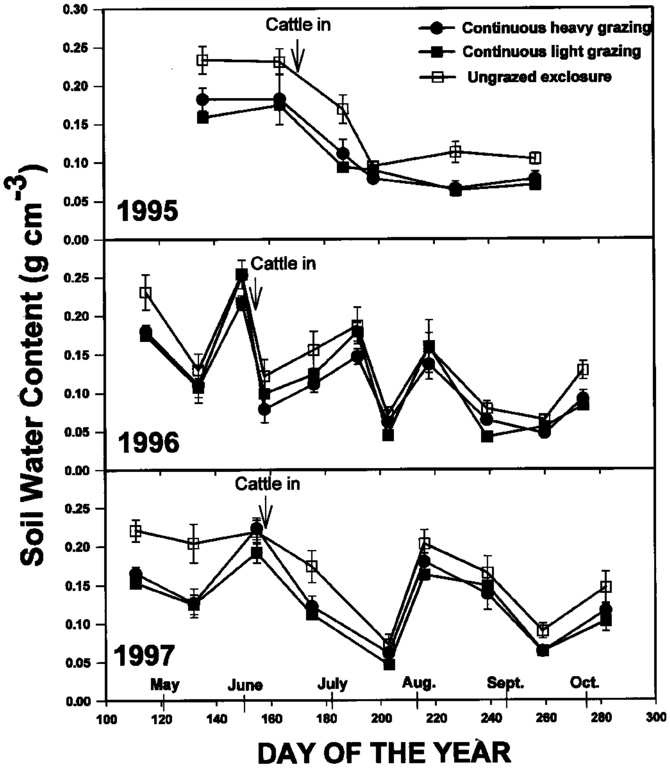

Fig. 2. Soil water content in the upper 30 cm of 3 mixed grass prairie pastures subjected to different grazing intensities. The X axis has the first day of the month marked. Data are means of 3 replications + standard errors.

piration rate and there was little difference between the heavily and lightly grazed pastures (Fig. 3C).

In 1996 only the heavily grazed pasture had greater CO_2 exchange rate than the exclosure on the first measurement date (24 April) (Fig. 4A). This trend continued for the next 2 measurement dates (13 May and 29 May), although differences were small. As in 1995, the heavily grazed pasture also had the greatest green vegetation index early in the season (Fig. 4B). Contrary to 1995, the CO_2 exchange rate and green vegetation index in the lightly grazed pasture were not higher than the exclosure in the spring of 1996. As in 1995, once cattle were put in the pastures the green vegetation index declined slightly in the continuous heavy compared to the continuous light and exclosed pastures. CO_2 exchange rate also tended to be lowest in the heavily grazed pasture during this period. During the spring of 1996 there were 2 measurement dates when soil respiration rate was slightly higher in the continuous heavy pasture than the continuous light and exclosure (day of the year 150 and 158) (Fig. 4C). There was no difference in soil respiration rate among the grazing treatments during the rest of the season.

On the first 4 measurement dates during the spring of 1997 (21 April– 24 June) the CO_2 exchange rate was higher in both the heavily and lightly grazed pastures compared with the exclosure (Fig. 5A). An ensuing drought caused CO_2 exchange rates to drop to near zero in all pastures by mid July. CO_2 exchange rates recovered following late July and early August precipitation, but there were no treatment differences for the rest of the season. Higher CO_2 exchange rates in the 2 grazed pastures was again accompanied by greater green vegetation index although not on day of the year 155 (Fig. 5B). Surprisingly, green vegetation index was highest in the heavily grazed pasture on 3 dates in July and August (day of the year 203, 216, 239) but this did not result in greater CO_2 exchange rate. There were 2 dates during the 1997 season when the continuous heavy pasture had a higher soil respiration rate than the continuous light and exclosed pastures (Fig. 5C). In none of the three years were treatment differences in CO_2 exchange rate associated with air or soil temperature at the time of measurement (data not shown).

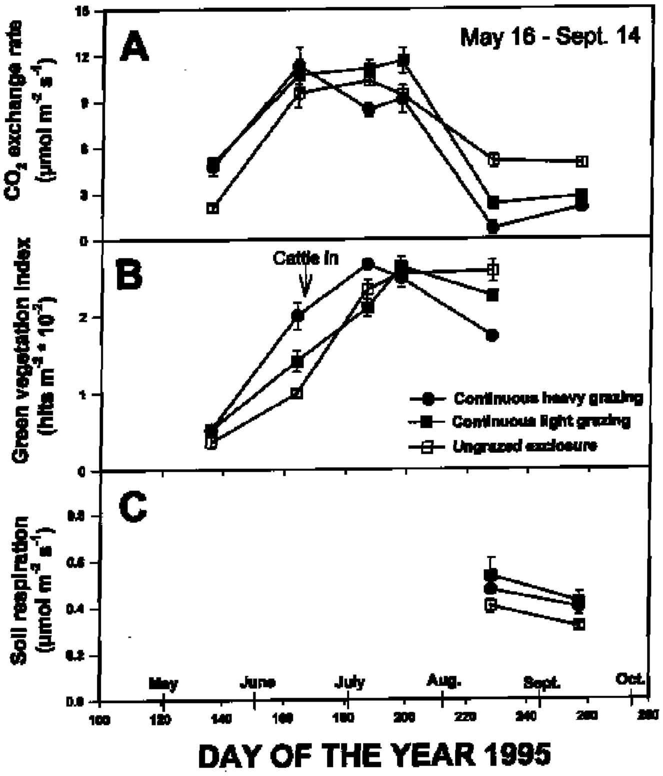

Fig. 3. 1995 data of CO_2 exchange rate (corrected for soil respiration when available; A), green vegetation index (B) and soil respiration rate (C) of 3 mixed grass prairie pastures subjected to different grazing intensities (the soil respiration equipment was not available until the final 2 dates). The X axis has the first day of the month marked. Data are means of 5 replications + standard errors.

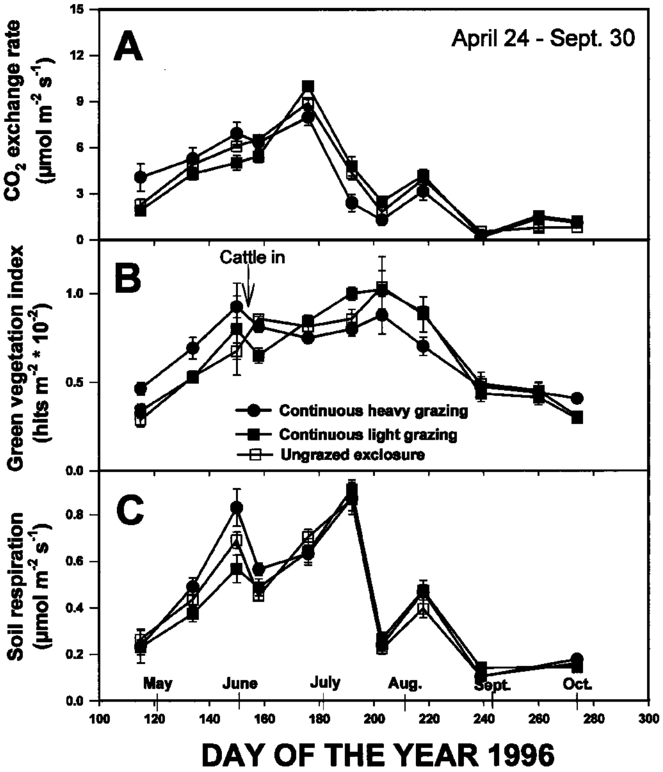

Fig. 4. 1996 data of CO$_2$ exchange rate (corrected for soil respiration; A), green vegetation index (B) and soil respiration rate (C) of 3 mixed grass prairie pastures subjected to different grazing intensities. The X axis has the first day of the month marked. Data are means of 5 replications + standard errors.

Our data do not allow us to calculate annual net primary productivity, however, by averaging the CO$_2$ exchange rate data over each season we can look at overall trends in carbon exchange resulting from 13 and more years of grazing. When the data are averaged over the entire season, within each year, they show no difference in the average CO$_2$ exchange rate among these 3 grazing systems, although in 1997 there is a trend for greater CO$_2$ exchange rate in the continuous heavy pasture, compared with exclosure (Table 1). Though the grazed pastures often had higher CO$_2$ exchange rate early in the season, the exclosure often had equal or higher rates during mid to late season.

Since changes in species composition may affect seasonal CO$_2$ exchange rate and soil carbon (Smoliak et al. 1972), the occurrence of the most prevalent species (as detected by the point frame) was averaged over the entire study (Table 2). There is relatively more blue grama in the continuous heavy and exclosed pastures than the continuous light pasture. Blue grama (C$_4$) appears to be replaced by the C$_3$ species fringed sage (*Artemisia frigida* Willd.) and scarlet globemallow (*Sphaeralcea coccinea* (Nutt.) Rydb.) in the continuous light pasture. The continuous heavy pasture has less western wheatgrass than the continuous light and exclosure, but more carex (*Carex eleocharis* Bailey) plants. Overall, there are only small changes in species composition induced by grazing for 13 plus years. Also, no significant difference in belowground biomass was detected in these pastures (Schuman et al., 1999). Our data differ somewhat from those of Schuman et al. (1999) who measured botanical composition as a percentage of harvested peak standing crop, and found higher amounts of blue grama in the continuous heavy treatment than both the continuous light and exclosure pastures. The differences noted above may be a result of the particular placement of our 1 m^2 frames in these large pastures, or that our data are averaged over many dates through the season rather than at peak standing crop.

Discussion

CO$_2$ exchange rates

Though there was year to year variation in this study, the seasonal pattern consisted of higher CO$_2$ exchange rates in the grazed plots (most consistently in the con-

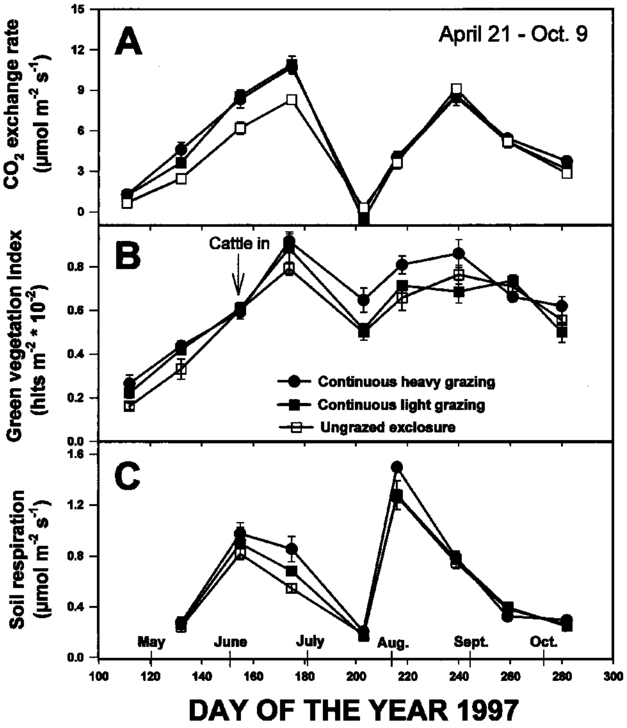

Fig. 5. 1997 data of CO$_2$ exchange rate (corrected for soil respiration; A), green vegetation index (B) and soil respiration rate (C) of 3 mixed grass prairie pastures subjected to different grazing intensities. The X axis has the first day of the month marked. Data are means of 5 replications + standard errors.

Table 1. The CO_2 exchange and soil respiration rates of grazed and ungrazed mixed grass prairie pastures near Cheyenne Wyoming (averaged over the entire growing season)[1].

	CO_2 exchange rate			Soil respiration rate		
Treatment	1995	1996	1997	1995	1996	1997
	(µmol CO_2 m^{-2} sec^{-1})					
Continuous heavy grazing	6.1 ± 0.8	3.9 ± 0.4	5.2 ± 0.5	0.43 ± .02	0.47 ± .04	0.66 ± .07
Continuous light grazing	7.2 ± 0.8	4.0 ± 0.4	4.8 ± 0.5	0.48 ± .04	0.41 ± .03	0.58 ± .06
Ungrazed exclosure	6.9 ± 0.6	4.0 ± 0.4	4.3 ± 0.5	0.43 ± .04	0.43 ± ..04	0.56 ± .06

[1] Data are means ± standard errors of 6, 11, and 9 measurement dates for CO_2 exchange rate and 2, 10, and 8 dates for soil respiration rate in 1995, 1996, and 1997, each of 5 replicate plots.

tinuous heavy pasture) compared with the exclosure in the spring (April, May, early June), with differences diminishing by mid June, followed by occasional higher CO_2 exchange rate in the ungrazed pasture late in the season. Treatment differences in CO_2 exchange rate were associated with differences in green vegetation index, indicating earlier spring green-up in the grazed pastures. There was no apparent correlation between treatment differences in CO_2 exchange rate and yearly climate variation.

We did not measure litter and standing dead in this study. However, Schuman et al. (1999), using these same pastures, showed that grazing greatly reduced litter and standing dead, while in the exclosure, 72% of the above-ground phytomass was litter and standing dead. We hypothesize that earlier spring green-up (measured as higher green vegetation index) and higher CO_2 exchange rates in grazed pastures is due to better light penetration and warmer microclimate conditions near the soil surface as a result of less litter and standing dead than in the ungrazed pasture. Our hypothesis is supported by Bremer et al. (1998), who attributed warmer soil temperature in clipped vs. unclipped plots to improved radiation penetration resulting from less litter and standing dead. We were unable to measure canopy light penetration in our system, as it is very difficult to assess accurately where plant canopy structure is low. Summarizing over the 3-year period of this study, we conclude that these intensities of grazing do not have a large effect on daytime carbon exchange of the mixed-grass prairie of Wyoming.

Soil respiration rate

When examined on a seasonal basis, we found no difference in soil respiration rate in grazed vs. ungrazed pastures (Table 1), but there were several dates over the 3 years when soil respiration rate was higher in the grazed vs. ungrazed pastures. These results differ from Bremer et al. (1998) who reported reduced soil respiration in grazed vs. ungrazed tallgrass prairie. In that study the reduction in photosynthetic surface area and available carbohydrates was reported to be the dominating factor in lowered respiration rates. In our ecosystem, photosynthesis was actually higher in the grazed pastures early in the season. Therefore, higher soil respiration rates in the spring may be indicative of greater carbon allocation to roots. Our maximum soil respiration rates were about 10% of those of the tallgrass prairie, indicating very different soil microbial and root respiration activity between tallgrass and mixed grass prairie ecosystems.

Green vegetation index and species composition

It was surprising in 1997 not to see a decrease in CO_2 exchange rate and green vegetation index in the heavily grazed pasture after cattle were put in the pasture. The introduction of cattle was followed by a severe drought period in 1997 (Fig. 2). Plant responses to drought, rather than grazing treatment, may have been the overriding factor in any treatment differences measured during and following the drought period in 1997.

There was no apparent relationship between the small differences in species composition in these pastures and the seasonal trends in CO_2 exchange rate. In a similar study (LeCain et al. 1998), conducted on the shortgrass prairie of eastern Colorado, long-term grazing elicited a shift in species composition to a greater dominance of blue grama. The prevalence of this warm-season grass was related to higher CO_2 exchange rate in the grazed pastures when warm temperatures occurred, while the exclosure, with a greater percentage of cool-season species, had higher CO_2 exchange rate when weather was cool. No such relationship was seen in the mixed grass prairie study. However, shifts in species composition in these pastures are likely to be more of a factor in the future (Schuman et al. 1999).

Effects of CO_2 exchange and soil respiration rates on soil carbon

Our data show only small differences in CO_2 exchange rate and soil respiration rate between grazed and exclosed pastures when the rates are averaged within each year (Table 1), suggesting little effect of grazing on soil carbon concentration in our study. However, our ability to make conclusions about effects of carbon

Table 2. The relative abundance[1] of major species on grazed and ungrazed mixed grass prairie pastures near Cheyenne Wyo., as determined by the point frame method.

	Grazing intensity		Ungrazed
Species	Continuous heavy	Continuous light	Exclosure
Blue grama (*Bouteloua gracilis* (H.B.K.) Lag. Ex Steud.)	37.0 ± 3	25.3 ± 2	36.5 ± 3
Western Wheatgrass (*Pascopyrum smithii* (Rydb.) A. Love)	10.5 ± 1.5	22.9 ± 2	22.8 ± 2
Carex (*Carex eleocharis* Bailey)	15.0 ± 1	3.6 ± 0.6	8.1 ± 0.9
Fringed Sage (*Artemisia frigida* Willd.)	8.1 ± 0.5	26.0 ± 2	6.0 ± 0.8
Scarlet globemallow (*Sphaeralcea coccinea* (Nutt.) Rydb.)	3.2 ± 0.3	12.0 ± 1	5.0 ± 0.5
Needle–and–thread grass (*Stipa comata* Trin and Rupr.)	3.2 ± 0.3	2.0 ± 0.3	6.0 ± 0.9

[1] Relative abundance is the percentage of point frame “hits” over 3 years worth of data on 5 replicate plots (125 measurements) ± standard error.

exchange on soil carbon are limited because our measurements were performed at 3 week intervals through the season and only during periods of maximum daily photosynthesis. We do not know the proportion of spring days during which grazed plots had higher CO_2 exchange rates, nor how many days during the summer that CO_2 exchange rate was lower in the continuous heavy plots, nor if treatment differences seen at midday occur diurnally.

The influence of observed seasonal trends in CO_2 exchange rate on soil carbon depends on interactive effects of grazing and rainfall on CO_2 exchange rate and seasonal patterns of partitioning of photosynthate between above and below-ground organs. On the northern mixed grass prairie most of the above-ground production typically occurs prior to July when soil moisture and temperature are favorable for growth of the dominant C_3 species (Sims and Singh 1978a, also see green vegetation index in Figs. 3, 4, and 5). Although a direct effect of grazing is to decrease carbon allocation to the roots during above-ground regrowth (Caldwell et al. 1981, Detling et al. 1979) much of the period of higher CO_2 exchange rate which we measured in grazed pastures occurred before cattle were introduced. Higher CO_2 exchange rate and productivity in grazed vs. ungrazed pastures during this part of the season are likely accompanied by greater carbon allocation to the roots. Over time this could increase soil carbon concentration. There was also a trend for greater soil respiration in the grazed compared to the ungrazed pastures early in the season, particularly in the heavily grazed pasture. This is another indication of improved biological activity and greater carbon allocation to roots during the early part of the season in grazed pastures, probably because of warmer soil temperature (Bremer et al. 1998).

In typical years, soils dry out as the season progresses and CO_2 exchange rate and plant productivity slows. The CO_2 exchange rate declines as defoliation by grazers lowers the photosynthetic surface area. This suggests less below-ground carbon allocation in grazed vs. ungrazed pastures during the later part of the season. However, much of the mid- to late-season photosynthate in range grasses is used in storage, rather than shoot or root growth, as plants prepare for summer or winter dormancy (White 1973). Most late season carbohydrates are stored in the stem bases and crowns and are utilized in winter respiration and leaf tissue regeneration in early spring (White 1973). Therefore, these carbon compounds may have less effect on soil carbon concentration than carbon used for structural root growth early in the season (Dormaar and Sauerbeck 1983). Further studies are necessary to determine precisely how seasonal differences in CO_2 exchange rate and soil respiration influence soil carbon in this ecosystem.

Conclusion

Our expectation that seasonal CO_2 exchange rate would be associated with the amount of green vegetation in the pastures was largely confirmed in this study. However, the discovery of higher CO_2 exchange rate and earlier spring green-up in grazed pastures was unanticipated, and perhaps the most interesting find. Overall, our data show that cattle grazing, at the intensities used in this study, elicits only small changes in ecosystem carbon exchange, soil respiration rate, green vegetation production and species composition. These results agree with studies conducted on the nearby shortgrass prairie, where the ecosystem has been found to be very tolerant of cattle grazing. Semiarid grasslands with a long history of grazing respond to grazing with only small changes in annual net primary productivity and community composition (Milchunas et al. 1988, Milchunas and Lauenroth 1993). In both systems up to 90% of the plant based carbon is below-ground (Schuman et al. 1999, Milchunas et al. 1998). Therefore, removal of even 50% of the above-ground plant material (as in the continuous heavy treatment) has only a small effect on ecosystem functioning.

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Alkaloid levels of a tall larkspur species in southwestern Alberta

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Abstract

Tall larkspurs (*Delphinium spp.*) are widely distributed in western North America and they kill more cattle on rangelands than any other poisonous plant. In Alberta, Canada, *D. brownii* Rydb. has a long history of causing cattle poisoning. The neurotoxic norditerpenoid alkaloid methyllycaconitine (MLA) was first detected in D. *brownii* over 50 years ago. A 2-year (1996 to 1997) survey was conducted on the levels of MLA in *D. brownii* collected at 5 sites in the foothills of southwestern Alberta. The vegetative stage of growth yielded the highest levels of MLA and the decline and change in concentration during that interval could be predicted on the basis of Julian day alone. The MLA levels during bud to pod development were not significantly different but they exceeded the reported levels for MLA in low larkspur by 5- to 10-fold. A new method is described for the determination of MLA by HPLC.

Key Words: Poisonous plants, *Delphinium brownii*, neurotoxic alkaloids, methyllycaconitine

Larkspur (*Delphinium spp.*), especially the tall larkspurs, constitute the most serious poisonous plant problem to rangeland cattle in North America (Nielson and Ralphs 1998, Wroe and Smith 1991, Fowler et al. 1982). Four species of tall larkspur predominate in western USA: D. *barbeyi* Huth, D. *glaucescens* Rydb., D. *occidentale* S. Wats., and D. *glaucum* S. Wats. (Ralphs et al. 1997). A large geographically separate population of D. *glaucum* also occurs in northwestern Saskatchewan (SK) and Alberta (AB), extending through northern British Columbia (B.C.), the Yukon, Western Mackenzie and Alaska (Brayshaw 1989). The 2 populations of D. g*laucum* are sometimes treated as distinct species (Hitchcock and Cronquist 1964). The population in the Pacific States is referred to as D. *glaucum* (mountain larkspur) and that in Alaska and Canada as D. *brownii* Rydb. (tall delphinium). According to Brayshaw (1989), the morphological features that separate them on a taxonomic basis are minor and indistinct and he does not treat them as separate species and all modern Floras of Alaska, Yukon, Northwest Territories, B.C., AB, SK agree. However, the chemical literature on tall larkspur in Canada always refers to D. *brownii*, so we have chosen to retain the 2 species concept.

Resumen

"Tall larkspurs" (*Delphinium* spp.) están ampliamente distribuidas en el oeste de Norte américa, y ellas matan mas ganado en los pastizales que ningún otra especie de planta tóxica. En Alberta, Canadá, *D. brownii* tiene un largo historial como causante de la muerte de ganado por envenenamiento. El alcaloide neurotóxico norditerpenoide metilicaconitina (MLA) fue detectado por primera vez en *D. brownii* hace 50 años. Se condujo un examen de dos años (1996 a 1997) de los niveles de MLA en *D. brownii* colectado en 5 sitios al pie de las montañas del sudoeste de Alberta. Los más altos niveles de MLA se registraron cuando la planta estaba en la etapa vegetativa de crecimiento y la disminución y cambio en la concentración durante ese intervalo pudieron ser predichas en base solo a los días julianos. Los niveles de MLA durante el desarrollo de yemas y vainas no fueron significativamente diferentes, pero ellos excedieron entre 5 y 10 veces los valores de MLA reportados en "Low larkspur". Se describe un nuevo método para la determinación de MLA por medio de HPLC.

The detection of methyllycaconitine (MLA) in D. *brownii* occurred over 50 years ago (Manske 1938, Marion and Manske 1946). The proof of structure (Benn et al. 1963), the precise stereochemistry (Pelletier et al. 1981, Edwards and Przyblyska 1982) and the mode of action of the alkaloid (Aiyar et al. 1979, Nation et al. 1982) were subsequently elucidated. It is now well established that MLA is the principal neurotoxic alkaloid in most native species of *Delphinium* in North America (Manners et al. 1991, 1993, Majak 1993). The objectives of this study were 1) to develop a new method for MLA determination by HPLC since earlier column packings for MLA determinations on HPLC (Manners and Pfister 1993, Majak et al. 1987) were not readily available and 2) to compare MLA levels in D. *brownii* at different stages of growth and at different sampling sites in southwestern Alberta where cattle losses due to the ingestion of D. *brownii* can be severe.

Materials and Methods

The 5 sampling sites were located between Bow Crow Forest (49^0 51'N, $114^0$0'W) and the OH Ranch (50°35'N, 114° 21'W) in the fescue (*Festuca campestris* Rydb.)-aspen (*Populus tremuloides* Michx.) parkland of southwestern Alberta, commonly known as the foothills. The elevations at the sites ranged from 1,400 to 1,600 m and the soils were loamy and characterized as Dark Gray Chernozem (Boralfic Boroll).

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Composite samples of *D. brownii* (100–200 g fresh weight, aerial portions) representing sequential stages of growth (vegetative, bud, flower, and pod) were collected randomly at each site during 2 growing seasons (n = 26 in 1996 and n = 31 in 1997). The number of samples at each stage of growth varied with site and year, depending on the duration of the phenological stage. When the larkspur plants became elongated and stemmy, the upper 50 cm of the shoot containing most of the leaves and the inflorescence was excised for analysis. The samples were freeze-dried, the alkaloids were extracted as described previously (Majak et al. 1987) and the extracts analyzed by HPLC utilizing a polymeric reverse phase column (PRP-1, 150 x 4.1 mm, Hamilton Co., part no. 79444) and acetonitrile - 0.1% phosphoric acid, 23:77, as the isocratic developing solvent at a flow rate of 1.8 ml/min with UV detection at 212 nm. The PRP-1 column minimized tailing of alkaloidal compounds without the use of ion-pairing reagents (Majak et al. 1987), which can accumulate as residues and affect instrument performance. The alkaloid was quantified by the external standard method with duplicate injections per plant sample using a 20 μl sample loop.

The effects of site and stage of growth on MLA concentration (% by weight) were determined by analysis of variance, or co-variance using the procedures of the SAS Institute Inc. (1989). Years were considered a form of replication. The data were transformed to logarithms for analysis to provide homogeneity of variance. Concentrations varied with collection date during the vegetative stage but not during the bud, bloom, or pod stages. For this reason, the data from the vegetative stage were analysed separately from the data for the other 3 stages. For the vegetative stage, the sources of variation in the analysis of co-variance were site, year, site x year, Julian day (co-variate) and the residual error. A test for non-parallelism at different sites and years was also carried out. For the bud, bloom, and pod data, the sources of variation in the analysis of variance were stage, site, stage x site, year, year x site x stage (experimental error, includes year x site and year x stage) and the residual error. Least squares estimates of log (MLA) concentration were made for each stage, site and year and back transformed for presentation. As is appropriate for back transformed logarithmic data, the variability was indicated by the coefficient of variation of the mean. This is the standard error divided by the mean and expressed as a percentage.

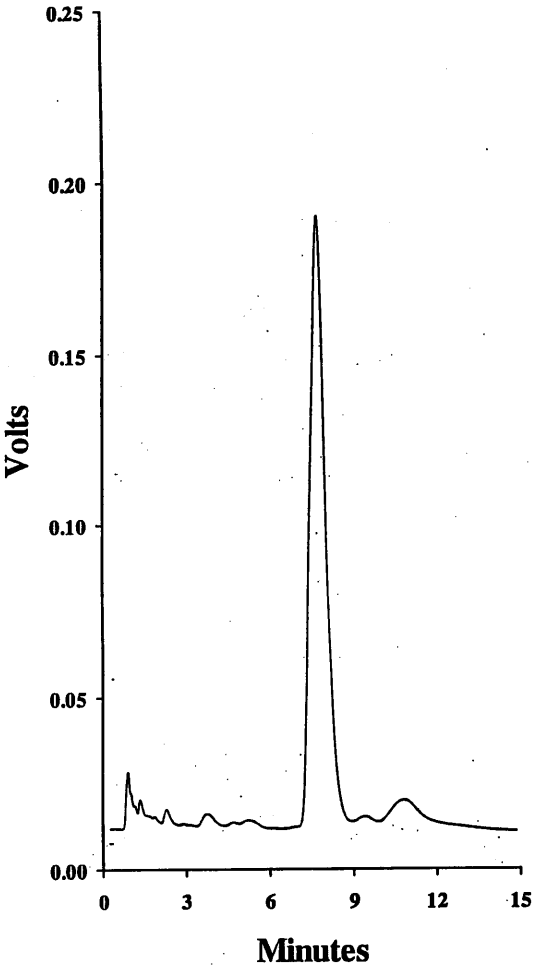

Fig. 1. HPLC separation of MLA (320 ppm) from a purified extract of freeze–dried D. brownii (0.5 g). Column: Hamilton PRP–1 (150 x 4.1 mm). Detection: 212 nm. Mobile phase: acetonitrile – 0.1% phosphoric acid (23:77).

Results and Discussion

The detection limit for MLA on the PRP-1 column was <10 ppm and the resolution on HPLC was equal to that described previously (Majak et al. 1987). For example, MLA (retention time = 7.4 min) was separated from nudicauline (retention time = 8.6 min) with near baseline resolution. Nudicauline differs from MLA only at C_{14} where MLA has a methoxy group and nudicauline has an acetyl group. In agreement with earlier studies (Benn et al. 1963) and as evidenced by the single peak on HPLC (Fig. 1), MLA was the major anthranoyl-type norditerpenoid alkaloid thus far detected in *D. brownii*. It is possible that geyerline and grandiflorine, previously reported in *D. glaucum* (Manners et al. 1998) were also present in *D. brownii* but only in trace quantities. These alkaloids were also resolved in our HPLC system.

The norditerpenoid alkaloids, browniine (Benn et al. 1963) and browniine acetate (Aiyar et al. 1978) have also been isolated from *D. brownii*, but these alkaloids would not be visualized by UV detection on HPLC owing to the absence of the anthranoyl-group. The absence of this group also renders these alkaloids much less toxic than MLA (Benn and Jacyno 1983, Manners et al. 1993). Ralphs et al. (1997) reported on the concentration of total toxic anthranoyl-type norditerpenoid alkaloids in *D. glaucum* (mountain larkspur) but they did not specify on the proportion of MLA. They concluded however, that of the 4 species of tall larkspur that were examined in the USA, D. *glaucum* had the highest levels of toxic norditerpenoid alkaloids: 1% on a dry matter basis with the range extending from 0.5 to 2%. The highest levels of MLA in *D. brownii* occurred during the vegetative stage of growth and the levels extended from 1 to 5%. These MLA levels were at least 2- to

Table 1. Levels of MLA (% by weight) in tall larkspur averaged for each stage, site, and year.

Stage				Site						Year		
Bud	Bloom	Pod	CV[1]	1	2	3	4	5	CV	1996	1997	CV
						(%)						
0.95	0.76	0.71	9.92%	0.94	0.89	0.80	0.71	0.69	11.3%	0.70	1.04	7.74%

[1] CV (mean) = (100 x SE) ÷ mean.

10-fold greater than those reported for low larkspur (*D. nuttallianum*) at the same stage of growth (Majak 1993). This may well account for the much higher incidence of larkspur poisoning in the foothills of Alberta than in the southern interior of B.C. where low larkspur is widespread but tall larkspur is absent. Tall larkspur is also seasonally persistent as compared to low larkspur, which is seasonally ephemeral. Field observations on grazing cattle in Canada suggest that the larkspurs are a preferred species during the vegetative stages of growth (Majak and Engelsjord 1988, B. Maynard, personal communication, OH Ranch).

During the vegetative stage, there was a significant ($P < 0.0001$) decline in MLA levels with time. The relationship between log concentration of MLA and time (Julian days after January 1) during the vegetative stage of D. *brownii* could be expressed as:

$$\ln [\mathrm{MLA}] = 6.1059 - 0.0310 \ (\mathrm{days}) \qquad \mathbf{(1)}$$

where $r^2 = 0.79$, SE (intercept) = 0.5824 and SE (regression coefficient) = 0.003465. During 1996 and 1997, the vegetative stage in *D. brownii* began at the end of May and ended during the beginning of July. The rate of decline was the same for all sites and years (no significant non-parallelism). On average, the MLA concentration declined by about 3% of its value each day. There were no significant differences in the intercepts among sites or among years.

During bud, bloom, and pod development, there were no significant differences in MLA levels among stages of growth or among sites at those stages but average values for MLA were higher in 1997 than in 1996 (Table 1). The levels of MLA in D. *brownii* at the more advanced stages of growth were still 5- to 10-fold higher than those reported for low larkspur (Majak 1993, Pfister and Gardner 1998). This again underlines the much greater toxicity of this species of tall larkspur.

The rainfall in the study area during July and August, 1996, which was the bud to pod growing period, was 5 to 10% of normal. The rainfall for the same period in 1997 was closer to normal. Whether this difference in moisture affected the MLA levels in *D. brownii* is not known. There are only a few reports on the effect of moisture stress on tall larkspur toxicity and they are inconsistent. Olsen et al. (1990), using a mouse bioassay, reported no difference in the toxicity of D. *occidentale* collected from a moist site and a dry site. Ralphs et al. (1997) compared toxic alkaloid levels in tall larkspur growing in shaded and unshaded areas. The alkaloid levels in *D. barbeyi* were higher ($P<0.02$) at the open site but significant differences were not detected in the alkaloid levels of *D. occidentale* from the 2 types of sites. In low larkspur, a seasonally ephemeral species, lower levels of MLA were associated with site conditions that reduced soil moisture stress (Majak et al. 1999). It is possible that moisture conditions affect alkaloids in climax species, such as tall larkspur, differently and more studies are required to resolve this issue.

In summary, a reliable method was developed for the analysis of MLA in *D. brownii* by HPLC. The vegetative stage of growth yielded the highest levels of MLA and the change and decline in concentration during that period could be predicted from Julian day alone. The MLA levels during bud to pod development did not show significant changes, nor were there differences in MLA levels among sites. The MLA levels in *D. brownii*, a tall larkspur, can be 5-to 10-fold higher than in *D. nuttallianum*, a low larkspur, and this may account for the much higher incidence of cattle poisoning from tall larkspur than from low larkspur ingestion in Western Canada.

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Seasonal chemical composition of saltbush in semiarid grasslands of Jordan

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Abstract

Saltbush (*Atriplex halimus* L.), a native shrub which is adapted to arid rangelands, was transplanted to the semiarid grassland at Jordan University of Science and Technology Campus in 1986. Our objective was to determine the seasonal changes in the chemical composition of the annual growth of leaves and stems of saltbush (*Atriplex halimus* L.) during 1995–96 and 1996–97. A strong positive correlation was found among P, Ca, crude protein, and nitrogen free extract and a strong negative correlation was found between fiber and P, Ca, crude protein, and nitrogen free extract. Nitrogen free extract (NFE) had a strong positive linear correlation with P, Ca, and crude protein. P, Ca, Ca:P ratio, crude protein, and NFE contents were found to be higher in leaves than in stems on all the occasions.

Leaves had relatively higher concentrations of P, Ca, crude protein, and NFE during the growing season (February to April). Crude protein of leaves reached its maximum in March (22.7%). The concentrations decreased, however, to 15% during the dry period (June to October). Crude protein content of stems ranged from 11.3 to 12.2%. Fiber content of leaves was lowest during February and March (16.9 to 18%), and reached maximum values during August and October. Saltbush is a good protein source for sheep during the dry season; however, P content would not meet nutritional requirements of ewes.

Key Words: *Atriplex halimus,* crude protein, dry season, ewes, fiber, leaves, Middle East, stems

Resumen

En 1986 se transplantaron arbustos de "Saltbush" (*Atriplex halimus* L.) (una especie nativa adaptada a pastizales áridos) en un pastizal semiárido de la Universidad Científica y Tecnológica de Jordania. Nuestro objetivo fue determinar los cambios estacionales de la composición química del crecimiento anual de hojas y tallos de "Saltbush" (*Atriplex halimus* L.) durante las estaciones de crecimiento de 1995-1996 y 1996-1997. Se encontró una fuerte correlación positiva entre P, Ca, proteína cruda, y extracto libre de nitrógeno. También se encontró una fuerte correlación negativa entre la fibra y P, Ca, proteína cruda, y extracto libre de nitrógeno. El extracto libre de nitrógeno (ELN) tuvo una fuerte correlación lineal positiva con P, Ca y proteína cruda. En todos los muestreos el contenido de P, Ca, la relación P:Ca, proteína cruda, y ELN fueron mayores en hojas que en tallos.

Durante la estación de crecimiento (Febrero a Abril), las hojas tuvieron un contenido relativamente mayor de P, Ca, proteína cruda y ELN. La proteína cruda de las hojas alcanzó su máximo valor (27%) en Marzo, sin embargo, la concentración disminuyó a 15% durante el período seco (Junio a Octubre). El contenido de proteína cruda de los tallos vario de 11.3 a 12.2%. El menor contenido de fibra de las hojas ocurrió en Febrero y Marzo (16.9 a 18%) y los valores máximos se alcanzaron en Agosto y Octubre. Durante la época seca, el "Saltbush" es una buena fuente de proteína para los ovinos; sin embargo, el contenido de P podría no satisfacer los requerimientos nutricionales de las borregas.

Atriplex spp. are halophytes that have considerable forage potential in the arid and semiarid rangelands of West Asia (Le Houerou 1992, 1995). In Jordan *Atriplex* spp. are thought to be a solution to feed shortages that occur during droughts and dormant seasons. Most forages usually have high nutritive value during early growth, but their nutritive value declines rapidly with maturity. Most shrubs generally have high levels of crude protein, phosphorous and calcium throughout the year (Stidham et al. 1982).

In Israel, *Atriplex halimus* L. furnishes protein, vitamins and minerals to sheep during summer and autumn (Benjamin et al. 1959). Sheep grazed on dormant crested wheatgrass ((*Agropyron cristatum* L.) had greater weight losses than those grazing a mixture of crested wheatgrass and fourwing saltbush (*A. canescens* (Pursh) Nutt.) (Otsyina et al. 1982). Protein content of *A. canesens* leaves had decreased from 25% in April to 10% in August before it gradually increased during winter to about 20%. The feed value of leaves again decreased during June through December (Thomson et al. 1997). Chatterton et al. (1971) reported a remarkable variation in the nutritive value of different parts of the plant *A. polycarpa* (Torr.) S. Wats. over the year.

Jordan has over 2.6 million sheep and 1 million goats, and the amount of supplemented feed stuff is estimated at 444 thousand tons (FAO 1994). Sheep in autumn depend on crop stubble and native pasture. Saltbush (*A. halimus* L.) is a native shrub found in many salty and arid regions of the Middle East including Jordan. It's a promising forage source and supplemental feed during dry seasons and emergencies, but the seasonal variation of its nutritive value and chemical composition has not been investigated. Our objective was to determine the seasonal changes in chemical

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composition of the current year's growth of leaves and stems of saltbush (*Atriplex halimus* L.) on semiarid grassland in Jordan.

Materials and Methods

Site Description

The saltbush on which this study was conducted grows on semiarid grassland located within the campus boundary of the Jordan University of Science and Technology (JUST) 22 km east of Irbid (32° 34' N, 36° 0' E). Altitude is 520 m, and the site is characterized by flat to gently rolling topography with less than 10% slope. The soil is a weakly cracked and deep silty clay. Natural vegetation is typical of Mediterranean semiarid grassland. Our study utilized 3 hectares of *A. halimus* L. transplanted in an adaptability trial during 1986–87 and protected from grazing. Mean annual precipitation for that site is 230 mm, and annual rainfall during 1995–96 and 1996–97 occurred during October to April. Highest accumulations and the most rapid plant growth occurred during the period from January to March (Fig. 1). Plant growth usually starts during December and stops by the end of April due to dry-hot conditions.

Sampling

Four100-m transects were randomly selected. In 1995–96 and 1996–97, 16 saltbush shrubs on each transect were selected randomly, and 8 shrubs per transect were utilized for the experiment each year. Samples were collected on 28 December, January, February, March, April, June, August, and October. On each sampling date, the current year's growth of 4 randomly selected shrubs was clipped, and the leaves and stems separated and dried at 70°C for 72 hours.

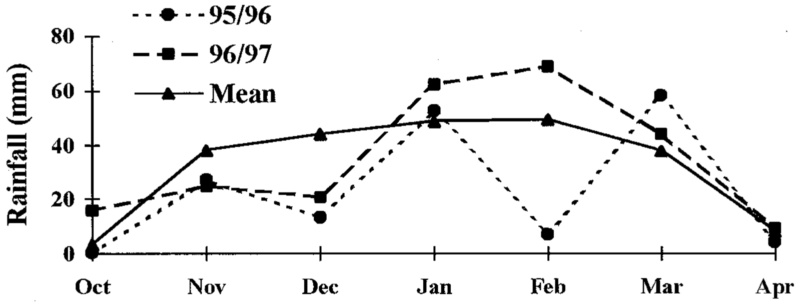

Fig. 1. Monthly rainfall (mm) for 1995–96, 1996–97 and long term means (n=11).

Chemical Analysis

One hundred-gram samples of oven-dry leaves and stems from each shrub were milled to pass a 0.4-mm screen and used for subsequent chemical analyses. Calcium was determined by atomic absorption spectrophotometer. Phosphorous was determined following Watanable and Olsen (1965) procedures. Crude protein (Nx6.25), nitrogen free extract (NFE) and fiber were determined according to AOAC (1984) procedures.

Statistical Analysis

The data were analyzed using a 2 x 8 x 2 factorial using a randomized complete block design. Factors were years (2), months (8), and plant parts (2) with 4 replications. Null hypotheses related to all 3 main effects and the pertinent interactions were tested at the P ≤ 0.01 level of significance. Analyses of variance did not show a significant year effect (Table 1), therefore, means of the chemical composition of leaves and stems were pooled over years. Means were separated by Fisher's Least Significant Difference (LSD) at P ≤ 0.01. Linear relationships among the chemical properties were determined by correlation techniques described by Steel and Torrie (1980).

Table 1. Significance levels in analyses of variance of various chemical components extracted from saltbush (Atriplex halimus L.) *in Jordan from* December 1995-October 1997.

Source of variation	df		P	Ca	Ca:P	CP	NFE	Fiber
replicate	(r-1)	3	ns	ns	ns	ns	ns	ns
year	(y-1)	1	ns	ns	ns	ns	ns	ns
plant part	(s-1)	1	**	**	**	**	**	**
year X plant part	(y-1)(s-1)	1	ns	ns	ns	ns	ns	ns
month	(m-1)	7	**	**	**	**	**	**
year X month	(y-1)(m-1)	7	ns	ns	ns	ns	ns	ns
plant part X month	(s-1)(m-1)	7	**	**	**	**	**	**
year X plant part X month	(y-1)(s-1)(m-1)	7	ns	ns	ns	ns	ns	ns
Error	(r-1)(ysm-1)	93						

** Significant at P<0.01
ns Not significant

Results

Simple linear correlation analysis (Table 2) showed strong positive relationships between P, Ca, crude protein, and nitrogen free extract, whereas fiber exhibited a strong negative correlation with P, Ca, crude protein, and nitrogen free extract. Analyses of variance did not show a significant year effect, however, there were significant differences between leaves and stems and significant seasonal effects in the composition of leaves and stems during the year at P≤0.01 (Table 1).

Leaves

Leaves of *Atriplex halimus* L. showed higher (P≤0.01) P, Ca, Ca:P ratio, crude protein, and nitrogen free extract (NFE) values than stems on any clipping date (Fig. 2). Leaves had maximum levels of P, Ca, crude protein, and NFE during the February to April growing season, and the Ca:P ratio increased gradually from 5 during February to 11.7 during October (Fig. 2C). Crude protein content ranged from 15.8 to 22.7% (Fig. 3A), with the highest values detected in February (20.8%) and March (22.7%). Crude protein decreased to about 15% during the June to October dry period. Nitrogen free extract (NFE)

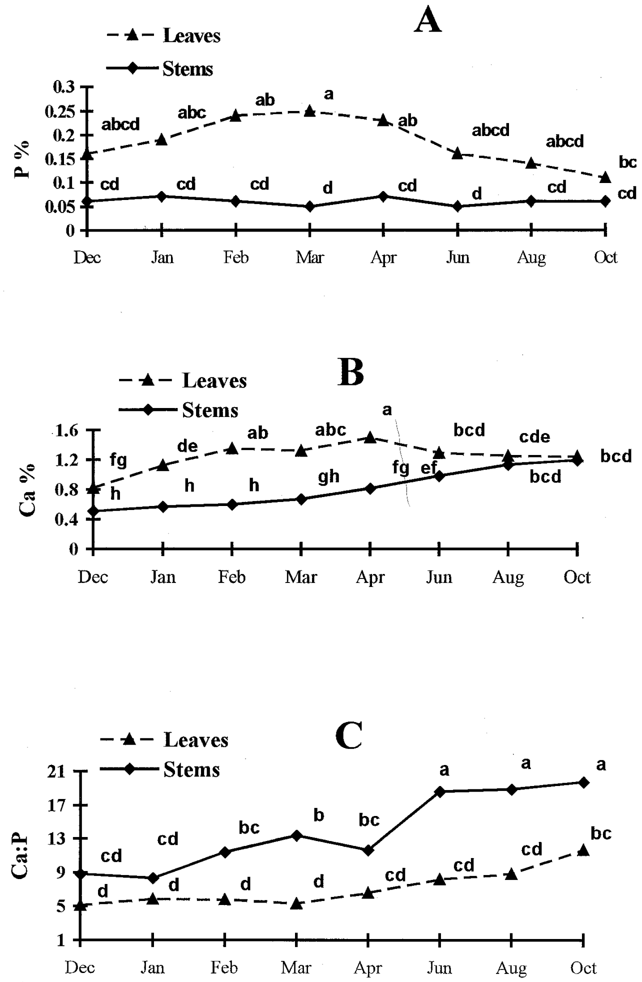

Fig. 2. Seasonal phosphorous (A), calcium (B) and Ca:P ratio (C) contents of saltbush (*A. halimus* L.) leaves and stems during 1995–96 and 1996–97 at Jordan University of Science and Technology Campus. Means within a component having a common letter do not differ significantly (P> 0.01).

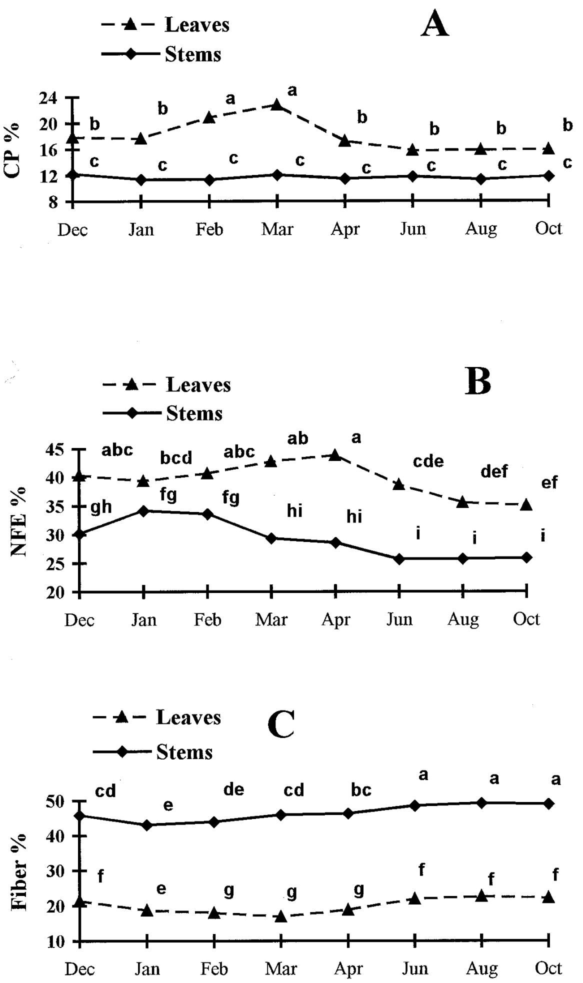

Fig. 3. Seasonal crude protein (A), nitrogen free extract (B) and crude fiber (C) contents of saltbush (*A. halimus* L.) leaves and stems during 1995–96 and 1996–97 at Jordan University of Science and Technology Campus. Means within a component having a common letter do not differ significantly (P> 0.01)..

increased gradually from 40% at the December sampling date, to 44% during April. Thereafter NFE gradually decreased to 35% in October (Fig. 3B). Fiber content increased from a low in February (16.9%) to a high of 22.6% in October (Fig. 3C).

Stems

Except for P and crude protein, where no seasonal changes occurred, the nutrient content of stems increased gradually from December to October (Fig. 2A and 3A). Crude protein content ranged from 11.3 to 12.2%. Ca content was 0.5% during December, and it increased gradually to 1.22% in October (Fig. 2B). During October, Ca concentrations of leaves and stems were equal. The Ca:P ratio increased gradually from 8.8 in December to 19.8 in October (Fig. 2C). Nitrogen free extract (NFE) was highest during January (34.1%) but started decreasing after February to a low of 25.8% in October (Fig. 3B). The crude fiber content of stems increased gradually from December (43%) to October (49%) (Fig. 3C).

Discussion

Jordanian rangeland has a unimodal precipitation pattern, with a short rainy period followed by an extended dry season furnishing limited opportunities for herbaceous forage production. Plant dormancy stimulates a decline in both quantity and quality of forage. Annual grasses may lose 75% of their protein content and up to 52% of their phosphorous during the dry season (Louis et al. 1983). Wheat and barley residue grazing starts immediatly after harvest in June and lasts until September. This provides the basic diet for sheep throughout the summer into autumn; when supplementary feeding begins (ACSAD 1983). The forage value of the crop residues deteriorates after a month of grazing, and the animals begin loosing weight. Supplementation with cotton seed meal or cereal grain at a rate of 100 g/day^{-1} could stop weight losses (Turminini 1991).

Sheep usually need supplementation for 6 months in a normal year and 9 months during drought years (Nesheiwat and Muhammed 1987). The CP content of saltbush (*Atriplex halimus* L.) is high, and would be a good protein source for livestock during dry summer and autumn periods. Protein is one of the most limiting nutrients for range livestock production and its supplementation is cost effective, because it improves forage intake and

Table 2. Correlation coefficients among some chemical components of *A. halimus* L. sampled in Jordan from December 1995–October 1997.

	Ca	Ca:P	CP	NFE	Fiber
P	0.66 **	-0.72 **	0.92 **	0.93 **	-0.87 **
Ca		0.04	0.89 **	0.50 **	-0.53 **
Ca:P			-0.68 **	-0.77 **	0.79 **
CP				0.90 **	-0.88 **
NFE					-0.85 **

** Significant at $P<0.01$

digestibility (Holechek and Herbel 1986). On Utah rangelands, Gade and Provenza (1986) compared the diet quality of sheep using crested wheatgrass and a wheatgrass-shrub mixture during winter. They found that sheep grazed on wheatgrass-shrub mixtures had higher forage intake, higher crude protein intake, and lower fiber levels in their diets than sheep grazing a pure stand of wheatgrass. In our study, saltbush (*A. halimus* L.) crude protein and Ca contents were sufficient to meet ewes maintenance and lactation requirements during any time of the year. Phosphorus was deficient for ewes, suggesting supplements would be necessary to adjust the high Ca:P ratio in their diet. Ewes require 7 to 9% crude protein for maintenance and 10 to 12% for lactation. They also need 0.15% to 0.20% P for maintenance and 0.25 to 0.30% for lactation (Holechek et al. 1994). The introduction of saltbush (*A. halimus* L.) into semiarid grassland of Jordan would elevate the nutritive plain of livestock and possibly minimize the need for grain supplements during summer and autumn.

Conclusion

Semiarid grasslands usually supply livestock with high food quality during spring but forage quality declines rapidly as grass mature. Saltbush showed relatively high levels of protein and nitrogen free extract throughout the year. Saltbush is drought resistant and can be grazed during droughty years. Introducing saltbush into Jordan's grassland may improve the quality of the livestock diets and minimize grain supplementation during summer and autumn. Phosphorous supplementation, however, would be necessary to adjust the Ca:P ratio.

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Grazing effects on spring ecosystem vegetation of California's hardwood rangelands

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Abstract

Three watersheds at the University of California's Sierra Foothill Research and Extension Center (SFREC), Marysville, Calif. were selected to study cattle grazing effects on the vegetation surrounding cold-water springs and their downslope creeks. Three spring-creek systems from each of 3 watersheds were randomly assigned to grazing treatments (9 total). Treatments were ungrazed, lightly grazed (1,500 kg•ha^{-1} residual dry matter), and moderately grazed (1,000 kg•ha^{-1} residual dry matter) based on degree of use in upland pastures encircling the spring-creek systems. Total herbaceous cover at springs varied significantly among the 6 years only once (greater in 1994 than all others) covarying with previous year's rainfall. Grazing intensity did not affect total herbaceous cover at springs. A year X grazing treatment interaction ($P<0.05$) was detected for total herbaceous cover at spring-fed creeks. Three years after grazing removal, total herbaceous cover on ungrazed creek plots surpassed cover at moderately grazed and lightly grazed plots. Moderately grazed plot herbaceous cover declined steadily throughout the first 3 years, while lightly grazed cover remained relatively stable. Plant community composition and stability by year and grazing treatment were analyzed with TWINSPAN. With few exceptions, stable plant communities persisted on sites regardless of grazing intensity or cover changes. Total herbaceous cover was sensitive to interannual fluctuations, especially under increased grazing intensities. This attribute renders cover a more useful gauge of ecosystem health than plant composition as the latter may not provide evidence of potentially deleterious grazing X climate interactions until after soil erosion or water table characteristics are seriously, perhaps permanently, altered.

Key Words: Riparian, creek, cover, grazing, species composition

Resumen

Se seleccionaron tres cuencas hidrológicas de la Estación de Investigación y Extensión Sierra Foothills de la Universidad de California con el objetivo de estudiar los efectos del apacentamiento del ganado en la vegetación circundante de manantiales de agua fría y sus arroyos pendiente abajo. En cada cuenca, tres sistemas de manantial-arroyos se asignaron aleatoriamente a los tratamientos de apacentamiento (9 en total). Los tratamientos fueron; sin apacentamiento, apacentacentado ligeramente (1,500 kg ha^{-1} de materia seca residual) y apacentacentado moderadamente (1,000 kg ha^{-1} de materia seca residual), los tratamientos se basaron en el grado de utilización de tierras arriba que circundan los sistemas de manatial-arroyos. La cobertura total de la vegetación herbácea en los manantiales varió significativamente solo una vez en 6 años (en 1994 fue mayor que los otros años) y los cambios se correlacionaron con la precipitación del año anterior. La intensidad de apacentamiento no afecto la cobertura total de la vegetación herbácea de los manantiales. En la variable cobertura total de la vegetación herbácea de los manantiales-arroyo, se detecto una interacción año x tratamiento de apacentamiento ($P<0.05$). Después de 3 años de que el apacentamiento se suspendió, la cobertura total herbácea de las parcelas de los arroyos sin apacentar superó a la cobertura registrada en las parcelas con apacentamiento ligero y moderado. La cobertura de herbáceas de las parcelas con apacentamiento moderado disminuyo paulatinamente durante los primeros tres años, mientras que la cobertura de las parcelas con apacentamiento ligero permaneció relativamente estable. La composición y estabilidad de la comunidad vegetal por año y tratamiento de apacentamiento se analizaron con TWINSPAN. Con pocas excepciones, comunidades estables de plantas persistieron en los sitios, independientemente de la intensidad de apacentamiento o los cambios de cobertura. La cobertura total herbácea fue sensible a las fluctuaciones interanuales, especialmente bajo las mayores intensidades de apacentamiento. Este atributo, en comparación con la composición de la comunidad, representa una mejor medida de la salud del ecosistema que este ultima puede no proveer de evidencia del daño potencial de la interacción apacentamiento x clíma hasta que la erosión del suelo o las características de agua freática son seriamente alteradas.

The ecology and management of California's annual grasslands, woodlands, and savannas have been well studied (Bartolome and Standiford 1992, Bartolome and McClaran 1992, Bartolome et al. 1994, Heady et al. 1992, Standiford et al. 1997). However, few studies examine cold-water spring ecosystems of these rangelands, or the potential for grazing effects on them (Allen-Diaz et al. 1998).

Managers assess range condition or health by comparing existing plant community composition to a standard (Dyksterhuis 1949, Busby et al. 1994). Plant species cover is the variable most often estimated for generating range condition classes. Although grazing management changes often effect changes in vegetation cover, Bartolome (1984) and Milchunas and Lauenroth (1993)

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suggested that species composition does not necessarily track cover variability and may lead to erroneous conclusions concerning long-term ecosystem productivity. Busby and Cox (1994) suggested that soil degradation and water quality parameters may be more important than plant species composition for assessing ecosystem health.

We tested the effects of different cattle grazing intensities on vegetation surrounding springs over 6 years on California's oak-dominated hardwood rangeland. We hypothesized that reduced grazing intensity would induce plant community composition change. However, we held no a priori notions regarding compositional change direction.

Study Site

Research was conducted at Sierra Foothill Research and Extension Center (SFREC). The study site was described in detail in Allen-Diaz et al. 1998. Briefly, SFREC has an average annual precipitation of 72 cm•yr^{-1}. Air temperatures in the region range from monthly averages of 32.0°C in July to 2.2°C in January. Dominant vegetation is blue oak (*Quercus douglasii* Hook. & Arn.)/gray pine (*Pinus sabiniana* Douglas) woodlands and savannas with introduced annual grass and forb understories. Soils in this area are classified as Auburn (loamy, oxidic, thermic, Ruptic-Lithic Xerochrepts) and Argonaut (fine, mixed, thermic Mollic Haploxeralfs) series (Herbert and Begg 1969).

As described previously, springs and their resultant creeks are quite small (about 0.5 m wide at the source). Wetland species (Table 1 for typical spring spp.) remain green in summer and sharply delineate a spring's boundaries, which extend an average of 3 m perpendicular to flow, forming oval-like borders. The highly palatable, perennial vegetation of spring ecosystems encourages intense cattle use. This is especially evident during summer months as upland annual grasses dry (Table 1 for typical annual grassland spp.). Concentrated utilization of springs creates visually striking vegetation impacts that motivated this study.

Three spring-creek systems were selected from each of 3 SFREC watersheds (Campbell, Schubert, and Forbes) for grazing treatment application (Allen-Diaz et al. 1998). Watersheds were selected for the presence of undeveloped springs, geographic proximity, and similar management histories. These watersheds had all been grazed by cattle at a moderate level (800 to 1000 kg•ha^{-1} residual dry matter) since 1960 when the ranch came under University of California ownership. Prior to this ownership change, it is believed that greater livestock use levels existed (Kinney 1996), however, these use levels have not been quantified. Impediments to wildlife herbivory do not exist, nor do we believe any ever have in the past.

Methods

Grazing treatment

Each pasture within a watershed was randomly assigned a grazing treatment, ungrazed (UG), lightly grazed (LG), or moderately grazed (MG); applied from 1993 through 1997. The approximately 2 ha pastures were grazed by cattle following autumn germination (usually November). Cattle were then removed for the winter and returned to pastures during the spring season annual vegetation rapid-growth phase (February through April). Residual herbage on a dry matter basis (RDM) estimates were then made and cattle were returned to pastures in May to meet target RDM levels (Table 2 for annual RDM estimates). The number of animals placed in a pasture during any period was variable as it was based on available upland forage. Indeed, more animals were often placed on the lightly grazed plots because of site and interannual productivity differences (Allen-Diaz et al. 1998).

Table 1. Partial herbaceous-layer flora of springs and uplands.

Species	Common name	Family
Springs		
Brachypodium distachyon L..	False brome	Poaceae
Briza minor L.	Rattlesnake grass	Poaceae
Carduus pycnocephalus L.	Italian thistle	Asteraceae
Cynodon dactylon L.	Crabgrass	Poaceae
Cynosurus echinatus L.	Dogtail	Poaceae
Cyperus niger Ruiz Lopez & Pavon	Sedge	Cyperaceae
Cyperus odoratus L.	Sedge	Cyperaceae
Eleocharis macrostachya Britton.	--[1]	Cyperaceae
Holcus lanatus L.	Velvet grass	Poaceae
Lolium multiflorum Lam.	Italian ryegrass	Poaceae
Mimulus guttatus DC.	Monkey flower	Scrophulariaceae
Paspalum dilatatum Poiret	Dallis grass	Poaceae
Polypogon monspeliensis L.	Annual beard grass	Poaceae
Rorippa nasturtium-aquaticum Hayek	Water cress	Brassicaceae
Rubus ursinus Cham. & Schldl.	Blackberry	Rosaceae
Stachys albens A. Gray.	Hedge nettle	Lamiaceae
Stellaria media Villars	Common chickweed	Caryophyllaceae
Typha angustifolia L.	Cattail	Typhaceae
Verbena bonariensis L.	--[1]	Verbenaceae
Vitis californica Benth.	California grape	Vitaceae
Uplands		
Avena fatua L..	Wild oat	Poaceae
Bromus diandrus Roth	Ripgut brome	Poaceae
Bromus hordeaceus L.	Soft chess	Poaceae
Bromus madritensis L.	Red brome	Poaceae
Carduus pycnocephalus L.	Italian thistle	Asteraceae
Centaurea solstitialis L.	Yellow star thistle	Asteraceae
Elymus glaucus Buckley	Blue wildrye	Poaceae
Erodium botrys Bertol.	Filaree	Geraniaceae
.*Erodium cicutarium* L'Her. ;	Filaree	Geraniaceae
Galium aparine L.	Common bedstraw	Rubiaceae
Geranium molle L.	Geranium	Geraniaceae
Hordeum murinum L.	Barley	Poaceae
Lolium multiflorum Lam.	Italian ryegrass	Poaceae
Medicago polymorpha L.	California burclover	Fabaceae
Nassella pulchra Barkworth	Purple needlegrass	Poaceae
Phalaris aquatica L.	Harding grass	Poaceae
Taeniatherum caput-medusae Nevski	Medusahead	Poaceae
Torilis nodosa L.	Wild carrot	Apiaceae
Trifolium hirtum All.	Rose clover	Fabaceae
Vulpia myuros C. Gmelin	Annual festuca	Poaceae

[1] No known common name

Table 2. Annual residual dry matter (RDM) estimates made each June from 3 clipped plots in pastures surrounding spring sites to estimate grazing intensity.

		Grazing Year (September-June)						
Watershed	Treatment	1992/3	1993/4	1994/5	1995/6	1996/7	Mean	SE
		($kg•ha^{-1}$)						
Campbell	UG[1]	2586	1404	2347	1227	1478	1808	274
	LG[2]	1256	462	2240	1066	790	1163	301
	MG[3]	1248	798	1685	1040	742	1103	171
Schubert	UG	6092	3031	5899	---[4]	1915	4234	1043
	LG	1453	1413	3461	1592	878	1759	442
	MG	1597	402	1013	1788	578	1076	272
Forbes	UG	5019	2648	5317	---[4]	3114	4025	670
	LG	5436	1807	5211	3403	3119	3795	680
	MG	2509	1399	2224	1434	1660	1845	222

[1] Ungrazed
[2] Lightly grazed
[3] Moderately grazed
[4] Data not available

Cattle were English-cross yearlings, including Angus, Red Angus, and Hereford breeds that averaged 455 kg (Table 3). Actual use data for pastures surrounding springs were provided in Allen-Diaz et al. (1998). Livestock were managed under a comprehensive SFREC health care program, which included immunization against locally common cattle diseases several times annually.

Livestock grazing during the growing season has little effect on forage composition or productivity on California's hardwood rangelands (Bartolome and McClaran 1992). Grazed California annual grass rangelands are managed so that target residual dry matter levels are achieved at the end of the annual grass growing season (late May) or before the new rains start (September) (Bartolome et al. 1980, Heady et al. 1992). Domestic grazing animals are generally allowed to graze rangeland pastures on a semi-continuous or periodic rotational basis so that *at the end of the growing season* RDM target levels for the grassland are met. Animal management objectives include maintaining or enhancing body weight, and animal numbers are adjusted depending on the quality and quantity of forage available at any time during the annual grass growth cycle. Other elements of the rangeland landscape, such as springs, are not managed for per se. Rather, these ecosystems experience cattle use levels in proportion to their desirability as green forage and place of water.

Experienced Research Center annual grassland range managers monitored grazing treatment intensity during each treatment period. Cattle were left on a site until a visually estimated residual dry matter (RDM) target level was attained during any grazing period. To quantify grazing treatment levels, upland RDM was measured annually (June) by comparing aboveground herbaceous biomass from 3 randomly-located 0.0625-m^2 clipped quadrats per treatment pasture.

Vegetation sampling

Depending on physical constraints imposed on transect length, a permanent 10-m or 5-m vegetation sampling transect was randomly established on each side of a spring and each side of a creek at each cohort in 1992 and was sampled annually in spring through 1997. Species cover was also estimated quasi-weekly 6 times from 11 April 1997 to 1 June 1997 to examine within-season variability. Transects were run parallel to spring or creek flow. The line-point method (Heady et al. 1959) was used to determine plant species cover 3 weeks after late spring (late May) cattle removal from grazing treatments. Vegetative "hits" were determined according to the first foliar intercept in the herbaceous layer. Total herbaceous cover was calculated as total hits minus non-vegetation hits divided by total hits. Plant species identification and nomenclature followed The Jepson Manual (Hickman 1993).

Statistical analyses

Potential differences in total herbaceous cover at springs and creeks among grazing treatments were assessed with split-plot, repeated measures ANOVA (S-PLUS 1993). Three watersheds comprised a blocking variable that effectively reduced error variance by partitioning site-to-site variability out of the ANOVA model. Each watershed was subjected to 3 grazing treatment levels (whole plot) repeatedly measured over 6 years (and 6 weeks for 1997; split plot). Homoscedasticity was verified for both factors but significant covariance among years indicated non-independence across factor levels rendering univariate analyses inappropriate for significance tests of temporal variation (Winer 1971). Hence, MANOVA was performed on year-wise orthogonal contrasts of total cover for tests of time. Orthogonal contrasts were created by multiplying total cover by a coefficient matrix whose determinant equaled zero. MANOVA was then performed using yearly responses as dependent variables (Venables and Ripley 1997). When significant main or interaction effects were detected, pooled standard errors of the differences among means were examined to ascertain which treatment levels gave rise to significant differences main or interaction effects.

Temporal changes in plant species composition across grazing treatments were assessed with TWINSPAN, a divisive, polythetic classification program (Hill 1979). Default cut-levels were used to classify each pasture-year combination.

Results

Grazing treatments did not affect herbaceous cover at springs. Interannual variation was significant only in 1994, when total herbaceous cover was greater than cover totals in 1995 and 1997 ($P < 0.05$).

Table 3. Cattle abundance and mean weight in each grazing period for 3 treatments. (Actual use dates and number of animals per treatment can be found in Allen-Diaz et al. 1998).

Grazing treatment period	Animal type	Animal weight
		(kg)
November-December 1992	cow	360-405
March–May 1993	cow	360-405
November–December 1993	cow	360-405
March–May 1994	cow	455
May 1994*	steer	225
December 1994–May 1995	cow	455
February 1996–May 1996	cow, calf	455, 214
November 1996–May 1997**	cow, calf, bull	455, 214, 475

*adjustment to reach RDM standards
**7 bulls for 2 days on Campbell LG

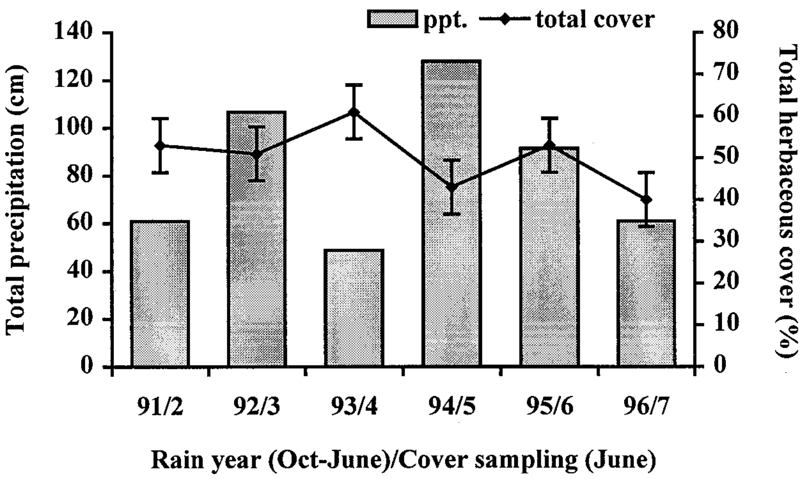

Fig. 1. Annual precipitation and total herbaceous cover at springs.

Precipitation well above average in the 1992/93 rain-year coupled with below average precipitation for the 1993/94 rain year probably contributed to increased cover in 1994 and reduced cover in 1995 (Fig. 1).

A significant grazing X year interaction was determined for total herbaceous cover at creek sites ($P < 0.05$). Grazing treatment groups did not differ significantly for 1992 and 1993 (Fig. 2). But, in 1994, ungrazed (UG) cover increased dramatically from 63% to 86% while the moderately grazed (MG) group declined from 74% to 59% total herbaceous cover. The UG group retained greater cover than MG and lightly grazed (LG) in 1995 and 1996, but not in 1997. The LG group maintained the most stable total herbaceous cover values over the study period ranging between 45–55%. The MG group cover ranged from 80% at the beginning of the study (1992) to 34% one year after the lowest rainfall year (1994).

TWINSPAN classification analysis showed that only one spring transitioned to a new community type, a result of *Rubus* spp. expansion at the Forbes moderately grazed (MG) spring plot (Fig. 3). The transition occurred between 1992 and 1993 and has an associated eigenvalue (λ) of 0.434 indicating a high *goodness-of-split* (Jongman et al. 1995). All other splits were based on dominant tree presence (*Salix* spp., $\lambda = 0.556$), *Typha angustifolia* L. presence ($\lambda = 0.474$), and *Rhamnus californica* Eschsch. presence ($\lambda = 0.359$), which changed little during the study.

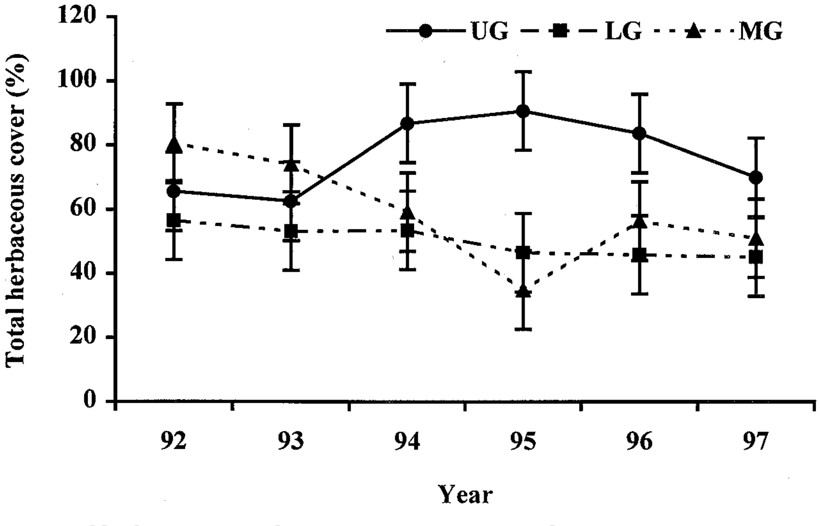

Fig. 2. Total herbaceous cover by grazing treatment at creeks.

Results based on 1997 quasi-weekly sampling showed no grazing treatment effects and no temporal variation in total herbaceous cover at springs. A year X grazing interaction for total herbaceous cover at creeks ($P < 0.01$) reflected a difference between LG and MG for the initial 1997 sampling week (11 April). Lightly grazed and MG groups then stabilized at ~50% herbaceous cover for the remainder of the 1997 6-week sampling period. The TWINSPAN results showed no compositional changes over the 6-week sampling period.

Discussion

Domestic livestock have grazed the Sierra Foothill Research & Extension Center (SFREC) area for about 120 years. Although grazing intensity has certainly varied during this period, springs and their resulting creeks likely experienced periods of intense utilization, especially during summer. With the introduction of SFREC range management (1960), use at springs remained concentrated but less continuous, allowing for vegetative recovery and regrowth of perennial vegetation during rest periods. At SFREC, cattle are moved often, usually dictated by research needs.

While mean residual dry matter (RDM) target levels were met for the 6-year period, moderate- and light-grazed targets were transposed in several years (Table 2). This resulted from difficulties in reconciling visual upland RDM estimates with visual observations of spring use and because the presence of particular species at certain sites (*Typha angustifolia* L., *Rhamnus californica* Eschsch.) somewhat physically deterred riparian use until surrounding annual grasses had been heavily utilized. Moderately grazed and lightly grazed (LG) targets were also occasionally transposed because of upland vegetation regrowth under more favorable weather conditions after animals had been removed. Hence, cattle were sometimes removed from pastures before upland RDM targets were met. We do not believe that the minor interannual differences in RDM target levels affected the overall 6-year results.

In fact, our study continued the 120-year history of periodic, intense use of the spring systems at both LG and moderately grazed (MG) treatment levels, but especially at MG levels. The ungrazed (UG) treatment can be thought of as release from 120 years of MG use. Grazing treatments, including complete protection, did

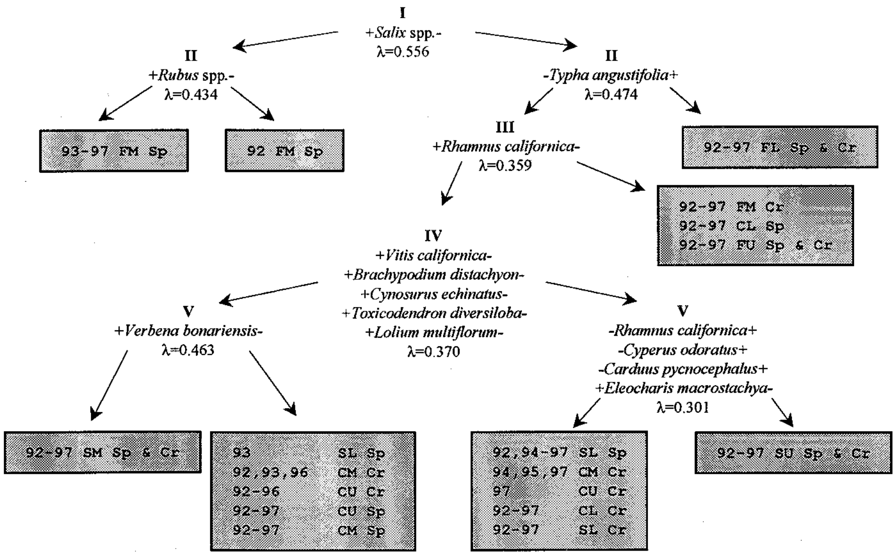

Fig. 3. TWINSPAN classification results. Roman numerals indicate different division levels. Numbers in shaded boxes indicate year, first letter denotes watershed (F=Forbes, S=Schubert, C=Campbell), second letter denotes grazing treatment (M=moderately grazed, L=lightly grazed, U=ungrazed), "Sp" denotes spring-site, "Cr" denotes creek-site. Classification divisions were based on presence (+) or absence (-) of noted species. Strength of a given division is measured by eigenvalue (λ; 0.00-1.00 range).

not alter total herbaceous cover at springs or species composition at springs or creeks during the 6-year study.

The finding that MG plots changed in total cover more among years at creeks and springs than either the LG or UG groups, possibly under the influence of rainfall fluctuations, is compelling. Annual rainfall patterns control variations in species dominance on California's annual grasslands (Pitt and Heady 1978). It appears that these same patterns could similarly influence herbaceous cover in the perennial vegetation of low-flow spring systems, but with a 1-year time lag (Fig. 1). We did not observe interannual rainfall induced shifts in vegetation composition, an anticipated result, because seed bank, edaphic characteristics, and water, which are known to affect annual uplands, are less limiting at spring ecosystems.

We speculate that prolonged drought in moderately grazed situations probably reduces herbaceous cover at both springs and creeks, but without an immediate impact on plant community composition until some low-cover threshold is crossed (sensu Bartolome 1984). We hypothesize that soil loss and decreasing water table depth would eventually produce compositional changes on moderately grazed systems, given drought conditions. As spring flows seasonally waned, the changing pattern of water table drawdown shown to affect composition in wet meadows (Allen-Diaz 1991) should eventually induce compositional transitions. Shallow-rooted annual species would move into formerly saturated areas. It is unknown whether these changes would be fluid enough that a return to pre-drought spring-flow would result in a linear, reverse transition to pre-drought species composition and spatial extent. However, given that this system has been moderately grazed for 120+ years, enduring several droughts, it seems apparent that the plant communities found presently represent some relatively stable result of Mediterranean-type climatic regimes. Monitoring to detect threshold response of these spring-creek systems under continued grazing exclusion and increased grazing intensity (target ~600 kg•ha^{-1} RDM) will continue.

Instead of showing more sensitivity to grazing, ample water supply seems to buffer deleterious grazing effects at springs and spring-fed creeks. This buffering apparently stabilizes perennial spring vegetation composition. We conclude that species composition is not sensitive to existing grazing systems that include periodic intense use coupled with overall moderate grazing levels on uplands. Instead, spring vegetation composition appears resistant to changes in both grazing and climatic conditions.

However, total vegetative cover appears to be a more useful metric for abiotic and biotic resource conservation in these systems. We base this conclusion on our finding that total herbaceous cover is sensitive to weather variability, especially under higher grazing intensities. Because total cover is directly linked to erosion rates and hydrologic processes (Busby et al. 1994, Busby and Cox 1994), total cover may prove to be an appropriate monitoring parameter for these systems.

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Switchgrass growth and development: Water, nitrogen, and plant density effects

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Abstract

Switchgrass (*Panicum virgatum* L.), an important component of the tallgrass prairie, is a productive warm-season forage grass. Interest in growing switchgrass for alternative uses has raised questions about resource use during production. The objective of our study was to examine how resource inputs affected interspecific plant competition in switchgrass. 'Alamo' switchgrass was established from seed in outdoor lysimeters in May 1993 and grown under 22 or 112 kg N ha^{-1}, and under field capacity or water-deficit conditions until August 1994. Plant spacing varied systematically from 10 to 70 cm. Plants were harvested in late summer each year and individual plant dry weight, tiller number, leaf area, and morphological development stage were measured. Soil moisture tensions below –45 kPa reduced switchgrass photosynthetic rates and xylem pressure potential. As plant spacing increased, tiller number, leaf area, plant dry weight, and morphological development stage increased. Plant dry weight and tiller number in the establishment year was not affected by N input. Established plants in 1994, however, responded to high N input at low plant densities with 50 to 100% greater leaf area and up to 3-fold greater plant dry weight compared to the low-N treatment. The increased plant dry weight at high N input resulted from increased individual tiller weight and not increased tiller number. Our data indicate that competitive responses of switchgrass plants at high plant densities were controlled by competition for aboveground resources, as plant yield and morphology at high densities were not affected by water or N inputs.

Key Words: *Panicum virgatum*, morphological development, stress

Resumen

"Switchgrass" (*Panicum virgatum* L.), un componente importante de las praderas de zacares altos, es un zacate forrajero productivo de estación caliente. El interés de cultivar "Switchgrass" para usos alternativos ha generado preguntas acerca del uso de recursos durante la producción. El objetivo de nuestro estudio fue examinar como la adición de recursos afectó la competencia interespecífica del "Switchgrass". En Mayo de 1993, mediante semilla, se estableció el zacate "Switchgrass" variedad 'Alamo' en lísimetros colocados en el exterior, las plantas se fertilizaron con 22 o 112 kg ha^{-1} de nitrógeno y crecieron bajo condiciones de capacidad de campo o déficit de humedad hasta Agosto de 1994. El espaciamiento entre plantas vario sistemáticamente de 10 a 70 cm. Las plantas se cosecharon a fines del verano de cada año y a cada una de ellas se les determino individualmente el peso seco, número de hijuelos, área foliar y desarrollo morfológico. Tensiones de humedad del suelo abajo de a –45 kPa redujeron las tasas fotosintéticas y el potencial de presión del xilema del "Switchgrass". Conforme el espaciamiento entre plantas aumento, el número de hijuelos, área foliar, peso seco y desarrollo morfológico también aumentaron. Durante el año de establecimiento, la adición de nitrógeno no afecto el peso seco ni número de hijuelos de las plantas. Sin embargo, en 1994, las plantas establecidas a respondieron a la adición alta de nitrógeno; a densidades bajas de plantas, el área foliar aumento de 50 a 100% y el peso seco por planta hasta en 3 veces comparadas con las plantas con una adición baja de nitrógeno. El aumento del peso seco de las plantas en el tratamiento alto en nitrógeno fue producto de un aumento del peso individual de los hijuelos y no de un incremento en el número de ellos. Nuestros datos indican que la respuesta competitiva de plantas de "Switchgrass" en altas densidades fue controlada por la competencia por los recursos arriba de la superficie del suelo ya que el rendimiento por planta y su morfología a altas densidades no fueron afectados por la adición de nitrógeno o agua.

Switchgrass is a warm-season perennial grass commonly grown in the Great Plains for harvested forage and grazing. Recent interest in alternative uses for switchgrass (e.g., biomass energy feedstock; McLaughlin and Walsh 1998) has prompted questions about how resource inputs (such as water and nutrients) affect growth, development, and plant relations of switchgrass. Water and nitrogen are the principal resources limiting productivity in perennial warm-season grass ecosystems (Epstein et al. 1996) and efficient use of these inputs in switchgrass production is critical.

Competition between plants is affected by plant population density (nearness and number of neighbors) and resource availability (Murphy and Briske 1992). In grasses, several morphogenetic changes, such as reduced tillering and increased shoot

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height, are presumably mechanisms for individual plants to adapt to resource availability (Ballare et al. 1995). These changes may buffer fluctuations in herbage yield. For example, Sanderson et al. (1996) reported that herbage yield of switchgrass was the same whether grown in rows spaced 10 or 100 cm apart because of compensatory responses in tiller number and size. At low plant population densities, individual plants may exploit larger pools of resources from above and below ground. If some soil resources are limited, input of additional water or nutrients should compensate for increased plant density.

The objective of our study was to examine how N and water affected competition among plants in switchgrass. We varied plant density, N fertility, and water availability and measured tillers and leaf area per plant, individual plant dry weight, and developmental stage to examine effects of these treatments on switchgrass morphology and development.

Materials and Methods

'Alamo' switchgrass seed was planted in sixteen, 1.8-m diameter by 0.6-m deep lysimeters (galvanized metal tanks) on 4 May 1993 at the Texas A&M University Agricultural Research and Extension Center at Stephenville, Tex. The lysimeters were outdoors in 2 rows spaced 2 m apart. The soil in each lysimeter was a Bunyan loam (fine loamy, mixed, nonacid, thermic, Typic Udifluvents). The lysimeters were filled so that the original soil profile and bulk density were maintained as much as possible. A 10-cm layer of pea gravel was placed in the bottom of each lysimeter and a 5-cm outlet was maintained for water drainage. The lysimeters were filled with soil in 1992 and allowed to settle until 1993. Analysis of soil samples taken to 15 cm in 1993 indicated 3.3 mg NO_3-N kg^{-1} of dry soil, 22 mg extractable P kg^{-1}, 108 mg extractable K kg^{-1} and a pH of 8.0.

The planting arrangement in each lysimeter was a systematic design for plant spacing experiments (Nelder 1962). Plots were arranged in a wagon-wheel layout with 8 radii (spokes) and 4 plants per radius. Each radius was planted along its entire length with switchgrass seeds. Plants were thinned on 8 June 1993 to 1 plant each at 10, 20, 40, and 70 cm from the center of the lysimeter. Plants were watered in all lysimeters to ensure establishment.

Treatments applied to the lysimeters included N fertilizer rates at 22 or 112 kg N ha^{-1} (as ammonium nitrate, no other fertilizer was applied) and soil water levels of approximately field capacity and 50% water deficit. The N fertilizer was applied in July of 1993 after seedlings had established (tillers had formed on the main stem), and in April of 1994. Beginning 7 July 1993, the water levels were imposed and maintained by an automated watering system controlled by tensiometers (Soil Moisture Equipment model 2725, Santa Barbara, Calif.) placed 30 cm deep in each lysimeter. The tensiometers had a magnetic switch that triggered a solenoid valve when soil water tension fell below a preset level of -10 kPa for the field capacity treatment and -50 kPa for the water deficit treatment. A timing device was programmed to query the solenoid valves at 0800, 1200, and 1700 hours each day. If the solenoid was switched on, water was applied for 1 hour. Water was distributed within the lysimeter via a drip irrigation system with 9 emitters spaced 10 cm apart and arranged in a circle. The experimental design was a randomized complete block with a 2 x 2 factorial arrangement of N and water levels in 4 blocks.

Photosynthetic rates were measured periodically to determine if treatments affected plant physiological functions. Photosynthetic rate of the most recent fully expanded leaf blade on 2 tillers from 2 plants at the 40-cm spacing in each lysimeter was measured on 7 dates in 1993 and 6 dates in 1994 with a Li-Cor 6200 portable photosynthesis system (Li-Cor Inc., Lincoln, Neb.). Preliminary measurements showed that plant density did not affect photosynthetic rates. Measurements were made during 1000 to 1400 hours on clear days. Only leaves in the fully exposed upper portion of the plant were measured. Leaves used for photosynthesis measurements were also used for xylem pressure potential measurements immediately after with a leaf pressure chamber (Scholander et al. 1965). In 1994, volumetric soil water content to a 30-cm depth was estimated with a calibrated time domain reflectometer (Trase System I, Soil Moisture Equipment Co., Santa Barabara, Calif.) on the days when photosynthesis measurements were made.

Plant height, tiller number per plant, and stage of morphological development (Sanderson, 1992) were measured weekly on each plant at each density on 4 radii beginning 28 June 1993 and 18 April 1994 and continuing until 1 September 1993 and 15 August 1994. On 9 September 1993 and 20 August 1994, plants in 4 radii from each lysimeter were harvested by hand to a 15-cm stubble. Tiller number per plant, morphological development stage of 5 tillers per plant, height of the 2 tallest tillers, and leaf blade area and dry weight (2 radii only) of each plant were measured. Plant and leaf blade dry weight were determined by drying at 55°C for 48 hours. Total Kjeldahl N was determined on leaf blades of plants in 1 radius from each lysimeter in 1993 and 1994. In August 1994, root mass was determined in each lysimeter by taking five, 7.5-cm diameter by 60-cm deep soil cores and washing roots from the soil over a 0.5 mm sieve. Roots were dried at 55°C for 72 hours to determine dry weight. In 1994, the plant crowns (stubble and plant material to a 5-cm depth) were dug from the soil and the total number of visible buds (crown and rhizome buds) were counted.

The data were analyzed as a 2 x 2 factorial with 4 replicates. Responses to plant spacing were determined by linear regression and a comparison of regression slopes and intercepts of each treatment (SAS 1988).

Results and Discussion

Soil Water Levels in Lysimeters and Plant Physiological Function

During 1993, soil water tension was relatively constant in lysimeters used for the field capacity treatment (Fig. 1). The water-deficit treatment developed soil water deficits during 15 July to 13 August, 19 to 23 August, and 27 August to 1 September. In each instance (except for 12 August) the water deficit was relieved by natural rainfall. All lysimeters were rewatered to field capacity on 12 August to start a second wet-dry cycle.

During 1994, there were 4 periods of low soil water in the water-deficit treatment: 20 May to 6 June; 21 June to 1 July; 11 to 23 July; and 26 July to 8 August (Fig. 1). The high-N, water-deficit treatment developed a lower soil water tension in the upper 30 cm of soil than did the low-N field-capacity treatment probably because there was a greater amount of transpiring biomass in the high N treatment. Despite irrigation, the field-capacity treatment developed relatively low soil moisture tensions during 27 May to 1 June, 1 July to 5 July, and 6 July to 11 July. Measurements of volumetric soil water content at 5 dates in 1994 confirmed the soil water tensions measured by tensiometer (Table 1). Rainfall was much less

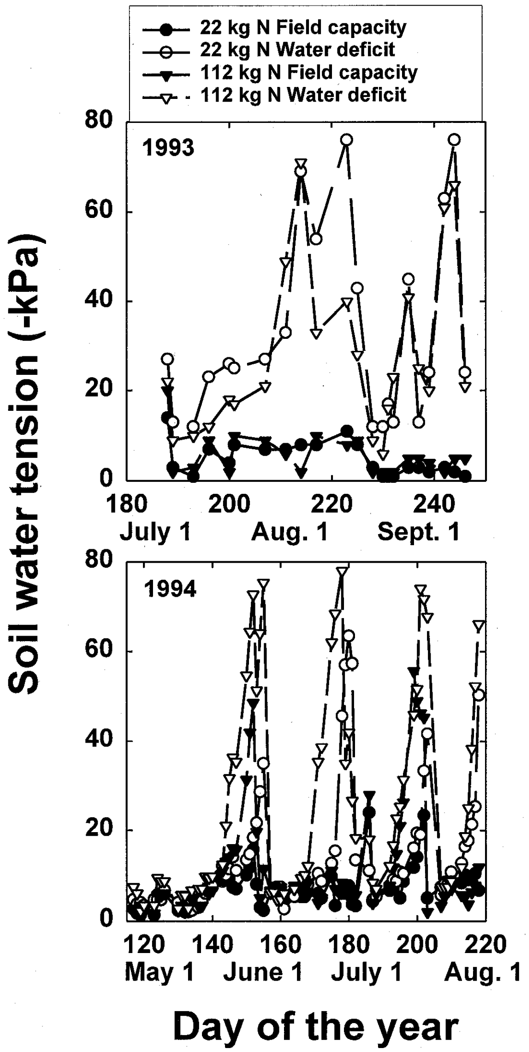

Fig. 1. Soil water tension (-kPa) as indicated by tensiometers placed 30-cm deep in the soil of each lysimeter. Data points are averages of 4 replicate lysimeters.

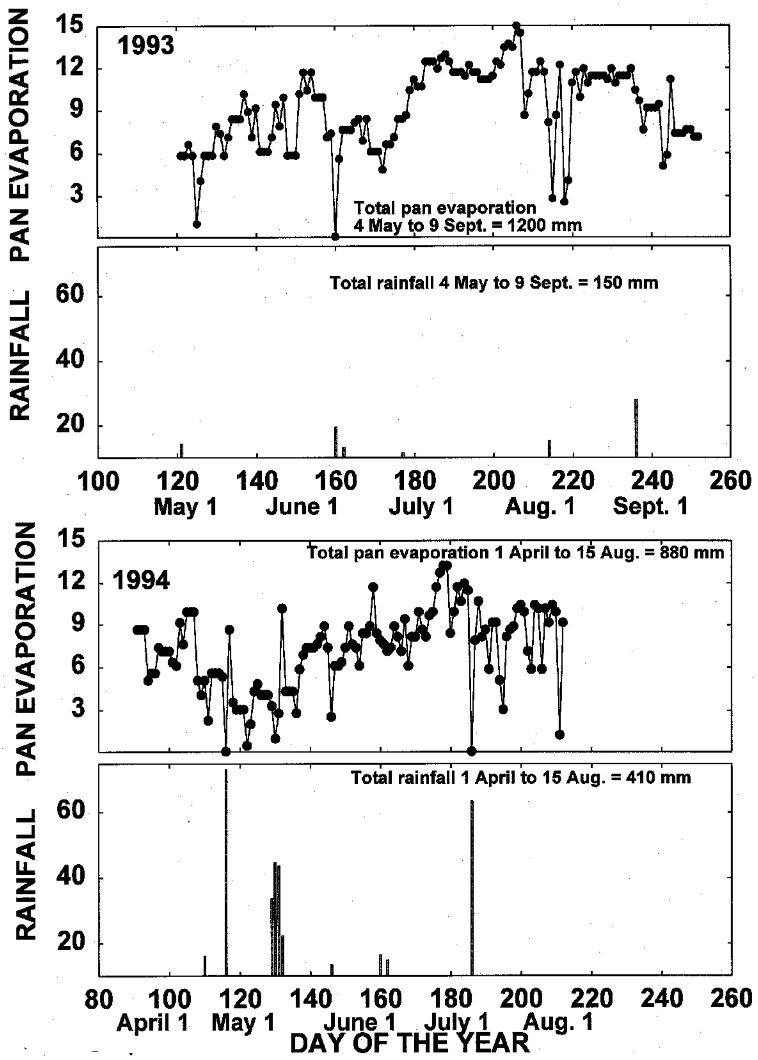

Fig. 2. Daily open pan evaporation and rainfall (mm) during 4 May (planting) to 9 September (harvest), 1993 and 1 April (greenup) to 20 August (harvest) 1994.

and pan evaporation was greater during the 1993 growing season compared to 1994 (Fig. 2).

We tried to time photosynthesis measurements to coincide with periods of water deficit to document effects on physiological function; however, because of limited time and climatic conditions (measurements were made between 1000 and 1400 hours on clear days), we were able to document water-deficit effects on photosynthetic rates only on12 and 30 August in 1993 and 29 June, 22 July, and 10 August in 1994. Switchgrass maintained relatively high rates of photosynthesis on 17 and 26 July 1993, which were not affected by N or water level (Table 1) and were similar to rates reported by Wullschleger et al. (1996) for Alamo switchgrass grown in the field.

On 12 August 1993, after water was withheld for 15 days, photosynthetic rate of plants in the water-deficit treatment was only 10% of that for plants in the field-capacity treatment, whereas xylem pressure potentials dropped from about –1.6 to –3.3 MPa. When all lysimeters were rewatered and plants allowed to recover until 20 August, photosynthetic rates and xylem pressure potential recovered to pre-stress levels. On 24 and 27 August, time and atmospheric conditions allowed us to obtain measurements only from the water-deficit treatments. Photosynthetic rates were lower on these dates than on 20 August, indicating a developing water deficit. On 30 August, it appeared that water deficit significantly reduced photosynthetic rates and xylem pressure potential compared to the field-capacity treatment.

In 1994, photosynthetic rates and xylem pressure potential were reduced in water-deficit treatments on 29 June, 22 July, and 10 August. On 22 July, only the high-N water-deficit treatment had significantly lower photosynthetic rates and xylem pressure potential than other treatments, whereas on 29 June and 10 August, both low- and high-N water-deficit treatments had lower photosynthetic rates and xylem pressure potential. Rainfall was abundant during April and May (Fig. 2) and precluded the development of significant soil water deficits in the spring.

Table 1. Photosynthetic rates, xylem pressure potential, and soil moisture in each treatment on several dates in 1993 and 1994

		1993			1994			
N level	Water treatment	Photosynthetic Rate	Xylem Pressure Potential	Tensiometer reading	Photosynthetic Rate	Xylem pressure potential	Tensiometer reading	Volumetric soil moisture content
(kg N ha^{-1})		(μmol m-2 sec^{-1})	(MPa)	(kPa)	(μmol m-2 sec^{-1})	(MPa)	(kPa)	(m^{3}m^{-3})
		17 July			3 June			
22	Water	25.6	–1.84	–26	25.7	–1.14	–29	0.12
112	deficit	30.8	–1.87	–18	15.5	–1.99	–64	0.07
22	Field	24.8	–1.70	–5	24.0	–0.87	–3	0.28
112	capacity	29.8	–1.67	–4	27.4	–0.92	–5	0.26
LSD[1]		NS	NS		NS	NS		0.07
		26 July			10 June			
22	Water	27.2	–2.15	–27	23.4	–1.06	–3	0.27
112	deficit	32.8	–1.74	–21	29.2	–1.16	–6	0.28
22	Field	34.9	–1.89	–7	22.9	–1.03	–5	0.27
112	capacity	32.1	–1.67	–9	26.5	–1.13	–6	0.25
LSD		NS	0.2		NS	NS		NS
		12 August			29 June			
22	Water	5.2	–3.20	–76	9.4	–1.73	–63	0.07
112	deficit	1.5	–3.46	–53	12.2	–2.12	–42	0.09
22	Field	30.2	–1.65	–11	23.0	–1.50	–8	0.27
112	capacity	34.5	–1.68	–8	23.0	–1.62	–5	0.25
LSD		3.6	0.3		5.1	0.2		0.04
		20 August			22 July			
22	Water	34.0	–1.90	–17	14.1	–1.38	–42	0.11
112	deficit	28.1	–1.78	–23	4.7	–3.40	–68	0.06
22	Field	28.4	–1.50	–11	15.4	–1.34	–5	0.28
112	capacity	33.3	–1.61	–8	17.7	–1.64	–2	0.28
LSD		NS	NS		4.0	0.05		0.03
		24 August			29 July			
22	Water	16.5	–1.95	–45	13.8	–1.36	–18	0.18
112	deficit	11.5	–1.83	–41	19.4	–1.61	–25	0.21
	Field	‡	‡		13.7	–1.29	–9	0.24
	capacity				19.3	–1.57	–4	0.21
LSD		NS	NS		3.3	NS		NS
		27 August			10 August			
22	Water	23.8	–1.89	–24	9.1	–1.76	–50	0.11
112	deficit	22.0	–1.81	–20	3.1	–2.66	–66	0.08
22	Field	‡	‡		16.2	–1.23	–7	0.21
112	capacity				18.2	–1.26	–12	0.18
LSD		NS	NS		4.9	0.59		0.06
		30 August						
22	Water	17.2	–2.24	–63				
112	deficit	12.4	–2.75	–61				
22	Field	31.1	–1.41	–4				
112	capacity	31.5	–1.57	–4				
LSD		13.7	–0.3					

[1] LSD = least significant difference at $P < 0.05$. ‡ Data were not taken.

Although we were not able to measure photosynthetic rates as often as we would have liked, it was clear that the water-deficit and field-capacity treatments differed in soil water levels and that these differences affected physiological function of switchgrass. When soil water tension was less than about –45 kPa, xylem pressure potential and photosynthetic rates were severely reduced indicating significant plant stress. Knapp (1985) reported photosynthesis rates near zero for switchgrass plants under severe water deficit (xylem pressure potential < –2.0 MPa) on the Konza prairie in Kansas.

Plant Dry Weight

In 1993, the dry weight of individual switchgrass plants was not affected ($P < 0.05$) by water or N inputs. Plant spacing had the largest effect on plant dry weight and all treatments increased linearly in weight with increased plant spacing (Fig. 3). During 1994, however, switchgrass plants responded strongly to increased N fertilizer, but not to additional water. Switchgrass plants increased in dry weight with increased plant spacing, but the response (slope of the regression line) was nearly doubled with increased N fertilizer. Thus, neither increased water nor N fertilizer were able to overcome the above-ground competition among plants at the higher plant densities.

The absence of a response in dry weight of seeding year switchgrass plants to or N input may indicate that the soil pool of N was adequate and that the young plants were able to explore and exploit a large volume of soil. In 1994, plants probably had a fully developed root system, which was able to draw more resources. Root dry weight was significantly higher for the 112 kg N treatment than in the low-N

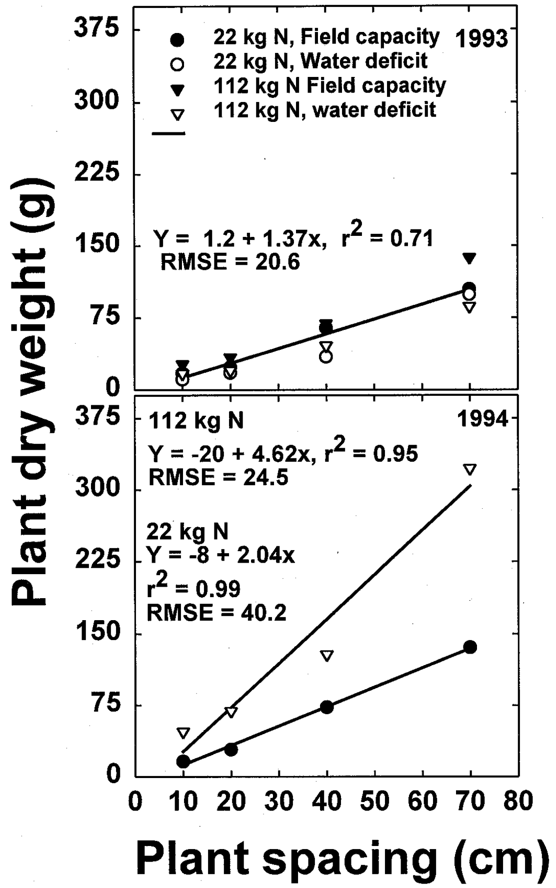

Fig. 3. Yield of dry matter per plant at 2 N and water levels in response to plant spacing. Data points in 1994 are the averages of 2 water treatments for each N level. RMSE = root mean square error.

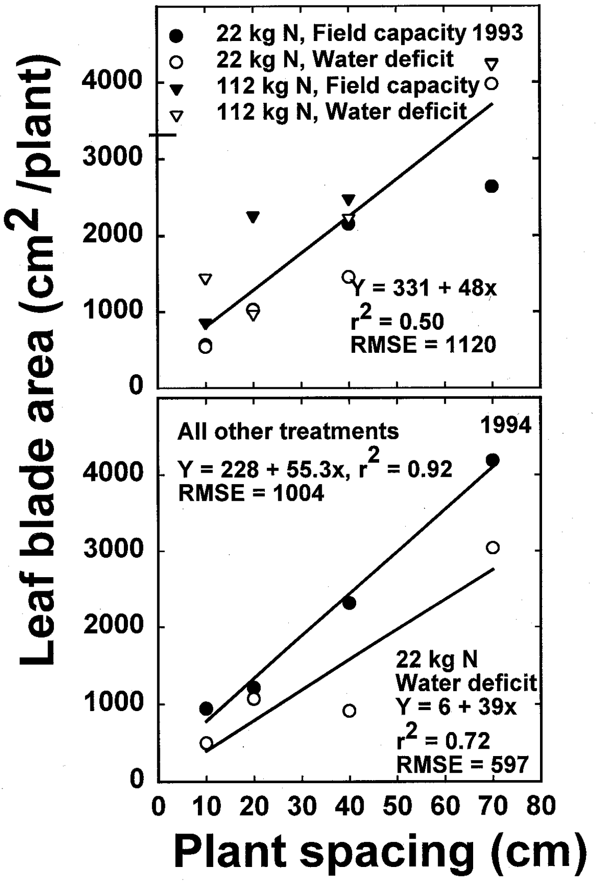

Fig. 4. Leaf blade area per plant at 2 N and water levels in response to plant spacing. There was no significant difference among the water treatments at 112 kg N and the 22 kg N field capacity water treatment, thus, these data were averaged for the regression response line. RMSE = root mean square error.

treatment at the end of the season in 1994, but was not affected by water level (Table 2). In 1993, all treatments were watered until 7 July to assure establishment. Significantly lower soil moisture tensions occurred after this, but all treatments were watered again on 12 August. Thus despite documenting significant differences in photosynthetic rates between water treatments on some dates (Table 1), the water deficit periods may not have been long enough to significantly reduce plant yields. Lower yields in 1993 compared to 1994 were a result of slow seedling growth and a shorter growing season (May to August in 1993 and March to September in 1994).

Leaf area per plant increased linearly with increasing plant spacing in 1993, but there were no significant differences among N or water treatments (Fig. 4). During 1994, the leaf area of plants grown with low N and under water deficit responded less (smaller regression slope) to wider plant spacing than the other treatments, which were not significantly different.

Table 2. Dry weight of switchgrass roots to a 60-cm depth in August 1994 as affected by nitrogen rate and soil water level.

	Nitrogen level (kg ha^{-1})		
Water treatment	22	112	Mean
	(kg root dry matter ha^{-1})		
Field capacity	11700	15300	13500
Water deficit	9900	13500	11700
Mean[1]	11000a	14400b	
SEM	1200		

[1] Means are significantly different at $P < 0.05$.

Leaf N concentration varied among years and treatments (Table 3). In 1993, plants grown with high N and under water deficit had one-third greater N concentration than other treatments. In 1994, there was no effect of water deficit, but the 112-kg N treatment had 36% greater leaf N than the 22-kg N treatment. There was an interaction among N and water treatments in leaf N concentration. Leaf N was not different between water treatments at the 22-kg N treatment, whereas leaf N increased with water deficit in the 112-kg N treatment.

Tiller Dynamics

Tiller number per plant increased linearly with increasing plant spacing and was not affected by N or water inputs in either year (Fig. 5). Thus, differences in yield per plant among treatments in 1994 probably resulted from increased tiller size rather than tiller number. Moreover, tiller

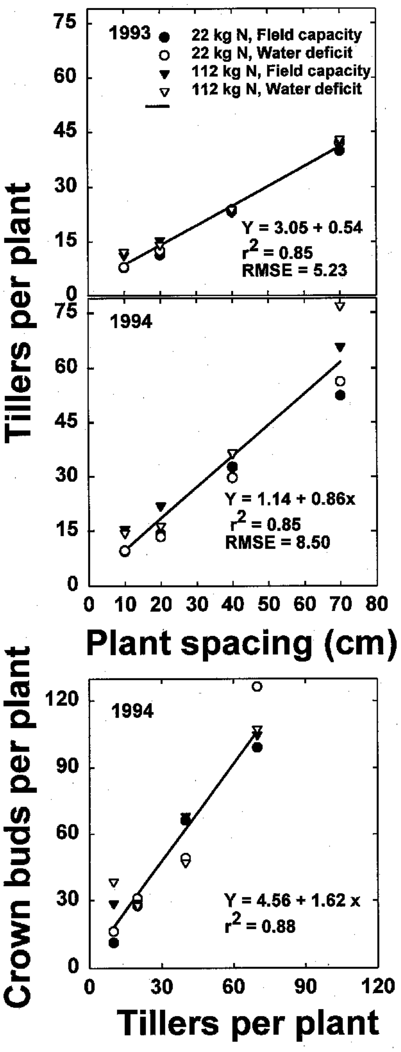

Fig. 5. Number of tillers per plant at 2 N and water levels in response to plant spacing in 1993 and 1994, and number of visible buds on the plant crown after harvest in 1994. RMSE = root mean square error.

number seemed to be affected more by aboveground competition than by competition for belowground resources. Similar to tiller number, the number of visible buds on the plant crown after harvest in 1994 increased linearly with increasing plant spacing and was not affected by N or water inputs (Fig. 5).

The pattern of tillering during the 1993 season was different among plant spacings (Fig. 6). Plants at the 40 and 70 cm spacings increased greatly in tiller number from July to September. At the 2 lower plant spacings, there was a small increase in tiller number during June, but tiller number remained relatively constant after that. Peak tiller recruitment occurred during early May and early July for plants at the 40 and 70 cm spacings in 1994. At the 10 and 20 cm spacings, there was no spring peak in tiller number, but there was a pronounced increase in tiller number in July. The increase in tiller number during May at the 40 and 70 cm spacings could have been from rhizomes and crown buds formed during the previous fall, whereas the increase in July may have been from axillary buds. Thus, at all plant spacings, switchgrass was able to initiate and maintain tillers until August, after which tiller mortality increased. Late-formed tillers may not have been able to develop functional roots. When new tillers form, they obtain water via the parent plant until they develop functional adventitious roots (Carman and Briske, 1982). If the root system does not develop, the tillers will die.

Table 3. Concentration of N in leaf blades of switchgrass in 1993 and 1994 as affected by nitrogen rate and soil water level.

Water treatment	Nitrogen level (kg ha^{-1}) 22	112	Mean
	(g N kg^{-1} dry matter)		
		1993	
Field capacity	8.2	10.8	9.5a
Water deficit	11.3	15.1	13.2b
Mean[1]	9.8a	13.0b	
SEM		1.11	
		1994	
Field capacity	5.8a	7.1b	6.4
Water deficit	5.5a	8.0c	6.8
Mean	5.6a	7.6b	
SEM		0.81	

[1] Means are significantly different at $P < 0.05$.

Morphological Development

Developmental stage of switchgrass plants increased with increasing plant spacing in 1993 (Fig. 7). Water deficit retarded morphological development, whereas N treatment had no effect. Plants in the water-deficit treatment had delayed inflorescence emergence and reproductive development compared with the field-capacity treatment (Fig. 8). In 1994, developmental stage responses to plant spacing differed between N treatments, but was not affected by water treatments (Fig. 7). Switchgrass plants had a lower developmental stage in the 22-kg N treatment compared with 112 kg N at the 10- and 20-cm spacings. There were no differences among treatments at the 40 and 70-cm spacing. Plants in the high N treatment exerted inflorescences earlier than low-N plants in 1994 (Fig. 8).

The pattern of morphological development in this experiment was similar to that reported by Sanderson (1992) and Sanderson and Wolf (1995). Nitrogen addition to individual switchgrass plants on the Konza Prairie increased the number of tillers that flowered and produced seed (Hartnett 1993) and increased plant density (in a pot experiment in the greenhouse)

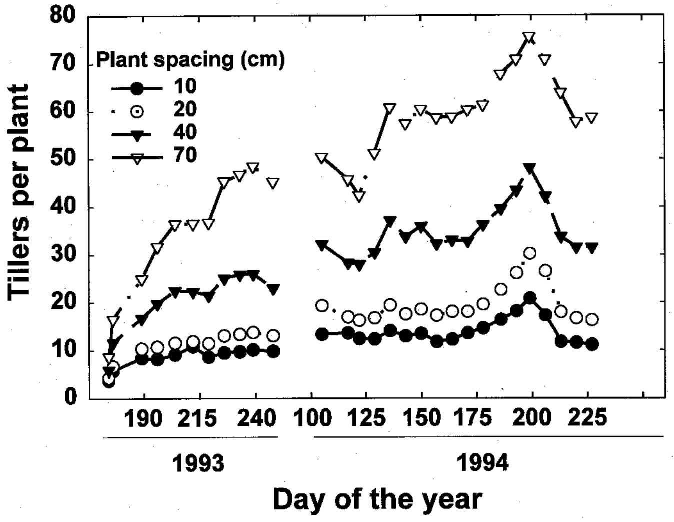

Fig. 6. Tillering patterns of switchgrass from planting to harvest in 1993, and from 15 April to 15 August 1994. Data points are averages of 2 N and water levels and 4 replicates.

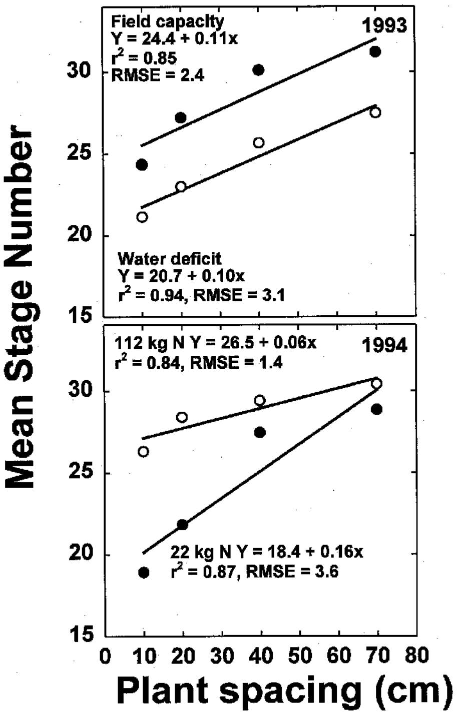

Fig. 7. Mean stage of morphological development at harvest at 2 N and water levels in response to plant spacing. In 1993, the data points are averages of 2 N levels, whereas in 1994 the data points are averages of 2 water treatments. Stage number 15 = vegetative plants with 5 elongated internodes; 20 = boot stage; 25 = 50% of the inflorescence emerged; 30 = anthesis. Morphological stages determined according to Sanderson (1992).

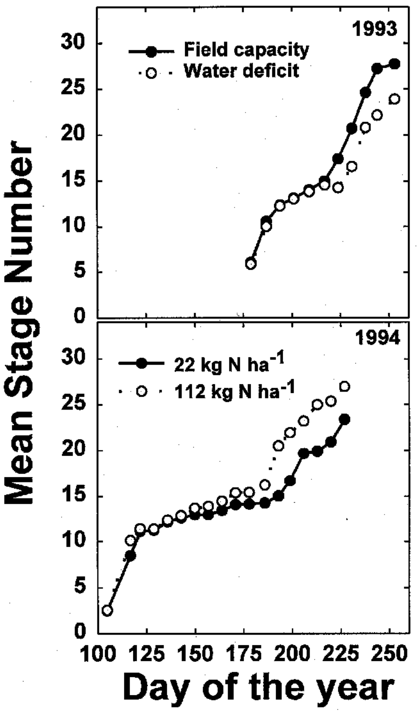

Fig. 8. Morphological development (mean stage number) pattern of switchgrass as affected by soil water level in 1993 and N fertility in 1994. Stage number 5 = vegetative plants with 5 fully expanded leave blades and no elongated internodes; 10 = beginning of internode elongation; 15 = vegetative plants with 5 elongated internodes; 20 = boot stage; 25 = 50% of the inflorescence emerged; 30 = anthesis. Morphological stages determined according to Sanderson (1992).

reduced reproductive growth of switchgrass (Hartnett 1989). Sanderson (1992) and Sanderson and Wolf (1995) reported no differences between wet and dry years in switchgrass development patterns. Thus, switchgrass development may be more sensitive to water stress during the seeding year than in subsequent production years after the plants have fully established.

Our data support the suggestion of Hartnett (1993) that N availability does not affect the rate of increase in clonal growth of switchgrass. Water availability and the canopy light environment of individual switchgrass plants were shown to be the dominant controls of individual plant tiller growth and dynamics (Hartnett, 1993). Our data were not clear-cut regarding the effects of water availability. We found that water and N affected tiller size, whereas tiller number was influenced mainly by interplant competition for aboveground resources.

This concept has practical application in managing stands of switchgrass that have decreased in density by natural thinning or mismanagement. If stands have thinned to a point at which individual plants are not able to compensate by increased tillering, production cannot be increased from these stands by adding more water or N fertilizer.

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Effects of nitrogen fertilization in leafy spurge root architecture

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Abstract

There is a dearth of information concerning the degree to which the amounts, periodicity, and spatial patterns of N applications can be manipulated to alter the rooting strategy of leafy spurge, and thus make it more susceptible to chemical and biological controls. This study was designed with the following objectives: (1) determine the effect of patchy N fertilization on shoot and root biomass, root distribution by depth, root plasticity, and the ratio of coarse vs. fine roots of leafy spurge; and (2) determine how leafy spurge scales root biomass to root lateral spread and root surface area, as well as how these scaling patterns are affected by N fertilization. The root architecture, plasticity, and response to patchy N fertilization was evaluated in 3 separate experiments conducted in large containers. Patchy fertilization did not alter the morphological characteristics of leafy spurge roots, but did cause a reduction in root biomass and a drastic change in the distribution of the root surface area within the plant's rooting volume. Fertilization both doubled the percentage of roots located in the top 10 cm of soil and shifted it toward the fertilized patches.

Key Words: Leafy spurge fertilization, root plasticity, root lateral spread

Resumen

Tenemos al presente un conocimiento limitado de como la cantidad, periodicidad, y distribución espacial de la fertilización con N puede ser manipulada para alterar la distribución de las raíces de leafy spurge y como consecuencia hacerla mas vulnerable a los controles biologicos y quimicos. Este estudio fue diseñado con los siguientes objetivos: (1) determinar como la aplicación espacialmente irregular de N afecta la producción de hojas, tallos, y raíces, la distribución de raíces a diferentes profundidades en el suelo, la plasticidad de las raíces, y la proporción de raíces gruesas en comparación con raices finas de leafy spurge; y (2) determinar la relación entre la biomasa, la expanción lateral y la superficie de las raices en cuestion, y como esa relación es afectada por la fertilización con N. La estructura, plasticidad, y la respuesta de raices a la distribución irregular de N fue evaluada en 3 experimentos conducidos en macetas grandes. La aplicación espacialmente irregular de N no afectó las caracteristicas morfologicas de las raices de leafy spurge, pero resultó en una reduccion en la proporción de la biomasa de la planta destinada a las raíces y un drastico cambio en la distribución espacial de las raíces dentro del volumen de suelo explorado por la planta. La fertilización simultaneamente duplicó el porcentaje de raices localizadas en los primeros 10 cm del suelo, y las concentró en las porciones del suelo fertilizadas.

Leafy spurge (*Euphorbia esula* L.) has evolved into an extensive weed control issue since first introduced to North America over 130 years ago (Selleck et al. 1962). The majority of current eradication strategies fall into 3 major categories (Lym and Zollinger 1995): physical (mowing, cultivation, competition), biological (grazing, insects), and chemical (herbicides). Leafy spurge eradication, however, has proven difficult primarily due to spurge's ability to persist under adverse conditions, a result of an efficient reproductive system and an extensive root system (Raju et al. 1963, Bowes and Thomas 1978, Galitz and Davis 1983, Messersmith 1983, Lajeunesse et al. 1995, Lym and Zollinger 1995). The heterorhizic complex root system of leafy spurge includes long roots having indeterminate longitudinal growth and the ability to undergo secondary (cambial) growth and short roots having limited cambial activity (Raju et al. 1963). Vertical ("long") roots can grow to depths up to 8.5 m, while horizontal roots can have lateral spreads of up to 5 m (Lajeunesse et al. 1995, Galitz and Davis 1983). The 2 primary modes of reproduction are through regenerative adventitious root buds and dehiscence of seed capsules (up to 5 m. from the parent plant) (Galitz and Davis 1983).

Nitrogen (N) plays a key role in the development and competitive abilities of plant species (Haynes et al. 1986), and the root morphological development of spurge has proven highly responsive to variant N, including responses in root:shoot ratios, percentage "long" and lateral roots, and number of root and shoot buds produced (McIntyre and Raju 1967). Recent studies have also shown that soil N plays a critical role in the overwintering strategy in leafy spurge root systems, and that seasonal fluctuations of root N are accurate indicators of plant health and determinants of potential regenerative vigour (Lym and Messersmith 1993, McIntyre and Raju 1967, Cyr and Bewley 1989, 1990). Furthermore, fall N fertilization has been shown to increase the effectiveness of spring applied herbicides (Regimbal and Martin 1985).

A renewed interest has arisen among plant ecologists in determining how root morphology and root plasticity (ability to redirect root growth to areas of high nutrient concentration) can affect plant performance and composition in patchy environments, and how the spatial distribution of nutrients themselves can alter biomass allocation to roots and root architecture (Campbell et al., 1991; Caldwell 1994; Jackson and Caldwell

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1996). Results from these studies have suggested that the ability of plants to compete for soil resources is highly dependent on: (a) the spatial distribution, concentration, and supply rate of soil nutrients; (b) the volume of soil explored by their root system; (c) the density and spatial patterns of root surfaces within the rooting volume; and (d) the rate of nutrient uptake. The available information for most native species and leafy spurge, however, is still quite limited.

Significant amounts of research have been done on leafy spurge physiology, eradication methods, and root organogenesis, but few studies have concerned themselves with elucidating how the competitive ability of leafy spurge can be influenced through interactions among the spatial distribution of soil nutrients (i.e. soil N), root architecture, and root plasticity. In particular there is a dearth of information concerning the degree to which the amounts, periodicity, and spatial patterns of N applications can be manipulated to alter the rooting strategy of leafy spurge, and thus make it more susceptible to chemical and biological controls. This study, thus, was designed with the following objectives:

1. Determine the effect of patchy N fertilization on shoot and root biomass, root distribution by depth, root plasticity, and the ratio of coarse vs. fine roots.
2. Determine how leafy spurge scales root biomass to root lateral spread and root surface area, as well as how these scaling patterns are affected by N fertilization.

Materials and Methods

The root architecture, plasticity, and response to patchy N fertilization of leafy spurge was evaluated in 3 separate experiments conducted from 1995 to 1997.

1. *Experiments 1 and 2*

Leafy spurge root rhizomes were randomly collected from a sandy soil type in the Sheyenne National Grasslands and planted in 60x60x60 cm wooden boxes (one 2.5 cm rhizome, with a bud, per box) equipped with detachable sides and filled with washed river sand from the Buffalo River, N.D. The boxes had two, 2 cm^2 hardware mesh panels inserted horizontally at depths of 10 and 30 cm. The mesh was intended to keep the roots in place after the sand had been removed so accurate measurements of vertical and horizontal distributions could be made. Half of the boxes in each experiment were fertilized with Sierra® slow release fertilizer prills (N-P-K:16-8-12 plus minor nutrients) at a rate of 37.5 gN/m^2. All prills were located in one side of the box (North), at 7.5 cm below the surface in a straight line half way between the plant and the outer edge of the container. The purpose of the design was to effectively test the degree to which root architecture was affected by nutrient patchiness. Before adopting this method, a series of preliminary tests were run to determine the design capability for maintaining nutrient patches. Nitrate (NO_3) was measured (due to its high mobility) for a 4 week trial period using different N concentrations. Although there was some movement of NO_3, we were able to maintain gradients ranging from 15 to 400 ppm.

The experiments were arranged as a completely randomized design with two treatments, fertilized and not-fertilized, and 5 replications per treatment. The experiments were conducted, outdoors, from May to September of 1995 (Experiment 1), and repeated in 1996 (Experiment 2). At the end of each experiment we proceeded as follows: (1) above ground biomass was clipped at the surface level; (2) the sides of the boxes were removed and the sand washed out; and (3) roots were harvested by depth (0–10 and 10–60 cm) and separated in two halves in accordance with the fertilization design. Aboveground biomass and roots were oven-dried for 12 hours at 60° C and weighed. In the first experiment, root subsamples by depth and halves were digitized using a Hewlett Packard high resolution scanner and analyzed for total root length, root diameter, and root surface area with the use of a Delta-T Scan imaging system.

2. *Experiment 3*

The third experiment was designed to determine how leafy spurge scales root biomass to root lateral spread. Cylindrical containers (50 cm in diameter, 90 cm in depth) were fitted with 2 cylindrical dividers (15 and 30 cm in diameter) made of wire netting (1 cm mesh). The mesh system was used to accurately measure root biomass by depth at fixed horizontal distances of 0-7.5, 7.5-15, and 15-25 cm from the rhizome (one 2.5 cm rhizome, with a bud, per box). The containers were filled with pure silica sand and planted with leafy spurge rhizomes. Half of the containers were fertilized using the same design outlined in Experiments 1 and 2.

The experiment was organized as a completely randomized design with 2 treatments, fertilized and not-fertilized, and 6 replications per treatment. The experiment was conducted in the greenhouse from May to September (1997). Above ground biomass was clipped at the surface level. Roots were rinsed out while still in the containers and clipped on the basis of 18 locations determined by 3 categories: (1) North side (fertilized) vs. South side (not-fertilized); (2) horizontal distance from rhizome (0–7.5 cm, 7.5–15 cm, and 15–25 cm); and (3) depth (0–10 cm, 10–20 cm, and 20–80 cm). Above and below ground biomass were dried and weighed. Roots were scanned, digitized, and analyzed for total root length, root diameter, and root surface area using the same method discussed in the previous section.

3. *Statistical Analysis*

Statistical differences between fertilized and not-fertilized treatments in terms of above ground biomass, root biomass, and root biomass by depth were analyzed using a t-test. Differences in the proportion of root biomass between the North side (fertilized side in the fertilized treatment) and the South side within each treatment were analyzed using a paired t-test with a null hypothesis of $H_o = 0.5$. The data in this case was transformed using the angular transformation (Bonham 1989). Combined P-values for the 3 experiments, where pertinent, were calculated using the Fisher test (Folks 1984). Differences in the distribution functions of root diameter vs. root surface area among treatments were tested using the Kolmogorov-Smirnov test (Sokal and Rohlf 1969). All results were considered significant at the $P<0.05$ level.

The scaling relationship of root biomass with root surface area and root lateral spread were analyzed using an allometric model of the form $\boldsymbol{y} = \alpha * \mathbf{RB}^{\beta}$ where $\boldsymbol{y}$ is either root lateral spread (rls in cm) or root surface area (RSA in m^2), and **RB** is root biomass (g). The equation parameters were estimated with the use of linear regressions on the log-log transformations: $\ln(y) = \ln(\alpha) + \beta * \ln(RB)$.

Results

Total leafy spurge biomass was unaffected by fertilization in 2 of the 3 experiments (Fig. 1A). In Experiment 2, however, total biomass in the fertilized treatment was more than 3 times higher than in the not-fertilized treatment, which resulted in a combined P-value for the 3 experiments of $P<0.001$. Total root surface area in Experiments 1 and 3 averaged 0.63 m^2, but there were no differences between the fertilized and not-fertilized treatment (Fig.

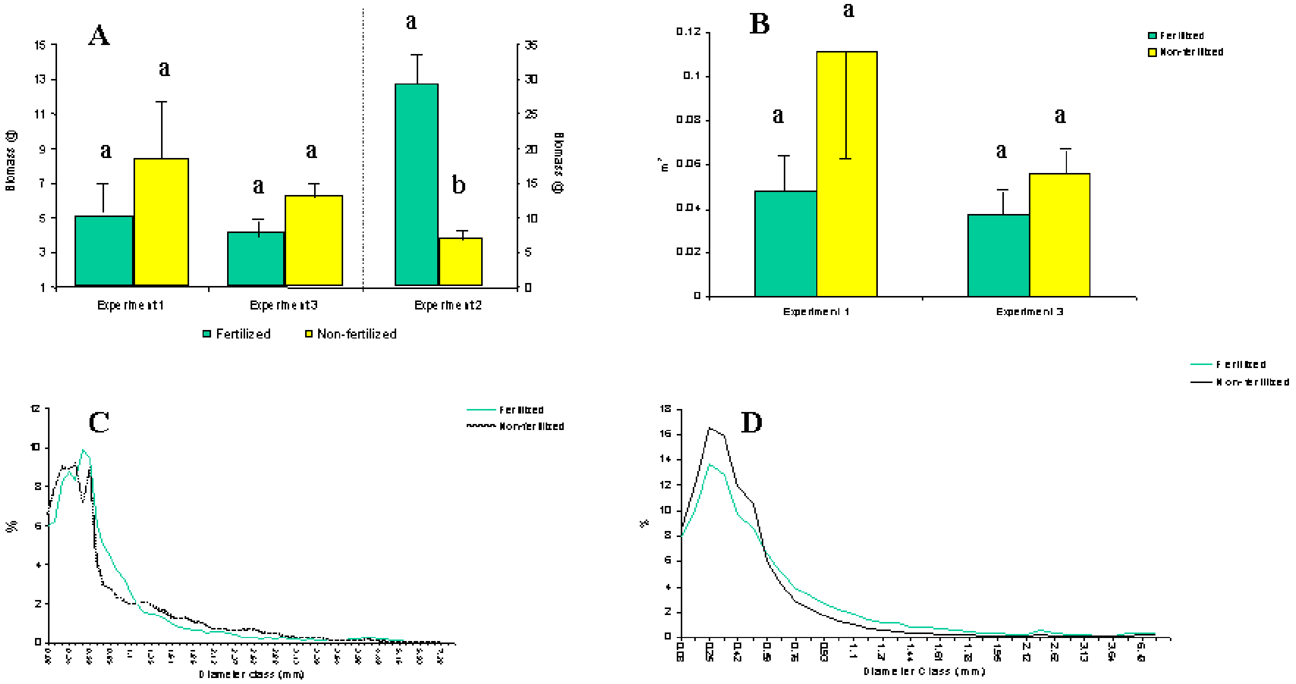

Fig. 1. Effects of fertilization on: A. Total plant biomass (g). B. Total root surface area (m^2). Percent distribution of total root surface area as a function of root diameter classes (in mm) in experiment 1 (C) and experiment 3 (D). Treatments with different letters within an experiment are statistically different at the P < 0.05 level. Vertical lines represent 1 SE.

1B). Fifty percent of the total root surface area in Experiment 1 and 70% in Experiment 2 (Figs. 1 C–D) were composed of very fine roots (diameters <0.5 mm), but there were no differences in either experiment between the distribution of the root diameter classes of the fertilized vs. the not-fertilized treatments (Figs. 1 C–D).

Root:shoot ratios and the vertical distribution of root biomass were significantly affected by fertilization (Figs. 2 A–C). In 2 of the 3 experiments fertilization reduced root:shoot ratio by an average of 50%: 1.29 vs. 2.49 (Fig. 2A), and doubled the percentage of root biomass allocated to the first 10 cm of the soil profile: 31% vs. 15% (Figs. 2 B–C). The combined P-values for the 3 experiments were $P < 0.001$ and $P < 0.006$ respectively. An analysis of data from Experiment 3, where 3 depths were available, showed that: (1) 70% or more of total root biomass was allocated below 20 cm; and (2) leafy spurge allocated only 11% of root biomass at depths of 10-20 cm, which was unaffected by fertilization (increases in root biomass in the 0–10 cm came from decreases in the 20–80 cm depth).

Leafy spurge showed a significant degree of root plasticity (Fig. 2D). In all 3 experiments leafy spurge allocated an average of 75% of its root biomass to the fertilized side of the containers in the fertilized treatments (Fig. 2D). No differences were found between the North and South sides in the not-fertilized treatments.

There was a significant allometric relationship between root biomass and root surface area, and root biomass and root lateral spread (Table 1). The equations for both the fertilized and not-fertilized treatments were remarkably similar showing very robust and stable scaling patterns. Fertilization, thus, did not affect the total area explored by the root system (Table 1) but simply changed the distribution of the roots within the given area (Figs. 2 B–D).

Discussion and Conlusions

Total biomass was unaffected by fertilization in 2 out of the 3 experiments, a result that was rather unexpected (Fig. 1A). Also interesting, was the fact that total biomass in Experiments 1 and 3 was very similar even though the experiments differed in the depth of the growth medium (60 cm vs. 90 cm), and location: outside vs. greenhouse. The total root surface area of these 2 experiments, furthermore, was also unaffected by fertilization (Fig. 1B). The statistical results in this case were caused by large standard errors, but there seems to be, nevertheless, a definite trend suggesting a decrease in root surface

Table 1. Allometric relationships of root lateral spread (rsl in cm) and root surface area (RSA in m^2) with root biomass (RB in g).

Experiment	Treatment	Equation	R^2	P-value
Experiment 1 (1995)	Fertilized	$RSA = 0.0325*RB^{0.9243}$	0.79	0.0028
	Not-Fertilized	$RSA = 0.03808*RB^{1.08}$	0.85	0.025
Experiment 3 (1997)				
	Fertilized	$RSA = 0.0155*RB^{0.95}$	0.83	0.031
	Not-Fertilized	$RSA = 0.0144*RB^{0.94}$	0.94	0.032
	Fertilized	$rls = 0.0616*RB^{0.91}$	0.80	0.0000001
	Not-Fertilized	$rsl = 0.0641*RB^{0.88}$	0.85	0.0000001

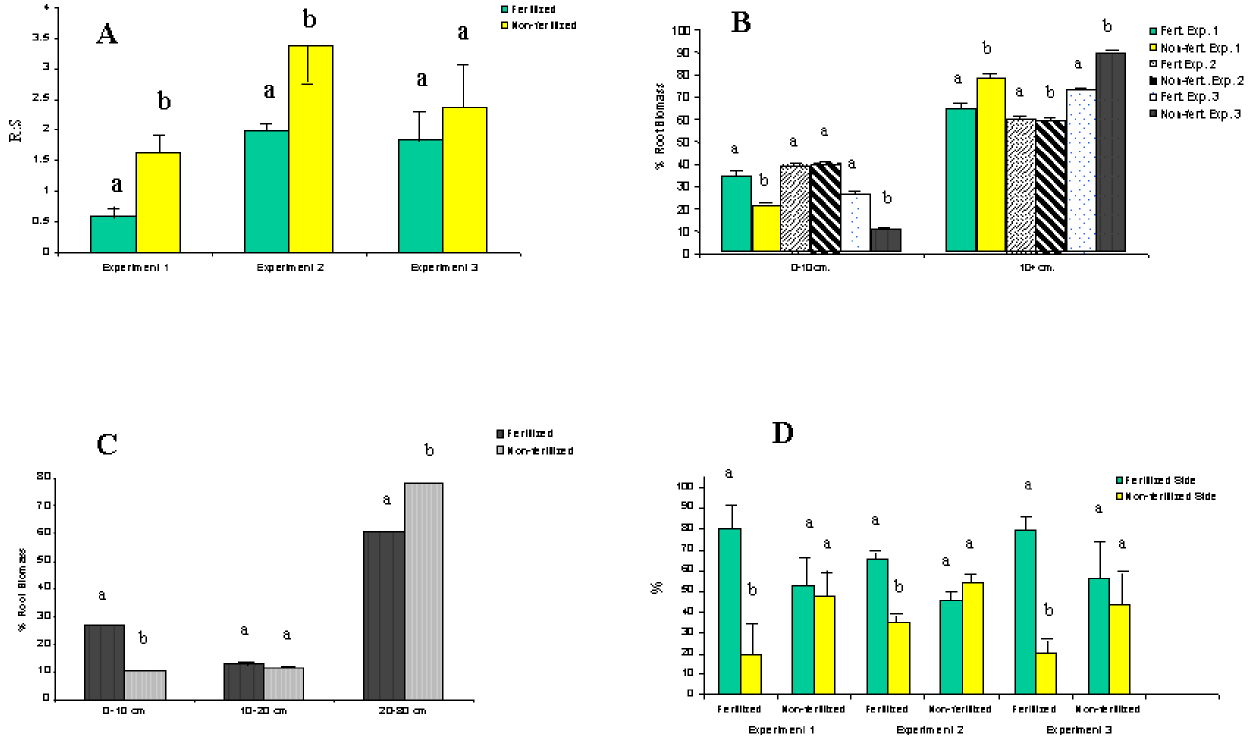

Fig. 2. Effects of fertilization on: A. Root:Shoot (R:S) ratio. B. Percent root biomass distribution in 0-10 cm and below 10 cm of depth for all 3 experiments. C. Percent root biomass distribution in the 0–10, 10–20, and 20–80 cm of depth for experiment 3. D. Percent biomass allocated to the fertilized and not-fertilized patches in the fertilized treatment and comparable areas in the not-fertilized treatment. Treatments with different letters within an experiment are statistically different at the P < 0.05 level. Vertical lines represent 1 SE.

area with fertilization (Fig. 1B). This trend, however, was not caused by alterations in root morphology but rather by a decline in root biomass. This interpretation is supported by 3 pieces of evidence: (a) fertilization decreased the amount of plant biomass allocated to roots (Fig. 2A), but did not change the way fertilized and not-fertilized plants scaled root biomass to root surface area (Table 1); (b) there were no changes in average root diameter and diameter distribution classes as a result of fertilization (Figs. 1 C–D); and finally (c) there is a substantial body of both empirical and theoretical data that suggests a trade-off in the way plants allocate biomass to roots: under high nutrient conditions plants increase their biomass allocation to leaves and shoots at the expense of roots, thus reducing their total root surface area (Tilman 1990, Ryser and Lambers 1995, Fransen et al. 1998, but also see Shipley and Peters 1990 for a different perspective). The lack of change in the distribution of root diameter classes as a result of fertilization was rather unexpected (Figs. 1 C–D). For most plants, fertilization tends to increase the average diameter of roots since, when nutrient concentration is not a limiting factor, thicker roots have the small axial conductance and high transport capacity needed to fully exploit a high nutrient environment (Ryser and Lambers 1995).

Patchy fertilization, in summary, did not change the morphological characteristics of leafy spurge roots. Its main effect was a reduction in root biomass and a drastic change in the distribution of the root surface area within the plant's rooting volume (Figs. 2 C–D). Fertilization both doubled the percentage of roots located in the top 10 cm of soil and shifted it toward the fertilized patches. This level of root plasticity is considerably higher than that observed in many other plants: a 3:1 ratio of root biomass in the fertilized vs. not-fertilized patches for leafy spurge (Fig. 2D) vs. an average of 1.5:1 reported in the literature for a variety of grasses and forbs (see Larigauderie and Richards 1994, Caldwell 1994, Fransen et al. 1998 and their respective citations).

The high vertical and horizontal plastic response shown by leafy spurge roots, while advantageous for nutrient acquisition, can potentially constitute a weakness. A considerable advantage of leafy spurge, is that the depth distribution pattern of its root system makes it less susceptible to direct competition from the roots of native species: more than 60% of the root biomass of most grasses and forbs native to the Great Plains is located within the top 30 cm of the soil profile (Jackson et al. 1996, Sun et al. 1997), whereas the majority of leafy spurge roots are located below 30 cm (Figs. 2 B–C). We hypothesize that patchy fertilization, by causing a decrease in leafy spurge root biomass, a shift of roots toward the top of the soil profile, and a concentration of these roots in small fertilized patches close to the surface, could increase the effectiveness of chemical and biological control methods because:

(a) Leafy spurge will have to compete for nutrients in a section of the soil profile dominated by the roots of native plants. Intense root competition in patchy environments has been shown to be a major mechanism for plant displacement (Caldwell et al. 1996).

(b) A reduced root system with a higher proportion of roots concentrated in small fertilized patches close to the soil surface, should increase the susceptibility of leafy spurge to drought, and more importantly improve the ability of both herbicides and insects to reach a substantial part of its root system.

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Rangeland management impacts on soil biological indicators in southern Alberta

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Abstract

Quantitative techniques are needed to determine the effects of cultivation and livestock grazing on biological indicators of soils of the Northern Great Plains. Our objective was to determine how various management practices, which were representative of those used since European settlement in the 1880's, affected 3 biological indicators of soil quality. The study was conducted at 3 sites that are representative of the major grassland ecosystems in Canada: a Mixed Prairie site with *Stipa comata* Trin. & Rupr. dominant in the Brown (Aridic Haploboroll) Soil Zone, a Mixed Prairie site with *S. comata* Trin. & Rupr. and *S. viridula* Trin. dominant in the Dark Brown (Typic Haploboroll) Soil Zone, and a Fescue Prairie site with *Festuca campestris* Rydb. dominant in the Black (Udic Haploboroll) Soil Zone. At each site, 6 treatments representing common production practices were imposed and compared with the native community in a randomized complete block design with 4 replicates and a plot size of 3 x 10 m. The treatments included: 1) monoculture seeding of 2 grass species; 2) alfalfa (*Medicago sativa* L. 'Beaver'); 3) continuous spring wheat (*Triticum aestivum* L. 'Katepwa'); 4) spring wheat and fallow rotation; and 5) abandoned cultivated land. Our hypothesis that mineralizable-N, and phosphatase and dehydrogenase activities would be influenced by cultivation was confirmed by significant changes in these indicators that were detected after only 180 days after treatment establishment. The pool of readily decomposable organic matter was reduced with cultivation and not replenished over the period of the study. The 3 biological indicators were sensitive to not only time following external management changes, but also to seasonal fluctuations. We conclude that soil biological indicators can be used to quantify temporal and botanical changes in diverse ecotypes within the Northern Great Plains.

Key Words: steady state, soil transformations, introduced grasses, abandoned land, monoculture

Resumen

Técnicas cuantitativas son necesarias para determinar los efectos de la cultivación y el pastoreo del ganado en los indicadores biológicos de suelos de la Grandes Llanuras Norteñas (Northern Great Plains). Nuestro objetivo fue determinar como diferentes prácticas de manejo, que eran representativas de aquellas utilizadas desde el asentamiento de los europeos alrededor de 1880, afectaron tres indicadores biológicos de la calidad del suelo. El estudio fue conducido en tres lugares que son representativos del ecosistema pastoril más grande de Canadá: un sitio de Pradera Mixta con *Stipa comata* Trin. y Rupr. dominante en la zona de suelos Marrones (Aridic Haploboroll), otro sitio con Pradera Mixta con *S. comata* Trin. y Rupr. y *S. viridula* Trin. dominante en la zona de suelos Marrones Oscuros (Typic Haploboroll) y por ultimo un sitio con Pradera de Festuca con *Festuca campestris* Rydb. que es la dominante en la zona de suelos Negros (Udic Haploboroll). En cada sitio se utilizaron seis tratamientos representativos de las prácticas de producción más comunes y se comparó con la comunidad de especies nativas en un diseño de "bloque seleccionado completamente al azar" con cuatro réplicas y un tamaño de parcela de 3 X 10 metros. Los tratamientos incluyeron: 1) siembra de monocultivo de dos especies de pastos;2) alfalfa (*Medicago sativa* L. 'Beaver'); 3) siembra continua de trigo de primavera (*Triticum aestivum* L. 'Katepwa'); 4) trigo de primavera y rotación con barbecho;y 5) tierra de cultivo abandonado. Nuestra hipótesis de que el N mineralizable y que las actividades fosfatasas y dehidrogenasas serían influenciadas por la cultivación fueron confirmadas por cambios significativos en estos indicadores que fueron detectados después de solamente 180 días después del inicio del tratamiento. La materia orgánica de rápida descomposición fue reducida con la cultivación y no fue restablecida durante el período del estudio. Los tres indicadores biológicos fueron sensibles no solamente a los cambios que siguieron a los manejos externos, pero como asi también a las fluctuaciones estacionales. Concluímos que los indicadores biológicos de suelos pueden ser utilizados para cuantificar cambios temporarios y cambios botánicos en diversos ecotipos de la Grandes Llanuras Norteñas (Northern Great Plains).

European settlement of the Northern Great Plains had a great effect on the stability of the soil through the imposition of cultivation and grazing by livestock. Southern Alberta is represented by 3 major grassland ecosystems: a Mixed Prairie site with *Stipa comata* Trin. & Rupr. dominant in the Brown Soil Zone (around 2% organic C), a Mixed Prairie site with *S. comata* Trin. & Rupr. and *S. viridula* Trin. dominant in the Dark Brown Soil Zone (around 4% organic C), and a Fescue Prairie site with *Festuca campestris* Rydb. dominant in the Black Soil Zone (around 11% organic C).

When settlers arrived on the southern Alberta plains, the soils were at a steady state (Jenny 1980) that included fire and free-

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roaming bison. Cultivation, introduction of new grass species, elimination of fire and replacement of bison with confined grazing of cattle, often at intense grazing pressures, interrupted the original steady state.

Biologically and biochemically mediated processes in soils are fundamental to terrestrial ecosystem function and may be early indicators of soil changes. Hence, to identify early warning indicators of ecosystem stress, an understanding of the underlying biological processes is needed (Dick 1994). For example, soil enzyme activity has been shown to have temporal responsiveness (Dormaar et al. 1984) which must be accounted for if used as an indicator of soil quality.

Assuming native grassland communities evolved for optimum utilization of the local environment, an experiment was designed to examine short-term effects of human interruption of the existing rangeland steady state in 3 ecotypes in the Northern Great Plains. We hypothesized that biological activities including mineralizable-N and enzyme activities would be good indicators of steady state interruption, and thus also be good indicators of changes in rangeland soil quality.

Materials and Methods

Site Description

The study was conducted at 3 sites, widely separated geographically, and representative of major ecotypes of the Northern Great Plains (Table 1). One site was at the Agriculture and Agri-Food Canada substation at Onefour (49° 07'N, 110° 29'W) and represented the *Stipa-Bouteloua* faciation of the Mixed Prairie. The second site was at the Animal Diseases Research Institute (ADRI) near Lethbridge (49° 43'N, 112° 57'W) and represented the *Stipa-Bouteloua-Agropyron* faciation of the Mixed Prairie. A third site was at the Agriculture and Agri-Food Canada substation in the Porcupine Hills west of Stavely (50°12'N, 113° 57'W) and represented Fescue Prairie dominated by rough fescue (*Festuca campestris*). The vegetation at these sites has been described by Moss and Campbell (1947) and Coupland (1961).

Methods

At each site, 6 treatments representing common production practices were imposed and compared with the native community in a randomized complete block design with 4 replicates and plot sizes 3 x 10 m. The treatments included 1) monoculture seeding of 2 grass species; 2) alfalfa (*Medicago sativa* L. 'Beaver'); 3) continuous spring wheat (*Triticum aestivum* L. 'Katepwa'); 4) spring wheat and fallow in rotation; and 5) abandoned cultivated land. On the 2 mixed prairie sites (Onefour and Lethbridge), the introduced grass treatments were crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) and Russian wildrye (*Elymus junceus* Fisch.). On the fescue prairie, smooth bromegrass (*Bromus inermis* Leyss.) and orchard grass (*Dactylis glomerata* L.) were sown. All plots were established in spring (Table 1) by cultivating and seeding, or abandoning a previously uncultivated native plant community. The native treatment was left intact and undisturbed during plot preparation. The abandoned plot was cultivated several times during the first summer and plants that emerged from live tillers were removed until the second year. All seedings were using 15-cm row spacing. The *Stipa-Agropyron-Bouteloua* and *Festuca campestris* sites were prepared and established in spring 1993 and the *Stipa-Bouteloua* site was established in spring 1994. Each site was enclosed with a 4-strand barbed-wire fence that excluded livestock.

Soil samples were taken through the centre of the plots to eliminate edge effect in fall and spring over a 3-year period, beginning in the fall of 1993, at the *Stipa-Agropyron-Bouteloua* and *Festuca campestris* sites, and over a 2-year period, beginning in the fall of 1994, at the *Stipa-Bouteloua* site (Table 1). Three subsamples from the Ah (=A1) soil horizon were taken by spade, composited, and hand-sieved in the field through a 2-mm screen. The samples were stored in sealed, double polyethylene bags at 4° C.

All analyses were made using moist soil and carried out within 3 weeks of arrival at the laboratory. Moisture content was determined gravimetrically. Mineralizable-N, as an index of biological N availability, was determined as described by Keeney (1982). Dehydrogenase activity, a common enzymatic activity to estimate microbial activity, was determined at pH 7.6 on fresh, moist soil by measuring the triphenylformazan (formazan) produced by reduction of 2,3,5-triphenyltetrazolium chloride when soil was incubated with 2-amino-2-(hydroxymethyl)propane-1:3-diol buffer (0.5 M) at 30° C for 5 hours (Ross 1971). Phosphatase activity, an indicator of capability to cleave phosphate esters, was determined at pH 6.5 on fresh, moist soil by measuring p-nitrophenol produced when soil was incubated with buffered disodium *p*-nitrophenyl phosphate tetrahydrate solution (0.115 M) and toluene at 37° C for 1 hour (Tabatabai and Bremner 1969).

Statistical Analyses

Each variable was analysed in a whole model as an unbalanced 3 (sites) x 7 (treatments) x 2 (seasons) x 2 or 3 (years) x 4 (replicates) split-split-split plot design (Table 2) using the GLM Procedure of SAS (1989). The potential bias resulting from repeated measurements over years was alleviated using the Box Correction Procedure (Milliken and Johnson 1984). The data were unbalanced because there were only 2 years for the *Stipa-Bouteloua* site and the grass species were combined as 1 treatment to yield 2 x the plot number for the new treatment. This was done to account for the differences in species among sites. The variables were highly responsive to the factors tested and meaningful interpretation required a more detailed examination of the data. This was accomplished by analysing the data by individual site, and the grass species as individual treatments, as a 7 (treatments) x 2 (seasons) x 2 or 3 (years) x 4 (replicates) split-split plot design. Further analyses consisted of evaluating only the first year effects in a 7 (treatments) x 4 (replicates) design for each season. The yearly trend of each index was also evaluated, for each

Table 1. Study site descriptions.

Location	Soil Zone	Soil Canada (Chernozemic)	Soil U.S. (Haploboroll)	Average Precipitation (mm)	Started	Soil Sampling Dates 1993	1994		1995		1996
Onefour	Brown	Orthic Brown	Aridic	310	6 Apr. 1994			1 Nov.	20 Apr.	28 Sep.	22 Apr.
ADRI	Dark Brown	Orthic Dark Brown	Typic	420	1 Apr. 1993	29 Sep.	21 Apr.	10 Oct.	8 Apr.	11 Oct.	1 May
Stavely	Black	Orthic Black	Udic	550	13 Apr. 1993	3 Oct.	22 Apr.	19 Sep.	17 May	14 Sep.	6 Jun.

Table 2. Analyses of variance for the whole model and by site of 4 variables to examine the influence of modified plant communities, site, season, and year on selected soil parameters.

Source of variation	Df	Probabilities/Means			
		Moisture	Mineralizable-N[1]	Dehydrogenase Activity[2]	Phosphatase Activity[3]
Whole model[4]		(%)			
Site			Means		
Stipa-Bouteloua		12	43	63	867
Stipa-Agropyron-Bouteloua		16	75	103	566
Rough Fescue Prairie		40	205	198	2914
Partial Models (by site)					
Stipa-Bouteloua[5]			P		
Treatment (T)	6	< 0.01	< 0.01	< 0.01	< 0.01
R x T (Error 1)	21				
Season (Se)	1	< 0.01	0.02	0.10	< 0.01
T x Se	6	< 0.01	0.02	< 0.01	0.06
R x T x Se (Error 2)	21				
Year (Y)	1	< 0.01	0.10	< 0.01	< 0.01
Se x Y	1	< 0.01	< 0.01	< 0.01	< 0.01
T x Y	6	< 0.01	< 0.01	< 0.01	0.22
T x Se x Y	6	< 0.01	< 0.01	< 0.01	0.02
R x T x Se x Y (Error 3)	111				
Year			Means		
1994/95		15	42	68	914
1995/96		12	43	63	867
Stipa-Agropyron-Bouteloua[6]			P		
Treatment (T)	6	< 0.01	< 0.01	< 0.01	< 0.01
R x T (Error 1)	21				
Season (Se)	1	< 0.01	0.02	< 0.01	0.14
T x Se	6	< 0.01	< 0.01	< 0.01	< 0.01
R x T x Se (Error 2)	21				
Year (Y)	2	< 0.01	< 0.01	< 0.01	< 0.01
Se x Y	2	< 0.01	< 0.01	< 0.01	< 0.01
T x Y	12	< 0.01	< 0.01	< 0.01	< 0.01
T x Se x Y	12	< 0.01	< 0.01	< 0.01	< 0.01
R x T x Se x Y (Error 3)	167				
Year			Means		
1993/94		19	95	68	719
1994/95		16	75	103	566
1995/96		18	83	106	466
Fescue Prairie[7]			P		
Treatment (T)	6	< 0.01	< 0.01	< 0.01	< 0.01
R x T (Error 1)	21				
Season (Se)	1	< 0.01	< 0.01	< 0.01	0.03
T x Se	6	< 0.01	< 0.01	< 0.01	< 0.01
R x T x Se (Error 2)	21				
Year (Y)	2	< 0.01	< 0.01	< 0.01	< 0.01
Se x Y	2	< 0.01	< 0.01	< 0.01	< 0.01
T x Y	12	< 0.01	< 0.01	< 0.01	< 0.01
T x Se x Y	12	< 0.01	< 0.01	< 0.01	< 0.01
R x T x Se x Y (Error 3)	167				
Year-			Means		
1993/94		50	306	189	4933
1994/95		40	205	198	2914
1995/96		40	197	180	2728

[1] NH_4^+-N released, mg kg^{-1} dry soil h^{-1}.

[2] Formazan released, nmole g^{-1} dry soil h^{-1}.

[3] P-nitrophenol formed, mg kg^{-1} dry soil h^{-1}.

[4] All effects were significant (<0.01) for each variable: Site (Si); Treatment (T); Si x T; Season (Se); Si x Se; Si x T x Se; Year (Y); Si x Y; Se x Y; Si x T x Y; T x Se x Y; Si x T x Se x Y.

[5] Brown Chernozemic soil.

[6] Dark Brown Chernozemic soil.

[7] Black Chernozemic soil.

site, as either the difference between 2 years with a t-test (*Stipa-Bouteloua* site) or with simple linear regression over 3 years (*Stipa-Agropyron-Bouteloua* and *Festuca campestris* sites). The trends were evaluated by subtracting the native soil (control) value for each indicator. This was done to remove the effect of environment at the time of sampling by assuming its effect on the control was the same as on the treatments (Table 4). Trends were thus established for each season, treatment, and replicate that were then evaluated by analysis of variance to test for the effect of season. Since the season by treatment interaction was significant ($P < 0.05$), in all but one case, (phosphatase activity on the *Stipa-Bouteloua* site), the data were reported by season and treatment. Mean separation was achieved using single degree of freedom contrasts (Steel and Torrie 1980).

Results

The indices of soil quality selected, i.e., mineralizable-N, and dehydrogenase and phosphatase activities, were highly responsive ($P < 0.01$) to the agronomic treatments and were influenced ($P < 0.01$) by site, season and year (Table 2). The main effects all influenced ($P < 0.01$) one another necessitating a more detailed examination to discern constituent response (Tables 3 and 4). The indices of soil quality tended to increase across sites with *Stipa-Bouteloua* < *Stipa-Agropyron-Bouteloua* < *Festuca campestris*. This response corresponded to increased soil moisture at the time of sampling (Table 2). Only phosphatase activity was lower on the *Stipa-Agropyron-Bouteloua* site than on the *Stipa-Bouteloua* site (Table 2).

The unadjusted (with the control) indices of soil quality tended to decrease with years since cultivation (Table 2). These means include the control (native prairie), so the trend describing the effect of years since cultivation was partially obscured by this analysis.

In the first year, cultivation and seeding affected the indices of soil quality ($P < 0.05$) in both fall and spring on each site (Table 3). The mineralizable-N and dehydrogenase activity were reduced by all treatments in both seasons on the *Stipa-Bouteloua* site and in spring only on the *Stipa-Agropyron-Bouteloua* and *Festuca campestris* sites (Table 3); however, both indices increased ($P < 0.05$) in response to treatment in fall on the *Stipa-Agropyron-Bouteloua* and *Festuca campestris* sites. Phosphatase activity tended to follow a similar pattern of response as the biological index and dehydrogenase activity, but with 1 exception in fall where the response to cultivation was less clear on the *Stipa-Bouleloua* site. Among the treatments in the first year, grass species tended to have lower mineralizable-N, and lower or simi-

Table 3. The influence of cultivation and modified plant communities on selected soil parameters in the year after establishment.

Treatment	Fall Mixed prairie[1]	Fall Mixed prairie[2]	Fall Fescue prairie[3]	Spring Mixed prairie[1]	Spring Mixed prairie[2]	Spring Fescue prairie[3]
			Moisture (%)			
1 Native	17 a[4]	24 bc	62 a	17 a	21 a	72 a
2 Grass 1[5]	15 ab	24 c	50 cd	13 c	8 e	36 cd
3 Grass 2[6]	15 b	25 abc	53 bc	13 c	8 e	32 d
4 Wheat Fallow	16 ab	26 ab	62 a	14 bc	13 c	48 b
5 Wheat continuous	17 a	25 abc	60 a	15 b	15 b	45 b
6 Alfalfa	16 ab	25 abc	48 d	13 c	9 e	35 cd
7 Abandoned	17 a	26 a	55 b	13 c	12 d	37 c
			Mineralizable-N[7]			
1 Native	68 a	57 e	313 b	64 a	116 a	556 a
2 Grass 1[5]	44 de	118 a	322 b	26 c	84 d	207 bcd
3 Grass 2[6]	47 cd	104 c	380 a	24 c	75 e	163 e
4 Wheat Fallow	51 bc	116 ab	398 a	34 b	96 b	244 b
5 Wheat continuous	53 b	111 b	380 a	34 b	88 cd	228 bc
6 Alfalfa	53 b	103 c	335 b	36 b	91 bc	200 cde
7 Abandoned	41 e	92 d	374 a	17 d	77 e	181 de
			Dehydrogenase activity[8]			
1 Native	106 a	44 d	104 e	97 a	87 a	431 a
2 Grass 1[5]	65 c	69 a	135 bc	52 de	70 b	210 bc
3 Grass 2[6]	68 c	60 c	149 a	52 de	63 c	202 c
4 Wheat Fallow	67 c	63 bc	136 b	55 cd	86 a	223 bc
5 Wheat continuous	73 bc	67 ab	125 d	62 c	82 a	202 c
6 Alfalfa	78 b	72 a	152 a	72 b	74 b	222 bc
7 Abandoned	68 c	59 c	129 cd	45 e	56 d	228 b
			Phosphatase activity[9]			
1 Native	1083 a	643 c	6962 a	922 a	826 a	9511 a
2 Grass 1[5]	986 b	796 ab	5407 b	789 bc	571 d	3059 c
3 Grass 2[6]	1007 ab	742 b	5635 b	702 e	571 d	2905 cd
4 Wheat Fallow	1091 a	830 a	6949 a	795 bc	689 b	3648 b
5 Wheat continuous	1082 a	795 ab	5408 b	770 cd	692 b	3465 b
6 Alfalfa	1049 ab	869 a	4870 c	834 b	692 b	2778 d
7 Abandoned	974 b	726 b	5732 b	718 de	620 c	2729 d

[1] *Stipa-Bouteloua*, Brown Chernozemic soil.
[2] *Stipa-Agropyron-Bouteloua*, Dark Brown Chernozemic soil.
[3] *Festuca campestris*, Black Chernozemic soil.
[4] Means having the same letter within a subset of the column do not differ significantly P>0.05.
[5] Grass species is crested wheatgrass in the mixed prairie and smooth brome in the fescue prairie.
[6] Grass species is Russian wildrye in the mixed prairie and orchard grass in the fescue prairie.
[7] NH_4^+-N released, mg kg^{-1} dry soil h^{-1}.
[8] Formazan released, nmole g^{-1} dry soil h^{-1}.
[9] P-nitrophenol formed, mg kg^{-1} dry soil h^{-1}.

lar dehydrogenase and phosphatase activities compared to wheat (Table 3). The 2 wheat treatments in the first year were identical and the differences ($P < 0.05$) detected between them (Table 3) are an anomaly likely produced by sampling.

Trends in the indices of soil quality over years since cultivation and seeding (Table 4) were, with a few exceptions, affected ($P < 0.05$) by treatment, season, and their interaction. On the *Stipa-Bouteloua* site, the trend of dehydrogenase activity was not ($P > 0.05$) influenced by either treatment or season while phosphatase activity was not ($P > 0.05$) influenced by treatment or the interaction of treatment with season. On the *Stipa-Agropyron-Bouteloua* site, only dehydrogenase activity was not ($P > 0.05$) influenced by season.

Over years since cultivation and seeding, mineralizable-N tended to decline in fall and increase in spring (Table 4). The treatment response, and differences between season, became greater from the *Stipa-Bouteloua* to the *Festuca campestris* sites. Dehydrogenase activity increased in both spring and fall in a similar manner ($P < 0.05$) across treatments on the *Stipa-Bouteloua* site. In the *Stipa-Agropyron-Bouteloua* site, dehydrogenase activity was mostly unaffected by years since cultivation and seeding while on the *Festuca campestris* site, dehydrogenous activity increased ($P < 0.05$) over all treatments in spring and tended to decrease in fall except where orchard grass was seeded (Table 4). In the fall, phosphatase activity decreased over years since cultivation and seeding on both the *Stipa-Bouteloua* and *Stipa-Agropyron-Bouteloua* sites but increased on the *Festuca campestris* site. In spring, phosphatase activity increased on the *Festuca campestris* site, but remained mostly constant on the other 2 sites (Table 4).

Discussion

Initial effect of cultivation

Cultivation and seeding had a dramatic effect on the indices of soil quality as measured by mineralizable-N, dehydrogenase activity, and phosphatase activity. These effects were mediated by site, season and treatment and influenced by time after cultivation and seeding. Since the first time measurement was made only 180 days after cultivation and seeding, we speculate that cultivation stimulated a rapid release of organic compounds through microbial decomposition of existing soil organic matter that was readily decomposed and was not replenished under the newly established cultivated species.

How are the indices related to soil organic matter and soil quality?

Site differences appear to be related to the decomposable nature of the organic matter. That is, the Ah horizon of Brown Chernozemic soils contained considerably more organic matter that was readily decomposable (Dormaar 1975) and less resistant to thermal decomposition (Lutwick and Dormaar 1976) than that under Black Chernozemic soils. Up to 39% of the organic matter of Brown Chernozemic soils was still in an undecomposed form compared with 5% in Black Chernozemic soils (Dormaar 1977). Comminution of root mass is significantly greater under Mixed Prairie than under the fescue prairie (Dormaar and Willms 1993).

It is clear that the variables of the 3 sites are different even in response to the treatments. For the 4 comparisons of the first 2 years, the phosphatase activities were consistently lower for the Dark Brown than for the Brown Chernozemic soil. Conversely, under growth chamber conditions phosphatase activity was Brown<Dark Brown<Black Chernozemic soils (Dormaar 1988). Although the rea-

Table 4. Trends of selected soil quality variables in 3 plant communities over a 2 or 3 year period since cultivation and reseeding, or abandonment, in both fall and spring after adjustment for the composition in native soil.

		Crested wheat-grass	Russian wild rye	Wheat-fallow	Continuous wheat	Alfalfa	Abandoned
Stipa-Bouteloua[1]							
Soil Moisture (%)	Fall	-0.25	0.5	5.50*[3]	4.25*	0.75	2.00
	Spring	1.5	1.25	0	0.25	3.25	1.25
Mineralizable-N[4]	Fall	3	-0.2	-1.2	-7	-7.2	3.5
	Spring	23.0*	27.0*	11.8	13	25.8*	31.5*
Dehydrogenase[5]	Fall	29.0*	18.5*	42.5*	35.75*	19.5	28.0*
	Spring	27.0*	30.8*	22.5*	17	28.5*	30.0*
Phosphatase[6]	Fall	-55*	-106*	-137*	-105	-19	-68
	Spring	29	70	22	67	50	19
Stipa-Agropyron-Bouteloua[2]							
Soil Moisture (%)	Fall	-1.88	-3.38*	-2.38	-3.25*	-3.75*	-3.25*
	Spring	0.12	0.88	0.5	0	0.62	0.5
Mineralizable-N	Fall	-31.1*	-21.6*	-34.4*	-35.6*	-25.8*	-23.2
	Spring	7.9	9.9*	-4.2	3.5	10.0*	13.6*
Dehydrogenase	Fall	3.6	-1.2	7.5	-5.5	1.4	3.2
	Spring	7.8	0	-8.1	-6.5	5.8	13.1
Phosphatase	Fall	-191*	-134*	-152*	-184*	-160*	-118*
	Spring	12	-38	-78	-120*	-37	-34
Fescue Prairie[2]							
		Orchard Grass	Smooth Brome				
Soil Moisture (%)	Fall	1.62	-4	-5.12*	-2.5	2	-3
	Spring	13.00*	11.50*	3.12	4.38	8.88	4.62
Mineralizable-N	Fall	-60.0*	-132.0*	-129.4*	-93.1*	-101.0*	-136.6*
	Spring	121.9*	103.0*	56.8*	80.0*	73.4*	87.6*
Dehydrogenase	Fall	33.6*	-15	-25.6*	10.1	-25.4	-7.4
	Spring	134.0*	123.2*	121.9*	146.1*	128.6*	151.4*
Phosphate	Fall	69*	342	-235	614*	809*	258*
	Spring	2176*	1949*	1655*	1661*	1945*	1679*

[1] Mean differences of adjusted values between the first and second years after establishment of qualitative constituents, n=8.
[2] Coefficients of linear regression equations of adjusted values over 3 years (n=12); average change of the coefficients over the 3 years.
[3] Asterisk denotes a significant ($P>0.05$) mean difference or coefficient (n=12).
[4] NH_4^+-N released, mg kg^{-1}dry soil h^{-1}.
[5] Dehydrogenase activity: Formazan released, nmole g^{-1} dry soil h^{-1}.
[6] Phosphatase activity: P-nitrophenol formed, mg kg^{-1} dry soil h^{-1}.

sons for this are not fully understood, a tentative explanation, for the spring differences at least, in the field, can be offered. If the ratio of soil organic carbon (C)/NaOH-extractable organic phosphorus (P) increases, it means more inorganic P bound to the soil organic matter complex has been released by the phosphatases present in the soil (Dormaar 1972, Dormaar et al. 1984). This leads to decreased levels of phosphatase activity and increased levels of available inorganic P. This available inorganic P, however, is immediately being taken up by the roots as the plant actively starts to grow again in the spring (Dormaar 1972). When the spring 1996 samples were obtained for this study, other samples were collected for a 1-time, early comparison of the various treatments (unpublished data). The ratios of total organic soil C over NaOH-extractable organic P for the average of all 28 samples (7 treatments x 4 replicates) per site are 248, 425, and 156 for the Brown, Dark Brown, and Black Chernozemic soils, respectively. Obviously, timing, i.e., attempting to sample at equivalent biological activity stages, would be desirable; however, weather conditions generally do not permit this. In addition, there are numerous other factors, such as soil moisture, depth of Ah horizon and chemical properties, that influence soil phosphatase activities (Speir and Ross 1978).

On the whole, with some exceptions at the *Stipa-Agropyron-Bouteloua* site, once native prairie has been disturbed, in spite of replacement with introduced grass species, biological activity in the soil has decreased in the first 2 or 3 years. Time will tell if the various treatments will be able to rebuild biological activity to the level of native prairie. This will depend on root mass and plant contributions to the rhizosphere ecosystem. The rhizosphere of the plant provides a surface for microbiological colonization which uses root exudates as an energy source. A major problem is to quantify the amounts of photosynthate that enters the rhizosphere and to identify the composition of root exudates. Only 1 study, and that in a growth chamber, quantified the amounts of photosynthate that enters the rhizosphere of 1 of the native grass species involved, i.e., *Bouteloua gracilis* (H.B.K.) Lag. (Dormaar and Sauerbeck 1983). Attempts have also been made to determine the impact of the interaction of root systems of 4 different plant species on the quantities and composition of root exudates. Dormaar (1988) and McKenzie et al. (1995) concluded that the properties of rhizosphere soil are system specific, that is, rhizosphere changes are a function of plant species, soil type, and time.

Dick (1994) noted that the primary value of measuring soil enzyme activities may not be to estimate biological activity per se, but rather as an integrative indicator of a change in the biology and biochemistry of soil. This may be due to the external management, such as monoculture of various crops or abandonment, or to environmental factors, such as location and time of the year. The study presented indeed has shown that the 3 biological activity parameters selected were quite sensitive to not only time following external management, but also to seasonal fluctuations. Comparing between sites does not seem realistic, since it is difficult to have each site at the same climatic conditions at the time of sampling. Comparing within sites supports the conclusions on a field scale that were obtained under growth chamber conditions by Dormaar (1988) and McKenzie et al. (1995). Biological activity parameters can be used as soil quality indicators on a routine basis to follow within-site temporal and botanical changes.

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Broom snakeweed establishment following fire and herbicide treatments

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Abstract

Broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt & Rusby) propagation was monitored from 1990 through 1998 following burning and herbicide control practices conducted on blue grama (*Bouteloua gracilis* [H. B. K. Lag.]) grasslands near Corona, N.M. Broom snakeweed usually germinated in April, May, or June (83% of 394 total) and mostly in 1991 and 1992 (81% of total) when spring moisture was sufficient. The majority of broom snakeweed seedlings (52% of total) emerged the first or second year after summer burning, especially in areas where grass yield and cover declined and bare ground exposure increased as a result of intense fires. Spring fires caused less damage to blue grama than summer fires, and the number of broom snakeweed seedlings produced (18% of total) was similar to non-treated rangeland (22% of total), but lower than numbers on areas burned in the summer. Grass yield and cover increased within a year of herbicide spraying and treated plots had significantly ($P < 0.05$) fewer broom snakeweed seedlings (8% of total) than burned and non-treated areas.

Key Words: Shortgrass prairie, germination, emergence, prescribed burning, picloram

Resumen

De 1990 a 1998 se monitoreo la propagación "Broom snakeweed" (*Gutierrezia sarothrae* [Pursh] Britt & Rusby) después de aplicar quema y herbicidas como practicas de control en un pastizal de "Blue grama" (*Bouteloua gracilis* [H.B.K. Lag]) situado cerca de Corona, N.M. El "Broom snakeweed" usualmente germino en Abril, Mayo o Junio (83% de un total de 394), principalmente en 1991 y 1992 (81% del total) cuando la humedad en primavera fue suficiente. La mayoría de las plántulas de "Broom sankeweed" (52% del total) emergieron el primero o segundo año después de la quema de verano, especialmente en áreas donde el rendimiento y cobertura del zacate disminuyeron y la cantidad de suelo desnudo aumento como resultado de fuegos intensos. Los fuegos de primavera causaron menos daño al "Blue grama" que los fuegos de verano, y el número de plántulas producidas de "Broom sankeweed" (18% del total) fue similar al del pastizal no tratado (22% del total), pero menor que las producidas en otras áreas quemadas en verano. El rendimiento y cobertura del zacate se incrementaron dentro del año en que se asperjo el herbicida y las parcelas tratadas tuvieron significativamente ($P < 0.05$) menos plántulas de "Broom snakeweed" que las áreas quemadas y las no tratadas.

The historical burning frequency on New Mexico's blue grama grasslands is unknown but Wright and Bailey (1982) speculate wildfires to have periodically occurred during periods of drought and probably at 15 to 25 year intervals. Today, wildfires on these shortgrass rangelands are usually started by accident (railroad box fires, downed power lines, etc.) rather than by natural causes (McDaniel et al. 1989). Prescribed burns are uncommon but occasionally landowners will conduct planned fires to remove broom snakeweed and other undesirable weeds and brush.

When burning blue grama grasslands, the majority of mature broom snakeweed can be eliminated provided fuel and weather conditions are suitable to produce heat of sufficient intensity to destroy the entire canopy (McDaniel et al. 1997). Extremely hot fires, however, often damage blue grama and other perennial plants, thereby creating micro-sites potentially favorable for establishment of low seral species, including broom snakeweed. Establishment of broom snakeweed seedlings shortly after burning can negate the economic benefits that are expected to accrue from prescribed fire (Torell et al.1989).

Research investigating broom snakeweed germination (Kruse 1970, Mayeux and Leotta 1981, Mayeux 1983), dispersal (Wood et al. 1997), and seed bank storage (Osman and Pieper 1988) have provided insight into how this species establishes on southwestern U.S. rangelands. Other research has focused on seedling survival (Nadabo et al. 1980), longevity (McDaniel 1989), and population dynamics (Torell et al. 1992). Broom snakeweed control by herbicides and the subsequent establishment of herbage and broom snakeweed has been reported in a number of studies (McDaniel and Duncan 1987, McDaniel 1989). In this study we examine some of the circumstances under which broom snakeweed is likely to establish after prescribed fire relative to herbicide spraying or no treatment. We specifically addressed the following 3 questions concerning broom snakeweed establishment on blue grama grasslands: (1) Under what conditions is seedling emergence most likely to occur? (2) What fire characteristics are likely to produce micro-sites favorable for seed germination? and (3) Can prescribe fires be conducted in ways to minimize broom snakeweed establishment?

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Materials and Methods

Description of Area

The study was conducted on the New Mexico State University Corona Ranch, about 23 km northeast of Corona, N. M. Two study sites were located about 10 km apart on blue grama dominated grasslands with level terrain and elevation near 1,870 m. Soils on both sites are comprised of the Taipa-Dean loam association, which are shallow and underlain by impervious limestone bedrock. The Taipa loam is classified as a fine-loamy, mixed, mesic, Ustollic Haplargid, and the Dean loam is a fine, carbonatic, mesic, Ustollic Caliciothid. Surface texture is a sandy loam to loam and soil depth is 0.5 m or less. Formed from piedmont deposits and derived from limestone quartzite and igneous rock, these soils are subject to wind erosion and are poorly drained, thus surface runoff is moderate to high (USDA 1970).

The NMSU Corona Ranch is characterized by a semiarid, continental climate with an average diurnal temperature range near 15°C (USDA 1970). Average daily maximum temperatures range from 6.4°C in January to 14.7°C in July. In summer, maximum daytime temperatures exceed 32° about 30 days each year. The growing season, or freeze-free season, is about 155 days a year. Average annual relative humidity is about 50%, but in late winter and early spring the daily average is about 30% and frequently falls below 15% by midday.

The primary sources of rain and snow in the region are from storms originating from the Pacific Ocean and the Gulf of Mexico. Winter precipitation is mainly snow, which averages 51 cm a year, and normally does not stay on the ground more than a few days (USDA 1970). Summer precipitation occurs mostly as intense, local, convectional thunderstorms of short duration. Mean annual precipitation averages 38 cm with about one-half this amount occurring from July to September.

Blue grama dominates the understory vegetation, but other important perennial grasses include wolftail (*Lycurus phleoides* [H.B.K.]), sand dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray), squirreltail (*Elymus longifolius* [Smith] Gould), and three awns (*Aristida* sp.). Broadleaf herbs are relatively uncommon, with scarlet globe mallow (*Sphaeralcea coccinea* (Nutt.) Rybd.) and verbena (*Verbena bracteata* Lag. & Rodr.) most important. Winterfat (*Ceratoides lanata* [Pursh] J.T. Howell) and cholla are scattered throughout the area, but broom snakeweed dominates the over story vegetation. Mature broom snakeweed is 15 to 45 cm in height and its spatial distribution ranges from irregular dense patches to widely scattered individuals. The relative dominance of broom snakeweed in this area varies through time and may be viewed as an increaser on disturbed grasslands (Pieper and McDaniel 1989).

Fire and Herbicide Treatments

Treatments were applied to 20- by 26.5-m plots arranged in a randomized complete block with 3 replications within the 2 study enclosures. Treatments in 1990 consisted of prescribed burns on 17 March (spring) and 13–14 June (summer); a herbicide spray using picloram (4-amino 3,5,6,trichloro-2-pyridinecarboxylic acid) at 0.42 Kg ha^{-1} applied with a trailer-mounted broom sprayer (6.4-m boom) on 26 March; and untreated controls. These treatments were reapplied to adjacent plots in 1991. High winds in spring 1991 prevented us from applying treatments to both sites at the same time, so burns were conducted on 20–23 March and 25–27 June at Site 1; and 5–6 April and 7–8 July at Site 2. Herbicide sprays were applied on 11 March at Site 1 and 5 April at Site 2 using a hand held CO_2 sprayer (3.3-m boom).

Burns were started as head fires using a hand-held drip torch containing a 1:1 gasoline-diesel oil mixture. Around each plot a 6.7-m buffer was installed using a grader to remove vegetation and to create a mineral break. A detailed description of the methods used to characterize each burning event has been described elsewhere (McDaniel et al. 1997). Burns for this experiment were conducted near the prescribed environmental conditions recommended by Wright and Bailey (1982) for general burning of low-volatile fuels typical of blue grama grasslands. They suggested burning a head fire with air temperatures between 21 to 27°C, relative humidity 20 to 40%, wind speed from 3.6 to 6.5 m sec^{-1} and wind direction from the southwest. While we tried to adhere to this prescription, we rarely experienced all of the weather requirements. Thus some burns were conducted outside the recommended air temperatures or relative humidity ranges (Carroll 1994, Hart1992).

Seedling Monitoring

After treatments were applied, nine, 1-m^2 permanent subplots were arranged inside every main plot using 3 by 3 equally spaced rows to monitor broom snakeweed seedling emergence and survival. Metal spikes (10 cm) marked the corners and nylon twine defined the perimeter of each subplot. Mature broom snakeweed plants within each subplot were initially mapped in a notebook and tagged with a common colored (telephone) wire secured around the plant's base for future identification. Beginning 1 month after treatment, subplots were visited near mid-month through October 1998 to mark and map newly emerged seedlings and to census survival of previously tagged plants. New seedlings were color coded to indicate the month of emergence on the subplot diagram. Death of a seedling was similarly denoted by circling the colored mark with the corresponding month of death. Thus, individual life spans for each seedling could be determined. The proximity of each newly emerged seedling was measured in relation to the nearest live grass plant and later was grouped as emerging within grass or emerging outside grass (bare ground). Data collected within the subplots allowed us to compare broom snakeweed emergence and survival over time, and to determine seedling differences among burned, herbicide, or nontreated areas. Differences in the total seedling number produced by treatment over the various collection dates were analyzed using the GLM procedure within SAS (1984). The experimental design was a randomized complete block with site by replication by year as the error term. Means were compared by Fisher's Protected LSD test using the 5% probability level.

Influence of Burning on Seedling Emergence

In 1991, 27 fires were conducted in spring (20 March to 6 April) and 15 fires in summer (25 June to 8 July) under varying fuel load and air temperature regimes for the purpose of developing a burning prescription for maximizing broom snakeweed control with fire (McDaniel et al. 1997). Burning procedures and simple statistics related to conditions before, during, and after these fires have been discussed elsewhere (Hart 1992, McDaniel et al. 1997). The next year (August 1992) it was visibly obvious after walking across burned plots that broom snakeweed seedlings were more abundant on areas burned in summer than spring. Also, we noticed that seedling numbers were not equal among plots burned during the same season, and this offered us the opportunity to compare differences in broom snakeweed emergence after these fires.

Pre-burn vegetation measurements had been obtained in each plot using ten, 31.5 by 61 cm permanently marked quadrats (McDaniel et al. 1997). These quadrats were placed along 2 diagonal lines across each plot from corner to opposite corner. Pre-burn measurements included aerial cover, density, and yield of broom snakeweed and grass. The same vegetational information collected during pre-burn measurements was also obtained every October from 1991 through 1998. Environmental variables monitored during each burn, and reported in McDaniel et al. (1997), included air temperature, soil temperature at 10 cm, relative humidity, wind speed, and wind direction. Fire characteristics evaluated included fire temperatures measured with thermocouples and heat sensitive tablets, rate of fire spread, duration of heat, and degree seconds of heat (Hart 1992, McDaniel et al. 1997).

For purposes of this study, broom snakeweed seedlings were counted in each plot in August 1991, 1992, and 1993 using the same 10 permanent quadrats used to obtain other pre- and post-burn vegetation data. This allowed a comparison of seedling density after burning to average pre-burn, climatic, fire, and post-burn measurements in each plot. Few seedlings were counted in 1991 and 1993; thus only 1992 data are reported. Simple linear and nonlinear regression analyses, and stepwise discriminant analyses (SAS 1984), were conducted with total seedling number per plot as the dependent variable. Environmental, fire, and pre- and post-burn vegetation measurements were used as independent explanatory variables to relate seedling establishment separately and combined across burning seasons. To examine these differences, least squares regression analysis were performed to evaluate the relationship between the 1992 seedling counts and 1991 burning information. The 1991 post-burn vegetation data were used because 83% of seedlings counted in 1992 emerged during the second quarter of the year (April to June). Thus, peak emergence had taken place before the growth of warm season perennial grasses in 1992.

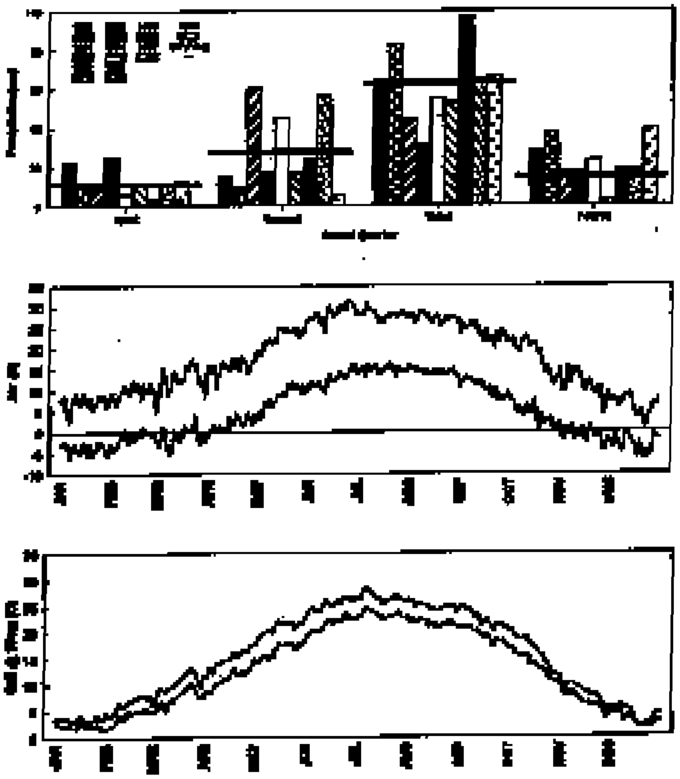

Fig. 1. Precipitation by quarters, and average minimum and maximum air and soil temperatures from 1990 to 1998 on the NMSU Corona Ranch.

Results and Discussion

Seedling Emergence and Survival

During the 9-year study period (1990–1998), annual precipitation at Corona, N.M. was near or slightly above the long-term average every year except 1993 and 1995, which were 28% and 38% below normal (Fig. 1); thus moisture conditions were seemingly favorable for broom snakeweed propagation and survival. Broom snakeweed seed can potentially germinate any month (Lane 1985), but during the course of this study fewer than 2% of new seedlings were counted in the first (January–March) or fourth (October–December) quarters of the year (Table 1). About 15% of seedlings emerged in the third quarter (July–September) when rain fall is usually most abundant. Air and soil temperatures, however, are elevated in these summer months and this probably reduces germination (Fig. 1). Kruse (1979) and Mayeux (1983) reported that broom snakeweed germination ceases when growth chamber temperatures exceed about 30°C.

The majority (83%) of broom snakeweed seedlings emerged during the second quarter (April–June), irrespective of year, site, or treatment (Table 1). This period roughly coincides to when alternating air and surface soil temperatures (10 cm depth) on our study area are near a 10 to 25°C range (Fig. 1). Kruse (1979) and Mayeux (1989) reported that optimal broom snakeweed germination occurs when growth chamber temperatures range between 10 to 25°C, under an 8-hour light period. An examination of average minimum and maximum soil temperatures during the second quarter indicates this optimal range occurs in the spring for about 6 to 8 weeks (about mid April to mid June). Interestingly, soil temperatures on our study area increase gradually in spring but decline rapidly in the fall; thus the optimal temperature range is shorter in autumn (Fig. 1). This may partially explain why few seedlings were counted in the fourth

Table 1. Absolute number of broom snakeweed seedlings counted, irrespective of treatment, from 2 study sites on the NMSU Corona Research Ranch. Counts were made monthly in nine, 1-m^2 subplots placed in each main plot (3 reps x 4 treatments x 3 months per quarter).

	Seedling emergence by annual quarters[1]				
Year	First	Second	Third	Fourth	Total
1990	0	3	4	0	7
1991	0	52	14	0	66
1992	2	211	34	6	253
1993	1	7	1	0	9
1994	0	17	2	0	19
1995	0	6	2	0	8
1996	0	7	0	0	7
1997	0	5	1	0	6
1998	0	18	1	0	19
Total	3	326	59	6	394

[1] First quarter, January, February, March; second, April, May, June; third, July, August, September; fourth, October, November, December

Table 2. Broom snakeweed emergence in relation to distance from individual grass plants, and seedling survival through the first growing season, irrespective of year, site, or treatment, on the NMSU Corona Research Ranch.

Distance	Seedlings Emergence[1]	Seedlings Survival[2]
(cm)	(%)	(%)
0 (within grass clump)	29	80
1–3	54	74
4–6	15	83
7–11	2	83

[1] Percent based on 394 seedlings.
[2] Percent of seedlings alive through first growing season.

quarter. Also, minimum air temperatures when broom snakeweed seed normally begins to disperse in late October are often near freezing, which probably impedes germination (Wood et al. 1997). Contributing to low fall germination may be the need for an after ripening period, which Mayeux and Leotta (1981) reported favors broom snakeweed germination.

In 1992, second quarter rainfall was 224% above normal and resulted in the highest yearly number of seedlings counted (64% of study total, Table 1). Relatively few seedlings emerged in 1990, 1993, 1995, or 1996 (4% of total) when second quarter precipitation was below the 30-yr average (Fig. 1). Precipitation was also below normal in the second quarter of 1991 but a single rain event on 13 May provided 26 mm of moisture and led to the second highest annual seedling total with most counted in mid-June. After this storm we noted the soil surface was saturated and remained wet for about 5 days. We speculate a storm of this intensity is near the minimum required to provide sufficient moisture to imbide seed and to allow germination. In greenhouse studies, Wood et al. (1997) reported optimum broom snakeweed germination occurs when soils are maintained at a minimum matric potential > -180 kPA for at least 4 days. In contrast, 1997 second quarter precipitation was nearly 200% above normal and only 6 seedlings emerged within all study plots at both sites. The low number of seedlings produced in 1997 may be because the seed bank held few viable broom snakeweed seed to support a new population. We speculate on this possibility because precipitation was below normal from beginning the first quarter of 1995 through the second quarter of 1996 and this drought caused the death of most adult broom snakeweed plants and resulted in a lack of seed production. Additionally, in 1995 highest average summer air temperatures ever recorded near Corona occurred and this contributed to a lack of flowering and loss of adult broom snakeweed plants. Broom snakeweed seed under natural conditions are not long-lived as most become non-viable within a year of being dispersed (Wood et al. 1997); thus, with essentially 2 years of no seed production it is likely that the seed bank was largely depleted when adequate soil moisture became available in spring 1997.

Irrespective of site, year, or treatment, the emergence of broom snakeweed seedlings in relation to a ground cover was distinct. About 71% germinated in open bare ground areas, whereas the remainder emerged directly within surrounding grass (Table 2). Percent aerial grass cover was variable over years and treatments, but usually exceeded 60%, whereas bare ground cover was below 25% (data not shown). A higher proportion of seedling emergence within open areas suggest a negative association with the grass overstory, which agrees with the observation that broom snakeweed is less prominent under increasing grass cover than in open disturbed areas (Jameson 1966, 1970, Ueckert 1979, Pieper and McDaniel 1989). Reduced emergence within grass may partially be related to a light requirement needed for normal germination by this species (Mayeux 1989). Interestingly, broom snakeweed survival through the first 2 growing seasons was equal (about 80%) among seedlings that emerged either within or outside grass plants (Table 2). This suggests that, once established, seedling survival to an adult may be more dependent on soil moisture and other environmental conditions than the presence of grass.

Seedling longevity was influenced by the date propagules emerged, and the amount and frequency of rainfall received, especially through the first growing season (Table 3). Broom snakeweed seedlings are vulnerable to dessication because they do not quickly develop an extensive root system to exploit soil water and nutrient resources (Osman and Pieper 1988). Excavations of entire seedlings in the field indicate root penetration is about 9.5 cm after 5 weeks, but only 27 cm after 29 weeks in southern New Mexico (Osman 1982). As the plant matures, it develops an efficient, shallow, fibrous root system that gives it access to soil water at about the same depth as associated perennial grasses (Ragsdale 1969, DePuit and Caldwell 1975). In this study, all seedlings that emerged in 1990 died the first season. However, most seedlings produced between 1991 to 1995 survived (60 to 89%) through the first growing season and later matured to flower the second year. Some 1991 to 1995 seedlings died annually (Table 3), mostly as a result of dry hot conditions in June or July; all but 11 of the original 365 seedlings produced through this time succumbed to 1995–1996 drought conditions. Eight of these seedlings were still alive when the study terminated in October 1998.

Broom Snakeweed Emergence After Treatment

In the study, most broom snakeweed seedlings emerged in 1991 and 1992; thus statistical comparisons between treatments were only made for these years (Table 4). Plots burned in summer 1990 had significantly ($P < 0.05$) more broom snakeweed seedlings the next year than untreated areas; and more seedlings than spring burned and herbicide treated areas the next 2 years. There was an equivalent number of broom snakeweed seedlings in 1990 spring burned and non-treated areas the first year, but fewer seedlings emerged in the spring burned plots the second year. Only 11 seedlings emerged over the 9-year study in plots sprayed with herbicide in 1990, which was less than those counted in spring and summer burned and non-treated areas.

Table 3. Broom snakeweed seedling survival by year, irrespective of treatment or site on the NMSU Corona Research Ranch.

Year Emerged	Number Emerged	Survival at end of growing season 1990	1991	1992	1993	1994	1995	1996	1997	1998
1990	7	0	0	0	0	0	0	0	0	0
1991	66	—	40	30	28	24	10	0	0	0
1992	253	—	—	220	195	167	99	8	6	5
1993	9	—	—	—	7	6	3	1	1	1
1994	19	—	—	—	—	16	11	1	1	1
1995	8	—	—	—	—	—	11	1	1	1
1996	7	—	—	—	—	—	—	1	1	1
1997	6	—	—	—	—	—	—	—	2	2
1998	19	—	—	—	—	—	—	—	—	17

Table 4. Total number of broom snakeweed seedlings produced annually within treatments from 1990 through 1998 on the NMSU Corona Research Ranch.

		Annual Seedling Total[1]									
Treatment	Year Applied	1990	1991	1992	1993	1994	1995	1996	1997	1998	Total
		(no.)									
Non-Treated		3	11b	20b	1	6	2	2	0	4	49
Spring burn	90	3	12b	14c	2	1	1	0	2	4	39
Summer burn	90	1	42a	21b	0	2	0	5	0	1	72
Herbicide	90	0	1c	3d	1	2	0	0	4	0	11
Spring burn	91	—	—	35b	1	1	0	0	0	3	40
Summer burn	91	—	—	146a	2	5	3	0	0	4	160
Herbicide	91	—	—	14c	2	2	2	0	0	3	23

[1]Observations were made in nine, 1-m^2 frames per plot with each treament replicated 3 times at 2 sites. Total measurement area is 54-m^2. Treatments within columns followed by the same letter are not significantly different (P<0.05).

From treatments applied in 1991, summer burned areas accounted for nearly 68% of the total number of broom snakeweed seedlings that emerged the next year (i.e. 1992; Table 4). New seedlings in 1991 spring burned and non-treated areas were similar, and again the fewest number of seedlings were produced in herbicide-sprayed plots. The trend of a relatively high number of seedlings the year after summer burning compared to other treatments indicates that fire probably does not harm seed already distributed on the surface, nor does it later impede broom snakeweed germination. The relatively low number of seedlings in herbicide treated areas compared to burned areas may partially be attributed to the enhancement of grass cover after spraying (Mc Daniel and Duncan 1987). Although spring and summer fires and herbicide spraying eliminated most of the mature broom snakeweed plants after one year (Mc Daniel et al. 1997), the fires always increased bare ground exposure and reduced grass cover relative to herbicide spraying (Table 5; Hart 1992, Carroll 1994).

Influence of Fire on Emergence

In August 1992, broom snakeweed seedlings were more abundant ($P < 0.05$) in the 15 plots burned in summer than the 27 plots burned in the spring 1991 (2.0 ± 1.9 and 0.59 ± 0.83 seedling m^{-2} respectively). There was wide variability among plots in seedling emergence ranging from 0 to 3 seedlings m^{-2} after spring burning, and 0 to 6 seedlings m^{-2} after summer burning.

Least squares regression analysis revealed no significant correlation between broom snakeweed emergence and any of the climatic, fire, or pre-and post-burn vegetation data from spring-burned plots (Table 6). Multiple regression analysis with fire and post-burn vegetation variables accounted for less than 20% of the variation in seedling density following spring burning (data not shown). It was noted by McDaniel et al. (1997) that fires in spring moved faster and burned cooler relative to summer fires, and subsequently resulted in less damage to blue grama. We speculate that when grass growth recovers quickly after fire, then the likelihood for broom snakeweed reestablishment is reduced.

As air temperatures and total fuel biomass increased during summer burning, so too did fire temperatures, total burn time, duration of heat, and degree-seconds of heat (McDaniel et al. 1997). When fires became very intense and produced excessive heat, then post-burn grass yield and cover was reduced for 2 or more years (Hart 1992). Broom snakeweed seedlings were negatively related to increasing grass yield (r = -0.73) and positively related to increasing bare ground cover (r = 0.69). About 9% of seedlings emerged in spring and summer burned plots averaging less than 10% bare ground cover, whereas the remainder emerged where bare ground exposure was higher.

Management Implication

On our study area near Corona, NM, broom snakeweed propagation was most common in the second quarter (April, May, and June) with moist surface soil temperatures ranging between 10 to 25°C. Broom snakeweed seed can potentially germinate any time during a year, and we suspect that propagation elsewhere will depend on localized soil temperature and moisture conditions. For example, while little propagation was noted on our study area during the first or fourth quarters of the year, under a milder climate near Las Cruces, N.M. broom snakeweed emergence was common in January and February (Barnett 1996).

Over this 9-year study broom snakeweed propagation was irregular with only 1991 and 1992 having a substantial number of seedlings produced. There are several possible explanations for why germination was higher in these years than others. Rainfall was plentiful the year after treatments were established. Also, although most adult broom snakeweed plants were killed by the burning and herbicide treatments, there was still a high number of potential progeny in the seed bank the first

Table 5. Percent aerial cover of broom snakeweed, grass, herbs, winterfat, litter, and bare ground when sampled in September 1990 and 1991 after broom snakeweed control on the NMSU Corona Research Ranch.

	Aerial Cover[1]							
	September 1990				September 1991			
	Non-treated	Spring Burn	Summer Burn	Herbicide	Non-treated	Spring Burn	Summer Burn	Herbicide
	(%.)							
1990 Treatments								
Broom Snakeweed	8a	0.7b	0.7b	0.0b	11a	1b	1b	0.0b
Grass	66c	70b	62c	76a	70b	74b	72b	86a
Herbs	4b	4b	7a	0.03c	3bc	4ab	6a	1c
Winterfat	1a	1a	1a	0.2a	2a	1a	1a	1a
Litter	5b	3c	2c	12a	6a	5a	6a	5a
Bare ground	15bc	22ab	27a	12c	9bc	13ab	15a	7c
1991 Treatments								
Broom Snakeweed	—	—	—	—	11a	4b	1b	2b
Grass	—	—	—	—	70b	70b	60c	80a
Herbs	—	—	—	—	3b	4b	15a	2b
Winterfat	—	—	—	—	2a	2a	0a	2a
Litter	—	—	—	—	6a	7a	8a	7a
Bare ground	—	—	—	—	9ab	13a	15a	7b

[1]Means within rows and sample date with the same letters are not different ($P < 0.01$). Treatments were replicated 3 times at 2 sites within years. Analysis of variance revealed no difference ($P < 0.01$) among sites so data were pooled for final analyses.

Table 6. Simple linear correlation coefficients obtained on 1991 spring and summer burns with dependent variable snakeweed seedlings m^{-2}.

	Correlation Coefficients		
Variables	Spring	Summer	Combined
Pre-burn Data			
Grass Cover	–.09	–.33	–.05
Snakeweed Cover	–.02	.26	.08
Litter Cover	.12	.26	–.23*
Bareground Cover	.15	.25	.10
Grass Yield	–.18	–.28	–.01
Snakeweed Yield	–.15	.33	–.04
Snakeweed Density	–.07	.33	.06
Grass Moisture	–.25	–.43	–.05
Snakeweed Moisture	.25	–.43	.07
Soil Moisture	.25	.43	–.30**
Climatic Data			
Air Temperature	.11	.59**	.51***
Soil Temperature	.16	.29	.48***
Wind Speed	–.07	.34	.16
Relative Humidity	–.12	–.50*	–.32**
Wind Direction	–.18	.58**	–.25*
Fire Measurements			
Total Burn Time	.07	–.59**	–.12
Max. Therm. Temp.	.02	.58**	.41***
Tempil-Strip-Temp.	.16	.65***	.60***
Rate of Spread	.20	.65***	.29*
Duration of Heat	.13	.22	.31*
Deg. Seconds Heat	–.003	.46*	.44***
Post-Burn Data			
Grass Cover	.03	–.23	–.20
Snakeweed Cover	–.31	–.39	–.21
Litter Cover	.19	.48*	.50***
Bareground Cover	–.09	.69***	.03
Grass Yield	–.30	–.73***	.12
Snakeweed Yield	–.26	–.46*	–.28**
Snakeweed Density	–.27	–.47*	–.30**

*Significant at P < .10.
**Significant at P < .05
***Significant at P < .01.

year after treatment. Broom snakeweed seed is not long-lived, with most becoming nonviable within a year of dispersal (Wood et al 1997). Thus, if adult plants are eliminated by fire, herbicide, or natural causes, the greatest opportunity for a large number of seedlings to become established should be shortly after the death of mature plants. We speculate, based on our study, that if 1 or 2 years lapse without seedling establishment, then the return of broom snakeweed to an area will be retarded and occur only after a slow year-by-year build up of the population.

Broom snakeweed control practices that provide for greater grass yield and less bare ground exposure should act to minimize, but not necessarily prevent, future broom snakeweed propagation. In this study, herbicide spraying was the only treatment to significantly increase grass yield and cover relative to non-treated rangeland, and was the most effective control practice examined for reducing broom snakeweed establishment. Other research and commercial spraying experience has shown that with time, broom snakeweed may reestablish after herbicide control, even with a 4 to 6 fold increase in grass production (McDaniel and Duncan 1987). However, the magnitude of broom snakeweed establishment on herbicide treated areas should be less than if the rangeland were burned or not treated.

When prescribed fires are conducted in a manner so as to eliminate mature broom snakeweed plants but minimize damage to associated grasses, then there is a greater likelihood for long-lasting broom snakeweed control. In McDaniel et al. (1997) we reported less broom snakeweed control with spring fires (65% average mortality) than summer fires (92% average mortality). In this study, fewer broom snakeweed seedlings emerged after these same spring fires than summer fires, which brings into question, what is the optimal burning time for long-lasting broom snakeweed control? Our recommended conditions for burning blue gramma grasslands in central New Mexico (McDaniel et al. 1997) includes air temperatures from 22°C, relative humidity 10–20%, soil moisture 3–10%, and pre-burn fine-fuel moisture below 15%. The fine-fuel should be uniformly distributed and exceed 500 kg ha^{-1}. Obtaining these prescribed conditions was difficult on our study area at all times of the year. However, we believe these conditions, irrespective of burning time, are capable of maximizing both broom snakeweed control while lowering the risk of seedling emergence after fire.

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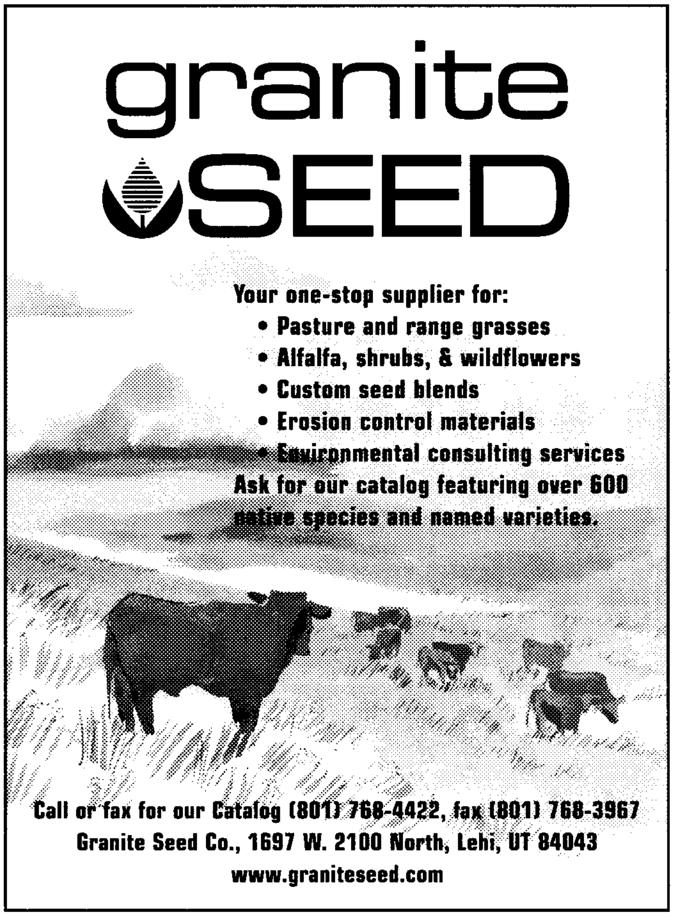


Book Reviews

The Politics of Ecosystem Management. By Hanna J. Cortner and Margaret A. Moore. 1999. Island Press, Washington, DC, and Covelo, California. 1979 p. US$25.00 paper. ISBN 1-55963-672-6.

How should ecosystems be managed so that such systems are ecologically sustainable in the long run? This is the central question that is studied in this book. The authors use the book's 8 chapters to analyze the above question in detail. Rather than provide a tedious chapter by chapter review, in what follows, I shall assess the contents of chapters 1, 2, 5, 7, and 8. These chapters are interesting, and contain some of the more thought-provoking ideas of this book. As such, a focus on these 5 chapters should provide the reader with a good idea of the intellectual contributions of *The Politics of Ecosystem Management.*

Chapter 1 studies the connections between politics and ecological approaches to resource management. To their credit, the authors clearly state that the "way society chooses to deal with its public problems...will necessarily shape how ecosystem management fares in the next century" (p. 6). Moreover, this chapter notes that a key aspect of ecosystem management consists of the maintenance of the resilience of ecosystem structures and processes. Now, the term "resilience" has 2 meanings in ecology, the first due to C.S. Holling and the second due to S.L. Pimm (see the paper by C.S. Holling et al. in the 1995 book *Biodiversity Loss: Economic and Ecological Issues*). Which meaning do the authors have in mind? We're not quite sure because parts of the book suggest the Holling meaning, other parts suggest the Pimm meaning, and the authors never explain exactly what they mean by resilience. This omission has the unfortunate effect of muddying some of the subsequent discussion about ecosystem management.

With the recent history of U.S. resource management in the background, Chapter 2 studies the shift toward what the authors call "ecosystem management." This chapter makes 2 salient points. First, the authors point out that in recent times, "public involvement policies have resulted in a politics of interest, creating an adversarial style of public involvement in resource management dominated by national interest groups" (p. 28). Second, on the basis of this point, the authors conclude that the typical American's view of what ecosystems are, and ought to be, appears to be undergoing a fundamental shift towards a more holistic perspective.

The philosophical underpinning of ecosystem management is the subject of Chapter 5. After discussing the thinking of the Enlightenment Era, this chapter argues with some justification that Enlightenment thinking has had 4 negative effects on modern society. These effects include an emphasis on human control over nature, a narrow conception of reason, the definition of science as positivism, and the subjugation of humans by humans. In particular, as far as the definition of science as positivism is concerned, the authors note that "positivism not only....served as a tool for the mastery of nature, but....also limited the nature of scientific inquiry to preconceived categories and principles" (p. 79).

These observations are fine, but in their call for changes in the nature of scientific inquiry, the authors occasionally let their zeal get the better of them. For instance, they call for the creation of a "civic science" that "addresses the paradox of expert versus open decision making by encouraging citizens to serve as lay scientists" (p. 84). Can one implement this kind of a scheme to better serve the goal of ecologically sustainable resource management? Second, if citizens are able to serve effectively as lay scientists, then why not dispense with experts and the attendant "expert culture" altogether? These issues are inadequately addressed by the authors.

With the goal of ecological sustainability in mind, Chapter 7 focuses on the enhancement of governmental performance and democratic values. The authors note that a reexamination of extant laws, a rethinking of the notion of property rights, altering a number of administrative organizations, and an alignment of market operations will be necessary to achieve the ultimate goal of sustainability. Although this chapter makes a number of useful points, it also raises several questions. Here are 3 examples. First, it is now well known (see the paper by M. Common and C. Perrings in *Ecological Economics*, 1992, Vol. 6, pp. 7–34) that ecosystems—or more generally ecological-economic systems—are jointly determined. As such, it is unclear why the authors focus exclusively on ecological sustainability and not on the sustainability of the joint system.

Second, the chapter says that integrating "the goal of ecological sustainability into economic approaches....can do much to resolve the paradoxes of sustainability by avoiding the inadequacies of traditional economic conventions" (p. 127). Does this mean that an ecosystem manager's objective should be attainment of ecological sustainability with economic activities affecting the manager's task as constraints? Or, does this mean that an ecosystem manager should place equal weight on the ecological and the economic aspect of the management problem? The authors do not provide clear answers to these questions.

Finally, a key issue in ecosystem management concerns the ability of our political and other institutions to deal with issues that arise once one adopts a multidisciplinary approach to the task of managing ecosystems. For instance, consider the issue of the substitutability between different kinds of natural capital. The study of this kind of substitutability is important in ecosystem management for at least 2 reasons. First, knowledge of the substitutability between different kinds of natural capital is essential for making prudent species conservation decisions. Second, a knowledge of this kind of substitutability is helpful in valuing the stock of, say a nation's natural capital. In turn, this valuation exercise is useful (see the paper by K.G. Maler in Environmental and Resource Economics, 1991, Vol. 1, pp. 1–15) in correctly computing this nation's net national product (NNP). Very little is known about how existing political institutions would cope with this kind of substitutability issue. Consequently, the authors should have provided a much more expansive discussion of these kinds of management issues that arise in a multidisciplinary context.

In Chapter 8, the authors speculate on the future of ecosystem management. In the course of their speculations, they make 2 significant points. First, we are rightly told that if "ecological sustainability is to assume a dominant position in natural resource management, [then] American society must embrace sweeping and profound changes...." (p. 139). Second, the authors remind us that short-term economic gains may well have to be sacrificed to protect biodiversity or prevent degradation of the reproductive capability of land or waters" (p. 140). Unfortunately, the clarity of these 2 points is muddied a little by the multiple meanings that the authors attach to the notion of sustainability. The greater part of this book focuses on the notion of ecological sustainability. However, in this last chapter, in addition to the notion of ecological sustainability, we are introduced to the notions of democratic sustainability (p. 136) and social sustainability (p. 137). Parsimony in attaching meaning to the notion of sustainability would have better served the authors in their call for a more integrated and inclusive approach to ecosystem management.

Although it is not possible to heap unqualified praise on *The Politics of Ecosystem Management*, the book contains much to be enthusiastic about. Consequently, it seems appropriate to conclude by noting that most of this book is worth your time.—*Amitrajeet A. Batabyal*, Utah State University, Logan, Utah.

Carbon and Nutrient Dynamics in Natural and Agricultural Tropical Ecosystcms. Edited by L. Bergström and I.I. Kirchmann, with numerous text contributors. 1998. Oxford University Press, 198 Madison Avenue, New York, NY 10016-4314, USA. Cabinao@cabi.org. US$90.00 cloth. ISBN 0-85199-2188.

This book was writtcn following a symposium held in Zimbabwe to acknowledge a 10-year celebration of a *Soil Biology and Fertility* project in that country. Those who attended included project workers, tropical soil fertility scientists and guest researchers. All of these participants held the view that declining soil fertility is a serious problem not only in Africa but also in other tropical regions around the world. A major theme of the symposium was therefore to find ways to minimize this problem. The book includes 5 major topics, each of which is comprised of subtopics, and an index,

Part I reminds readers of the nutrient dynamics in soils. Authors in this section looked examined soil organic matter (SOM) turnover when different types of land management are applied for various tropical ecosystems. Since legumes are important in tropical soil fertility, their relationships to N release, soil plundering and soil organic matter (SOM) dynamics were explored. Not surprising, some legume litters readily provide nitrogen for crops, whereas those rich in tannins may hinder nitrogen uptake. Parallel to this mechanism is plant residue decomposition. In animal-based systems such as improved grass-legume tropical pastures, legumes provide aboveground litter/manure recycling that contributes to the SOM build-up. With increases in SOM there would be higher rates of carbon turnover, which lead to increased activity of soil fauna, and to soil aggregation. Land use practices such as deforestation and long-term cultivation of tropical soils lead to reduced levels of SOM, which impact aggregate stability by increasing the dispersion of clays in water.

Part II deals with crop residue decomposition. Authors in this section discussed some low-input means for soil fertility management based on locally available biological resources. Incorporating high quality tree prunings, nitrogen-15-labeled maize residues in Zimbabwean soils increased maize yields due to improvements in nitrogen availability and uptake. Similarly, the use of coffee husks in Ugandan banana production resulted in substantial increases in banana yields. Thus, litter and crop residues represent valuable organic resources for small-scale African farmers who cannot afford to use industrial fertilizers. Equally important is the quality of such plant residues because of their influence on residue decomposition and nutrient release.

Part III examined tree-soil-crop interactions in agroforestry systems. Influence of the canopy on understory vegetation and soils was reviewed from a low-cost and low-technology agricultural systems perspective. The studies illustrated that trees and shrubs in arid areas may improve soil fertility of soils below their crowns. Others found that rain and sunlight are intercepted by woody vegetation, minimizing their impact on the soil beneath tree/shrub canopies. As tree/shrub canopies and other characteristics are likely to change, however, ecosystem and landscape level changes are questionable, requiring more studies that would also consider global climate change. Models can provide useful tools for understanding the functioning of agroforestry systems, not just at a specific location or ecoregion, but also for other areas.

Part IV of the book dealt with ecosystem dynamics. Authors in this section compared natural ecosystems and agroecosystems, focusing on carbon (C) and the best ways to achieve nitrogen management practices. When natural vegetation replaced by crops, soil organic matter usually declines. Differences in C occurred within 5 cm of the topsoil, maize fields having 50% less soil organic C than adjacent natural woodland. Even though the soil fauna density, biomass, and diversity were higher in natural systems, spatial variability resulted in lower C in the woodlands than in maize fields. A simulation study that assessed N uptake and leaching in maize fields resulted in reduced N uptake, which reflected soil-water stress in low rainfall seasons.

Part V, which is the final chapter of the book, discussed the present and future of agriculture in the tropics. In the final remarks, the authors provided information on investigating and managing soil fertility in Africa, an analytical framework for land use change, and the soil biology and fertility research outlook.

This book is a valuable resource for soil scientists, agronomists, students and ecologists with interest primarily in tropical soil biology and fertility. Also, it will be of interest to policy-makers in natural resource management. *T. Mbabaliye*, Washington State University, Pullman, Washington.

The Pheasants of the World. Biology and Natural History. Second edition. By Paul A. Johnsgard. 1999. Smithsonian Institution Press, Washington D.C. 398 p. US$50.00 cloth. ISBN 1-56098-839-8.

Last week while driving to my office I heard on the radio news that Washington State was considering ending the fall ring-necked pheasant season early because of low populations of pheasants reported in several areas where their populations are normally high. Sparse cover and wet winter and spring weather, not to mention hunters, can be tough on pheasants in eastern Washington, but I hadn't noticed any particular shortage of pheasants this year following last year's mild winter. And I tend to notice pheasants, because some of my earliest memories are of my father making a living, one might say, raising game birds, especially ring-necked pheasants, for our commercial hunting and fishing preserve in northeastern Ohio. So the second edition of Paul A. Johnsgard's *The Pheasants of the World* recalled personal history beyond its technical edification.

Long a prolific writer of technical, semi-technical and popular books on natural history, Paul Johnsgard has, in this revised second edition, contributed a significant review of the Old World family *Phasianidae.* This edition updates the first edition published over 15 years ago. Recent research on pheasants has come from research institutions, captive breeding programs, and from commercial and hobbyist breeders of these birds. Dr. Johnsgard has utilized all of these sources.

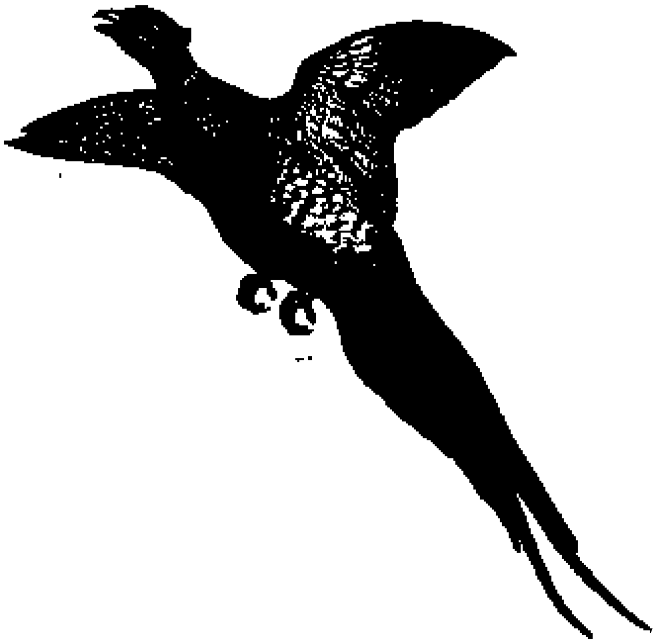
The Pheasants of the World consists of 2 main sections. Part 1 consists of 8 short chapters covering general ecological topics of the pheasant family including taxonomy, hybridization, growth and development, individual and social behaviors, ecology and population biology, mating behavior and social signaling, reproductive biology, and aviculture and conservation. The discussions here are succinctly semi-technical, but within these 83 pages are found some interesting tabular data, (much of it from the 1940's–1980's), and ultimately, general coverage of pheasant biology and ecology.

Part 2 of the book consists of taxonomic keys, and of species descriptions arranged by genus. Individual species descriptions include varying topics such as other vernacular names, species distributions, descriptions of subspecies, identification features, measurements, habitats, predators, behaviors, avicultural traits, and population status and conservation outlook. Descriptions for some species, such as the common or ring-necked pheasant (*Phasianus colchicus*) are more detailed, while those for some of the more obscure species are predictably shorter. Many of the 49 species descriptions include hand-drawn illustrations, most by the author. While all pheasants are exotic to the Western Hemisphere, some are long-introduced species (e.g. golden pheasant), while others are still largely indigenous to their Asian areas of origin. Dr. Johnsgard's book includes an appendix of derivations of scientific and vernacular names, an extensive bibliography, and a detailed general index.

As its title and content might suggest, *The Pheasants of the World* is better characertized as a review of the *Phasianidae* than as any kind of synthesis. Beyond review of the strikingly ornamental pheasants, the book offers little thermatic message, other than a pensively analytical ambivalence toward captive breeding by zoos and its role in species preservation. Stylistically, the text has the flavor of a review, with abundant, although rarely excessive, citations of literature, and straightforward, scientific narrative. Combination of these features yields a readable reference.

More colorful than the text is section of glossy plates including half- and full-age photographs of living birds and some full-page 19th Century colored plates by Joseph Wolf, both with minimal captions. These plates add much to the book for the casual reader, but *The Pheasants of the World* will be reference interest to scientists and students, and would seem a must for avicultural hobbyists as well. The book offers much scope and considerable depth to amateur bird breeders, especially to those who specialize in the less common exotic species, individuals who are usually far outside the purview of those who try to commercially raise ring-necked pheasants.

I haven't heard whether Washington State has decided to shorten the ring-necked pheasant season this year. Poor pheasants. Introduced into marginal exotic habitats full of hunters, they often seem to have a rough go of it, and so, for that matter, do some people who raise them for a living. Both certainly, have their pleasant moments, but *pleasant* and *pheasant* are a letter away from *peasant*, simple spelling deletions that, like surviving commercial pheasant farming, are easily accomplished. It is all just a matter of getting the *h* and *l* out.—*David L. Scarnecchia,* Washington State University, Pullman, Washington.



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