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The Trail Boss

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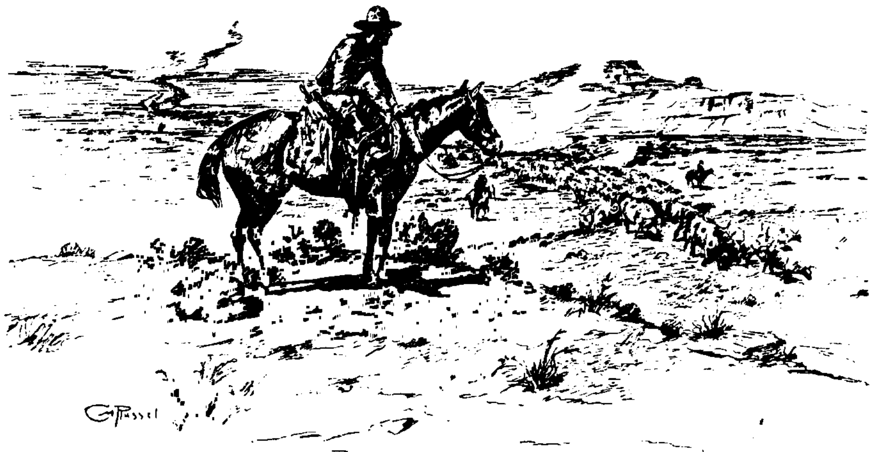

THE TRAIL BOSS

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Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range

ROBERT P. GIBBENS AND RELDON F. BECK

Abstract

Between 1915 and 1932, permanent 1 × 1-m quadrats were established on grasslands of the Jornada Experimental Range in southern New Mexico. Quadrat records accumulated from 1915 to 1979 on grasslands dominated by black grama [*Bouteloua eriopoda* (Torr.) Torr.], poverty threeawn (*Aristida divaricata* Willd.), tobosa [*Hilaria mutica* (Buckl.) Benth.], and burrograss (*Scleropogon brevifolius* Phil.) were used to examine changes in perennial grass basal area and forb densities. Quadrats originally dominated by black grama had large reductions in basal area during droughts, and basal area increased slowly following droughts. By 1979, black grama no longer occurred on 77% of the quadrats. Quadrats originally dominated by poverty threeawn changed to a mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) type. Perennial grass basal area on quadrats dominated by tobosa and burrograss decreased during droughts, but recovery was relatively rapid. Antecedent precipitation was associated with only 10 to 38% of the variation in perennial grass basal area. Perennial forb densities were low and fluctuated among years in all types. Annual forbs and grasses displayed large fluctuations in densities among years. The necessity of basing management of Chihuahuan Desert ranges on the perennial grass component is borne out by the low densities of palatable perennial forbs, and the extreme fluctuation and unpredictability in densities of annual forbs and grasses.

Key Words: black grama, poverty threeawn, tobosa, burrograss, arid rangeland

Striking changes have occurred in former grasslands of the northern Chihuahuan Desert. The most obvious and best documented change has been the widespread encroachment of shrubs into former grassland areas (Buffington and Herbel 1965, York and Dick-Peddie 1969). Few areas remain that can be classified as grassland, and Küchler's (1964) classification as shrub-steppe is appropriate for most rangelands of the region. The original grassland types still occur but have been reduced in area, and dominance is often shared with shrubs.

Permanent quadrats, charted on a yearly basis, were once widely used to follow vegetation dynamics in grasslands (Weaver and Albertson 1944, Albertson and Tomanek 1965). Beginning in 1915, permanent quadrats were established on the Jornada Experimental Range in southern New Mexico. Data from these quadrats were the base for evaluating vegetation changes caused by grazing and climatic fluctuations (Nelson 1934, Paulsen and Ares 1962). These quadrat data also furnished a base for determining demographic characteristics of grasses (Wright and Van Dyne 1976, 1981; Gross 1984) as well as other species (Dittberner 1971).

The purpose of this study was to examine changes in grass basal area and forb numbers that have occurred in 4 grassland types during a 64-year period, 1915 to 1979.

Materials and Methods

This study was conducted on the Jornada Experimental Range 37 km north of Las Cruces, New Mexico. The 78,266-ha Experimental Range lies principally on undulating plains of the closed Jornada basin. Average elevation of the plains is near 1,260 m. On the east, the Experimental Range extends to the crest (2,833 m) of the San Andres mountains. Mean monthly maximum temperatures are highest in June (36° C) and lowest in January (13° C). Long-term average annual precipitation is 230 mm with 52% occurring in July, August, and September. Summer precipitation is mostly from high intensity, short duration, convective storms covering small areas. Winter precipitation comes from low intensity frontal storms covering broad areas. Snow is infrequent. The frost-free period averages 200 days, but the effective growing season, when soil water and temperature are favorable, is often 90 days or less.

The Jornada Experimental Range was established in 1912 and placed under the administration of the Bureau of Plant Industry. In 1915 it was transferred to the U.S. Forest Service and has been operated by the Agricultural Research Service since 1954 (Ares 1974). In 1915, 34 permanently marked, 1 × 1-m quadrats were established and charted. Additional quadrats (including only those where markers still exist) were established in 1916 (8), 1919 (14), 1921 (3), 1924 (2), 1926 (17), 1929 (2), 1931 (1), and 1932 (2), total (104). A decimeter grid was used to chart the quadrats until 1925 and a pantograph was used thereafter (Campbell 1931). Grass basal area was determined by counting squares (equivalent to 1/10,000 m) on the grid paper used in charting or, in later years, with a planimeter. With few exceptions, all quadrats were charted each year until 1947. After 1947, only a portion of the quadrats were charted each year, resulting in discontinuous records for individual quadrats. Charting was discontinued in 1979.

Besides grass basal area, species and numbers of forbs present on the quadrats were recorded. The forb density data must be viewed with caution because the quadrats were usually sampled in September, October, November, or even December, when probably some forbs had dehised, or palatable forbs had been bitten off by livestock, rabbits, or rodents. It was possible to determine the total number of species recorded for each quadrat sampling because notations like "unidentified perennial forb A" were used for unidentified species. In the 64 years, there were only 168 individuals for which no designation as to annual or perennial forb was given. These were not included in density calculations. We believe the forb numbers were determined with enough precision to allow relative comparisons among years and grassland types.

Quadrat locations were carefully selected to represent average species composition in the major grassland types and were usually placed at 0.8-km intervals along lines radiating from permanent watering points (Nelson 1934). Quadrats were placed on grasslands dominated by black grama [*Bouteloua eriopoda* (Torr.) Torr.] (57 quadrats), tobosa [*Hilaria mutica* (Buckl.) Benth.] (22 quadrats), burrograss (*Scleropogon brevifolius* Phil.) (12 quadrats), poverty threeawn (*Aristida divaricata* Willd.) (6 quadrats), and blue grama [*Bouteloua gracilis* (H.B.K.) Griffiths] (6 quadrats). A single quadrat was on a gypsiferous area dominated by gypgrass (*Sporobolus nealleyi* Vasey). Because the quadrats in the blue grama type and the gypgrass quadrat were charted infrequently after 1947, they will

Authors are range scientist, Jornada Experimental Range, USDA, Agricultural Research Service, Las Cruces, New Mexico; and professor, Animal and Range Sciences Department, New Mexico State University, Las Cruces.
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not be discussed. Quadrats representing the black grama and poverty threeawn types are located primarily on shallow (30 cm) sandy loams (Simona series) underlain by an indurated caliche layer or on deep (to 152 cm) loamy sands (Wink and Onite series). The tobosa type is found primarily on deep (>152 cm) clay loams (Reagan series), and the burrograss type on deep, fine sandy loams (Dona Ana series) (Bullock and Neher 1980).

Precipitation records are from the centrally located Experimental Range Headquarters. Precipitation is reported on a crop year basis, i.e., crop year precipitation for 1916 is from 1 Oct. 1915 to 30 Sep. 1916. Correlation and regression techniques were used to examine relationships between precipitation and grass basal area and forb numbers. Regressions with precipitation were done on an accumulative basis with a separate regression performed for each accumulation, e.g., grass basal area in a given year was examined in relation to precipitation in September of that year, then with September plus August precipitation, then with September plus August plus July precipitation, etc., until 48 preceding months of precipitation were added. Only those regression coefficients associated with the maximum coefficient of determination (R^2) were tested for significance ($P<0.05$).

Plant nomenclature follows Correll and Johnston (1970).

Results and Discussion

Black Grama Type

The early quadrat records (1915–1925) show a relatively low black grama basal area (Fig. 1). Contemporaneous reports (e.g., Jardine and Forsling 1922, Nelson 1934) attribute the low basal area to unfavorable rainfall patterns. Also, it is likely that livestock grazing, which was proper according to the concepts of the times but would be rated as heavy today, contributed to the relatively low basal area. An early grazing strategy on the Experimental Range was to reduce grazing of the black grama type during the growing season (July–September) and reserve the forage for the dry spring months (March–June) (Jardine and Hurtt 1917).

During the 1926 to 1934 period, there was a large increase in black grama basal area, reflecting relatively more favorable rainfall patterns (Fig. 1). However, the severe drought of 1934 resulted in a sharp decrease in black grama basal area. Canfield (1939) found no new growth in 1934 on any of the black grama quadrats he was studying on the Experimental Range. By 1935 average basal area of black grama on the 57 quadrats was only 3.1%, compared to the high of 9.6% attained in 1932. Paulsen and Ares (1962) found black grama basal area was reduced to about the same level during dry years, irrespective of grazing intensity or amount of antecedent basal area. Black grama and other perennial grasses partially recovered from the 1934 drought by 1936, and basal area was relatively stable until 1947. Another severe drought occurred in 1948 and again perennial grass basal area was sharply reduced (Fig. 1). Relatively high rainfall in 1949 and 1950 resulted in a small increase in basal area, but the severe drought of the 1950s reduced perennial grass basal area to very low levels. The drought of the 1950s is believed to be the most severe in the Southwest in the past 350 years (McDonald 1956, Schulman 1956). Herbel et al. (1972) found the reduction in black grama during the 1950s was greatest on deeper soils and least on shallow soils underlain with impervious caliche layers. They hypothesized the caliche layer prevented deep percolation, holding water within reach of plant roots.

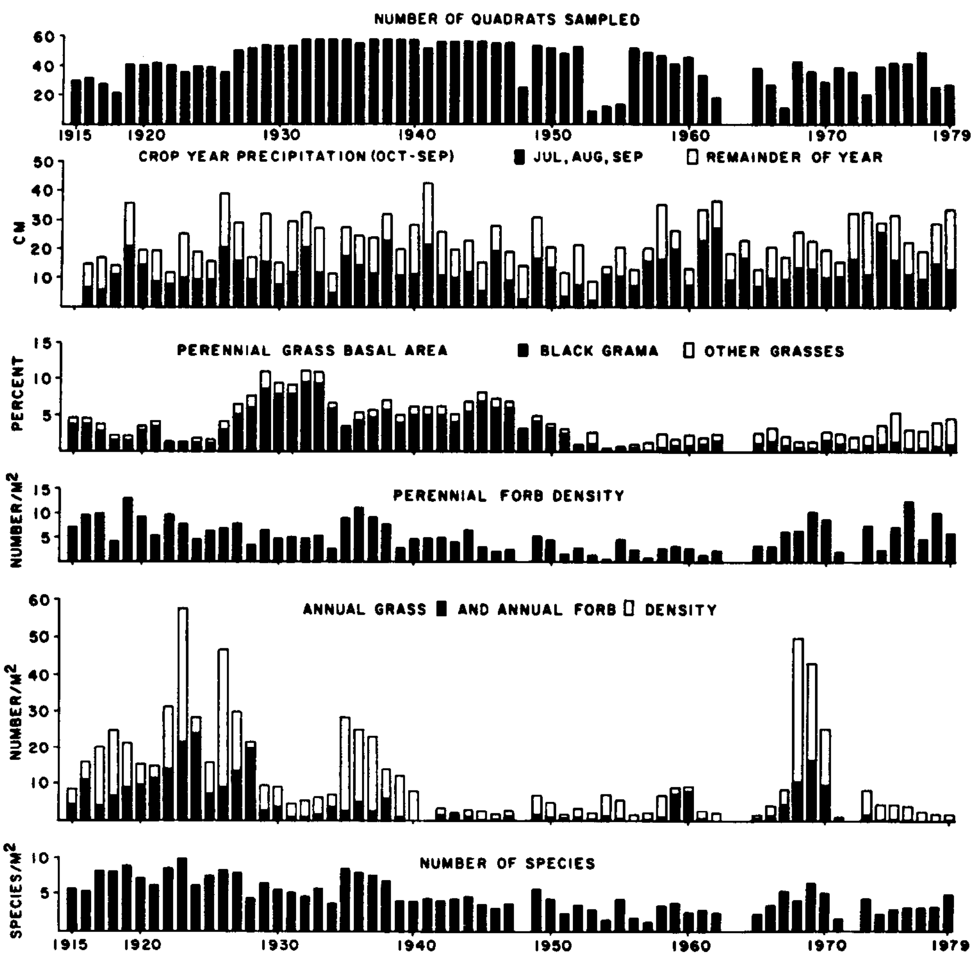

Fig. 1. *Number of quadrats sampled, crop-year precipitation, perennial grass basal area, perennial and annual plant densities, and number of species for the black grama type. Forbs were not counted in 1948 and 1972.*

Following the drought of the 1950s black grama basal area did not increase to former levels. Also, the proportion of basal area contributed by other perennial grasses increased (Fig. 1). The areas around the 57 quadrats were vegetated by a population of black grama plants originally; however, by 1979 there was a large decrease in areas with black grama. Black grama disappeared from 1 quadrat in each of the following years: 1934, 1935, 1939, 1942, 1944, and 1946. Following the dry 1948 season, black grama was lost from 3 more quadrats by 1950. During the severe drought of 1951–56 black grama disappeared from 26 quadrats and by 1961 did not occur on 9 additional quadrats. Thus, black grama no longer occurs on 44 quadrats, or 77% of the original sites. By 1981, shrubs were dominant on 24 (42%) of the quadrat sites (Gibbens and Beck 1987).

There was a small subset (6) of quadrats, established in 1915, where black grama persisted for 64 years. Black grama basal area on this subset of quadrats is similar to that portrayed in Figure 1. Average black grama basal area on the 6 quadrats was 4.0% in 1915. Basal area decreased during the 1920s but then increased to a high of 14.2% in 1932. Following the drought of 1934, basal area decreased to 5.9% in 1936, then increased to 10.4% by 1945. Black grama basal area was 2.1% in 1956, 6.0% in 1965, and 3.0% in 1977, the last year all 6 of the quadrats were sampled. Thus, a population of quadrats continuously occupied by black grama shows basal area changes reflecting climatic patterns. The widely separated quadrats have no readily apparent common factor to account for the survival of black grama.

Regression of total perennial grass basal area upon preceding accumulated precipitation revealed a maximum R^2 of 0.26 at 44 months, and the regression coefficient was significant ($P<0.001$). The low R^2 means that accumulated precipitation is not a good predictor of basal area, but is associated with 26% of the variation in basal area. Log transformations of data did not improve correlations of basal area and precipitation. Also, no improvement was found when only the subset of quadrats in which black grama persisted was examined. One reason for the low correlations with precipitation is the variability in basal area response within a given year. For example, in 1931 there were increases in black grama basal area on 24 quadrats and decreases in basal area on 26 quadrats. Between 1916 and 1950 there were only 2 years, 1928 and 1948, when all quadrats showed a consistent response (decrease) in black grama basal area.

Seven quadrats were established within livestock exclosures on the black grama type. Clipping studies have shown black grama is sensitive to degree and timing of defoliation, and basal area and reproductive potential (stolon and stoloniferous culm production) can be adversely affected by high rates of defoliation (Canfield 1939, Miller and Donart 1979). However, long-term changes in perennial grass basal area on the 7 protected quadrats were similar to those on quadrats that were grazed.

Neilson (1986), taking into account global climate patterns, analyzed long-term monthly weather records from Las Cruces, N.M. He hypothesized that the pristine black grama grasslands were established under and adapted to "little ice age" type climate and are only marginally adapted to the present, warmer climate. He contends that, with variable but consistent summer rains, the pattern of winter precipitation becomes critical in establishment of perennial life forms with warm-season (usually C_4) grasses favored

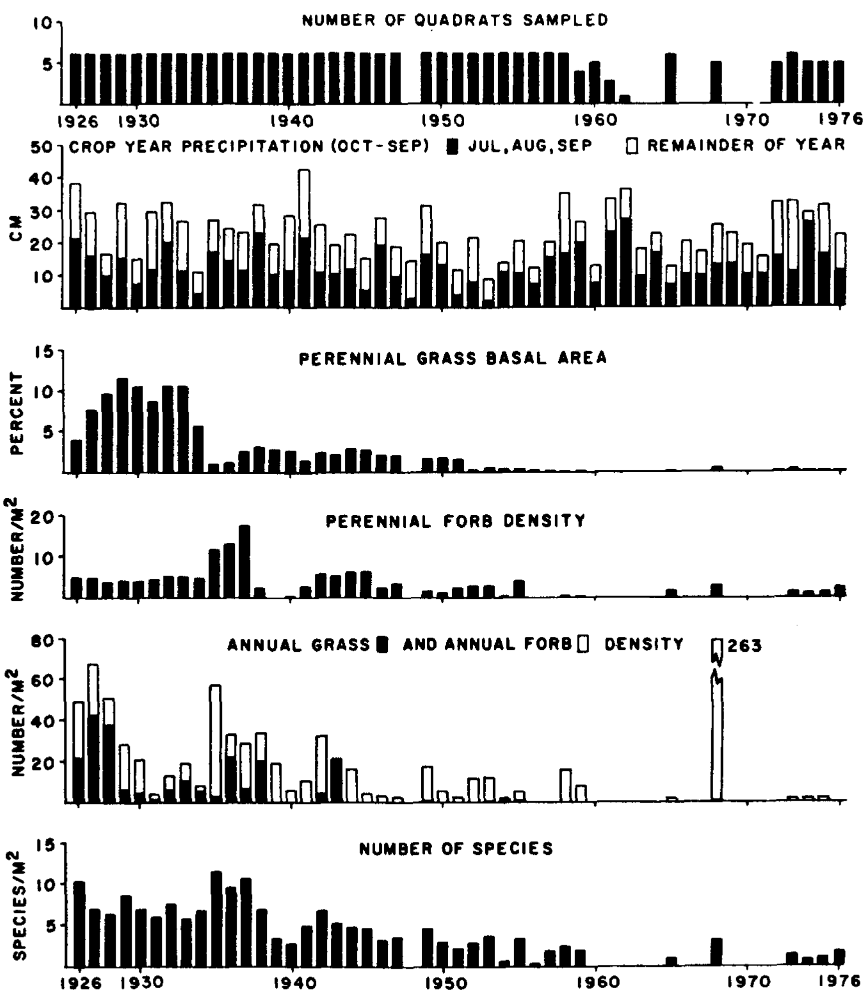

Fig. 2. *Number of quadrats sampled, crop-year precipitation, perennial grass basal area, perennial and annual plant densities, and number of species for the poverty threeawn type. Forbs were not counted in 1972.*

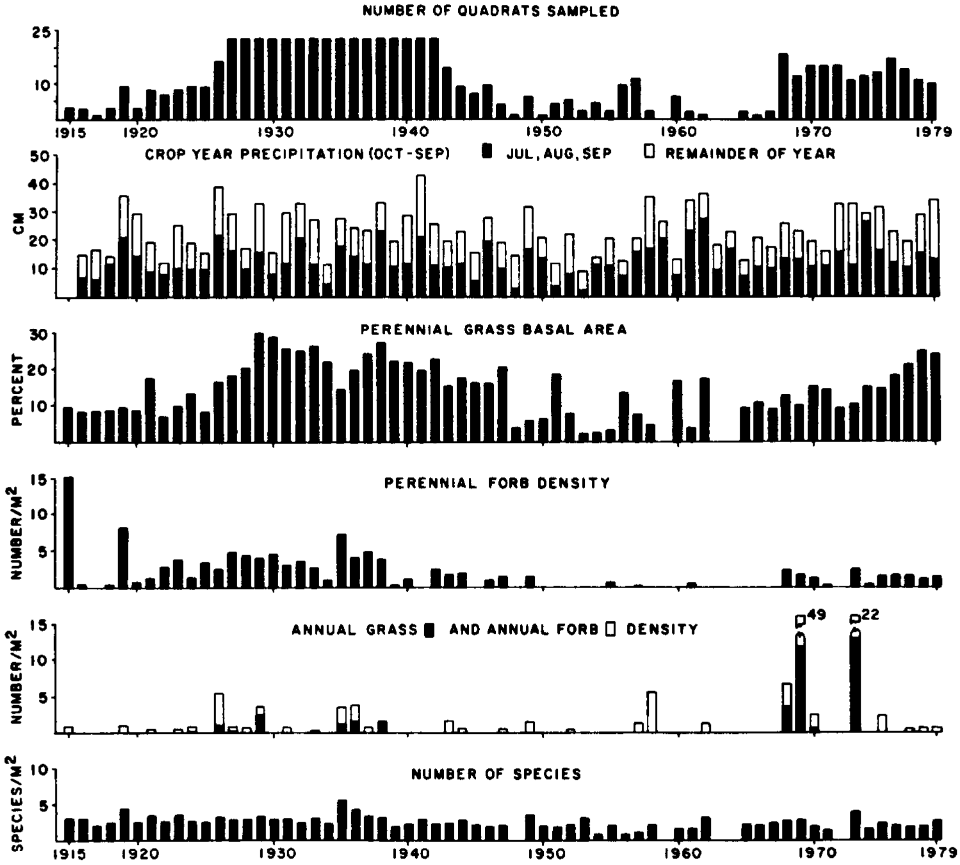

Fig. 3. *Number of quadrats sampled, crop-year precipitation, perennial grass basal area, perennial and annual plant densities, and number of species for the tobosa type. Forbs were not counted in 1948 and 1972.*

if winters are dry and cool-season (usually C_3) shrubs favored if winters are wet. He found periods of persistent interannual winter rainfall in the 1930s and following 1940 which coincided with periods of shrub establishment. Neilson's hypothesis is plausible and the quadrat records show that sexual reproduction (seedlings) of black grama is rare.

Perennial forb density fluctuated during the 64-year period but, unlike black grama basal area, the density of perennial forbs appeared to return to former levels following the drought of the 1950s. The same species of perennial forbs were encountered throughout the 64-year period. The species that were most frequent (based on all quadrat samplings) and most abundant (total number of individuals recorded) were the suffrutescent broom snakeweed [*Xanthocephalum sarothrae* (Pursh) Shinners], leatherweed croton [*Croton pottsii* (Kl.) Muell. var. *pottsii*], silverleaf nightshade (*Solanum elaeagnifolium* Cav.), two-leaved senna (*Cassia bauhinioides* Gray), trailing allionia (*Allionia incarnata* L.), and woolly paperflower [*Psilostrophe tagetina* (Nutt.) Greene].

The density of annual grasses and forbs was extremely variable among years (Fig. 1). Both annual grasses and annual forbs were characterized by years of low density and by years of what might be termed superabundance. Annual forbs were superabundant in 1924, 1927, 1936, 1937, 1938, 1968, 1969, and 1970. Annual grasses were most abundant in 1924, 1925, 1929, and 1969. Because amount and timing of rainfall are critical in the development of annual plant populations (Went 1948, 1949; Beatley 1974; Kemp 1983), one can expect little correlation between annual plant density and yearly precipitation amounts. Also, different species were most abundant in different years of superabundance, indicating a relatively wide range in optimum conditions for the various species. The most frequent and abundant annual grasses were sixweeks grama (*Bouteloua barbata* Lag.), needle grama [*Bouteloua aristidoides* (H.B.K.) Griseb.], and sixweeks threeawn (*Aristida adscensionis* L.). The most frequent and abundant annual forbs included lemon weed (*Pectis* spp.), dwarfpea (*Astragalus nuttallianus* A. DC.), purple rollleaf (*Nama hispidum* Gray), Russian thistle (*Salsola kali* L.), annual purslanes (*Portulaca* spp.), wooly tidestromia [*Tidestromia lanuginosa* (Nutt.) Standl.], and annual buckwheats (*Eriogonum* spp.).

Species richness (average number of species per quadrat) was highest in those years when annual plants were most abundant (Fig. 1). Species richness was lower during drought years. Species richness appeared to decrease during the 64-year period, but the discontinuous sampling of quadrats during the 1960s and 1970s makes verification impossible.

There were no significant regression coefficients for annual forb numbers and accumulated preceding precipitation. A significant regression coefficient ($P<0.05$) occurred between perennial forb numbers and 14 months of accumulated precipitation. However, the R^2 of 0.08 means a small percentage of the fluctuation in perennial forb numbers is associated with accumulated preceding precipitation.

Poverty Threeawn Type

Six quadrats (Fig. 2) were established in the poverty threeawn type in 1926, one of which was protected from livestock grazing. Small amounts of black grama occurred on 4 of the 6 quadrats. Threeawns are generally considered as secondary species in the black grama type (Paulsen and Ares 1962), but can be dominant on small areas.

Total perennial grass basal area increased to a high of 10.6% in 1932 (Fig. 2). The drought of 1934 caused a sharp reduction in basal area, which was only 1.0% in 1935. Although there was some increase in basal area after 1936, the dry 1948 season and the drought of the 1950s caused perennial grass basal area to decrease to less than 1.0%. No poverty threeawn occurred on the quadrats after 1952 and no black grama after 1958. The small amounts of perennial grass basal area present in the 1960s and 1970s were contributed by mesa dropseed [*Sporobolus flexuosus* (Thurb.) Rydb.] and fluffgrass [*Erioneuron pulchellum* (H.B.K.) Tateoka]. Besides droughts, a primary cause of the decrease in perennial grass area was the invasion of mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) and the formation of mesquite dunes, which now dominate the area where the quadrats are located, including the quadrat site protected from livestock. Norris (1950) concluded from exclusion studies that rabbits and rodents, or even rodents alone, exert enough grazing pressure in mesquite dominated areas to prevent improvement in cover of grasses and forbs.

Regression of total perennial grass basal area upon preceding accumulated rainfall showed a maximum R^2 (0.10) at 48 months, and the regression coefficient was significant ($P<0.05$). Separate regressions were calculated using only data from the years 1926–1947, when records were most complete, but there was no improvement in R^2 values.

There was little variation in perennial forb density from 1926 to 1934, with density ranging from 3.8 to 5.1 individuals per quadrat. Coincidental with the sharp decrease in grass basal cover in 1935, perennial forb density increased to a high of 17.7 individuals per m^2 in 1937 (Fig. 2). However, perennial forb density decreased sharply in 1938 and no forbs were recorded in 1939. In the early 1940s perennial forbs reached densities equal to those of the 1920s but the drought of the 1950s reduced densities to low levels, and records from the late 1970s indicate densities have remained low. The most frequent and abundant perennial forbs included rushpeas (*Hoffmanseggia* spp.), broom snakeweed and euphorbias (*Euphorbia* spp.).

Numbers of annual grasses and forbs fluctuated widely among years, even when perennial grass basal area was high (Fig. 2). Annual grasses were particularly abundant in 1927 and 1928, while annual forbs reached superabundance levels in 1935 and 1968. The most frequent and abundant annual grasses were sixweeks grama, needle grama and sixweeks threeawn. Annual forbs with high frequency and abundance included purslanes, purple rollleaf, desert baileya (*Baileya multiradiata* Harv. & Gray), threadstem carpet-weed [*Mollugo cerviana* (L.) Ser.], and buckwheats.

There was a definite decline in species richness from 1926 to 1979 (Fig. 2). This reflects the decline in numbers of both annuals and perennials, and indicates that the establishment of mesquite and the formation of dunes resulted in a depauperate flora. It is quite likely rodents, which are more abundant in the mesquite dune type than any other type on the Jornada plain (Wood 1969), contributed to the decline in number of species.

There were no significant relationships between accumulated precipitation and either annual or perennial forb numbers.

Tobosa Type

The tobosa type usually occurs on heavy soils in low-lying areas that receive some run-in water from overland flows (Herbel and Giles 1973). Five of the 22 quadrats in the tobosa type were on sites where tobosa was the only perennial grass. On the other quadrats, burrograss, ear muhly (*Muhlenbergia arenacea* Buckl.), alkali sacaton [*Sporobolus airoides* (Torr.) Torr.], and vine mesquite (*Panicum obtusum* H.B.K.) were found with tobosa, either singly or in various combinations. One of the quadrat sites was within a livestock exclosure. Only 3 quadrats were established in the tobosa type in 1915. These had a perennial grass basal area of 9.2% (Fig. 3). By 1927, when all 22 quadrats in the type had been established, perennial grass basal area was 19.2%. Basal area increased to 30.0% by 1929, but decreased thereafter. A sharp decrease in basal area occurred in 1935, following the drought of 1934. By 1938 basal area had returned to predrought levels, but declined somewhat in subsequent years. It is difficult to judge the effect of the drought of the 1950s from the average basal areas shown in Figure 3 because basal area appears to be a function of which of the original 22 quadrats were sampled in any 1 year. Also, which quadrats received run-in water in any given year is not known. However, using one particular quadrat as an example, tobosa basal area was 33.7% in 1929, 16.3% in 1949, 8.4% in 1952, and 39.0% in 1960. In this case at least, the drought of the 1950s caused a reduction in tobosa basal area but recovery was fairly rapid. Basal area on quadrats sampled in the late 1960s and 1970s indicates a return to amounts of basal area present before the drought of the 1950s. Tobosa remained present on all but 3 of the quadrats and the protected quadrat was one of those from which tobosa disappeared. Shrubs became dominant on 1 quadrat. The quadrat records indicated interpretations of basal area in the tobosa type varied considerably among recorders, and this is believed to contribute to the high variation among years.

Regressions of perennial grass basal area upon accumulated preceding rainfall showed a maximum R^2 of 0.38 at 43 months. The regression coefficient was significant ($P<0.001$).

Perennial forb density in the tobosa type was generally low, and particularly so after the 1950s drought (Fig. 3). The most frequent and abundant forbs included desert holly (*Perezia nana* Grey), broom snakeweed, euphorbias, and globemallows (*Sphaeralcea* spp.). With the exception of the years 1969 and 1973, density of annual grasses and forbs was low in the tobosa type (Fig. 3). Russian thistle, portulacas, dwarfpea, and hairy caltrop or carpet-weed (*Kallstroemia hirsutissima* Vail) were the most frequent and abundant annual forbs. Sixweeks grama, sixweeks threeawn, and annual lovegrass (*Eragrostis* spp.) were the most common annual grasses.

Species richness was low in the tobosa type and remained fairly constant (Fig. 3). The sod-forming tobosa apparently limits the number of species that can coexist.

When forb numbers were regressed upon accumulated precipitation, maximum R^2's occurred at 12 months for both annual (0.08) and perennial forbs (0.09). Regression coefficients were significant ($P<0.05$).

Burrograss Type

Like the tobosa type, burrograss normally occurs on heavy soils in low-lying areas (Paulsen and Ares 1962). Few of the 12 quadrats located in the burrograss type were placed on sites where burrograss was the only perennial grass. Associated grasses included early muhly, tobosa, alkali sacaton, and black grama. One quadrat was within a livestock exclosure. Basal area on the 1 to 6 quadrats sampled from 1915 to 1925 was low, not exceeding 6.5% (Fig. 4). Basal area increased markedly in 1926, a year of high rainfall. Large decreases in basal area occurred in 1934 and 1935 (Fig. 4). By 1938, basal area had increased to pre-drought levels. Basal area was reduced by the drought of the 1950s but was relatively high in comparison to other types throughout the 1950s. Basal area following the 1950s drought varied widely, but high years were equal to or above levels in the 1930s and 1940s (Fig. 4). The stoloniferous habit of burrograss enables this species to spread rapidly in years of favorable rainfall (Campbell 1931). Burrograss remained present on all but 2 of the quadrat sites. Basal cover on the quadrat protected from grazing was similar to that of grazed quadrats. Shrubs became dominant on 1 quadrat.

Regression of basal area upon accumulated precipitation revealed a maximum R^2 (0.38) at 41 months. The regression coefficient was significant ($P<0.001$). As in the other grassland types, more of the variation in basal area is associated with precipitation, if rainfall from the preceding 3–4 year period is considered.

There was a great deal of variation in perennial forb density with

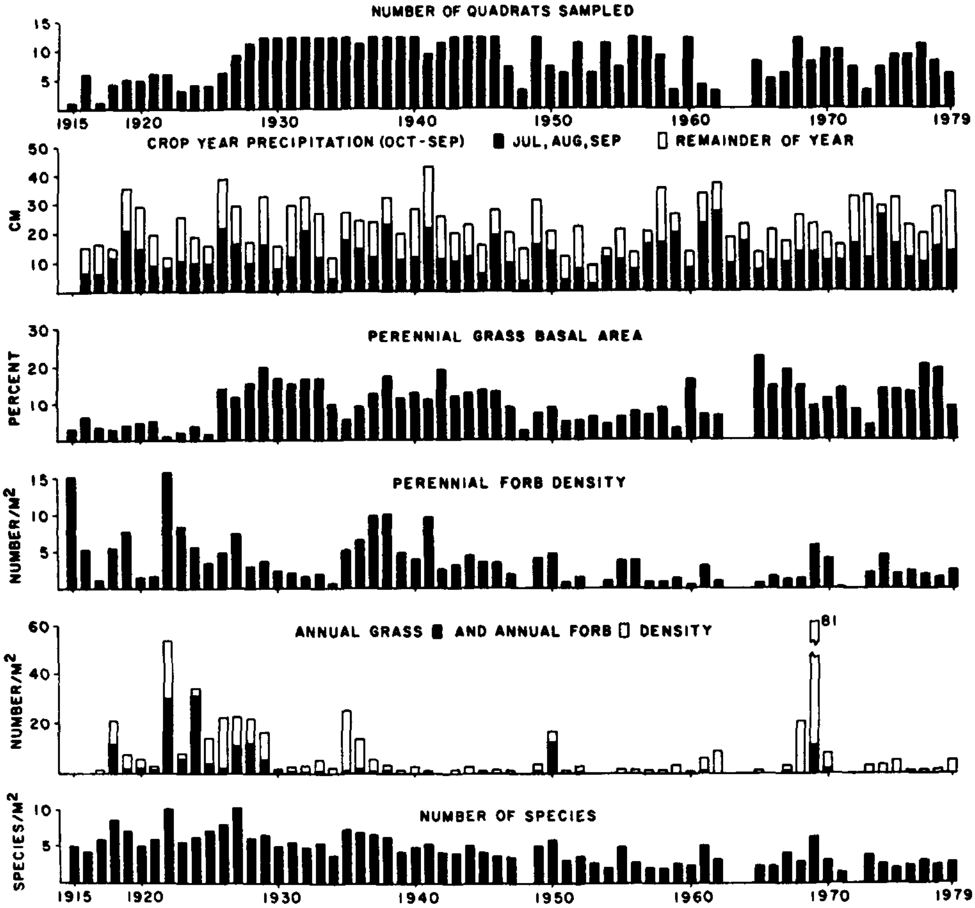

Fig. 4. *Number of quadrats sampled, crop-year precipitation, perennial grass basal area, perennial and annual plant densities, and number of species for the burrograss type. Forbs were not counted in 1948 and 1972.*

no clear correlation with either precipitation or perennial grass basal area (Fig. 4). The most frequent and abundant perennial forbs were Fendler bladderpod [*Lesquerella fendleri* (Gray) Wats.], leatherweed croton, broom snakeweed, and rushpeas. In most years, the number of annual grasses and forbs was low (Fig. 4). A notable exception was 1922, a year of low rainfall, when both annual grasses and forbs were exceptionally abundant. Also, 1969 had a superabundance of annuals. Mouseear, Russian thistle and bitterweed (*Hymenoxys odorata* DC.) were the most frequent and abundant annual forbs. Sixweeks grama, needle grama and sixweeks threeawn were the most abundant annual grasses.

Species richness was somewhat higher than in the tobosa type (Figs. 3 and 4). This appeared to be due to the greater abundance of annuals in the burrograss type. Species richness appeared to be lower in the 1960s and 1970s than in the 1920s and 1930s.

No significant relationships were found between annual and perennial forb numbers and accumulated precipitation. This was also true when the pre-1947 data set was examined separately.

Conclusions

These long-term quadrat records, accumulated at great expense, suffer from small sample size, a defect which was intensified by erratic sampling. However, the sheer length of the records allows some conclusions to be drawn. Perennial grass basal area is associated to some degree with 3 to 4 years of antecedent precipitation. The relationship between precipitation and perennial grass basal area is not strong because we do not have measured inputs at each quadrat site and because of our inability to define what is effective precipitation. Long-term, detailed studies of vegetation in desert areas receiving a high percentage of precipitation from localized, convectional storms should not be undertaken unless precipitation can be measured at each sampling site.

The few quadrats protected from grazing indicate that grazing has not had a significant impact upon perennial grass basal area. Drought years appear to have a tremendous influence upon perennial grass basal area and upon the composition of contributing grasses, particularly in the black grama type. The vulnerability of black grama to drought, and its relatively slow recovery, must be borne in mind when formulating grazing management plans. In contrast, tobosa and burrograss types offer a forage source less susceptible to drought and with relatively rapid recovery rates. The necessity of basing management of Chihuahuan Desert ranges on the perennial grass component is borne out by the low densities of perennial forbs and the extreme fluctuation and unpredictability in densities of annual forbs and grasses. The most serious problem is the widespread establishment of unpalatable shrubs which has occurred in spite of enlightened, conservative grazing management.

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Correlation of degree-days with annual herbage yields and livestock gains

MELVIN R. GEORGE, CHARLES A. RAGUSE, W. JAMES CLAWSON, CHARLES B. WILSON, ROBERT L. WILLOUGHBY, NEIL K. MCDOUGALD, DON A. DUNCAN, AND ALFRED H. MURPHY

Abstract

On California's winter annual rangelands precipitation controls the beginning and end of the growing season while temperature largely controls seasonal growth rates within the growing season. Post-germination accumulated degree-days (ADD) account for the length of the growing season and variation of daily temperature. Simple correlations of ADD and herbage yield or resultant livestock gains were determined at 5 locations in annual type range in northern California. Degree day values were determined by summing daily degree-days from the beginning of the growing season after germinating rainfall until the clipping or weigh dates. Accumulated degree-days accounted for 74 to 91% of the variation in seasonal herbage yield while accumulated days (AD) accounted for 64 to 86% of the variation. Together, ADD and AD accounted for 94 and 86%, respectively, of the variation in stocker cattle weights. Regression coefficients relating ADD to herbage yield appear to predict maximum site productivity. A procedure for estimating a seasonal herbage yield profile based on key growth curve inflection points and using simple field observations with 3 clipping dates and ADD is proposed.

Key Words: heat units, weather, sampling methods, modeling, seasonal production

Year-to-year variation in range herbage yield has frequently been attributed to variations in precipitation (Sneva and Hyder 1962). However, Duncan and Woodmansee (1978) were unable to show a relationship between herbage yield and precipitation on California annual rangeland. Pitt and Heady (1978) identified 5 annual range weather variables that explained 73% of the variation in March standing crop. Three of these variables were temperature related. Another set of 5 variables explained 90% of the variation in June standing crop. Two of these were temperature variables.

The annual range growing season can be partitioned into fall, winter, and spring periods. Fall precipitation and cooling winter temperatures determine the length of the fall growing season. The duration of slow winter growth is variable depending on the beginning and ending dates of the cold season. The length of the rapid spring growth period is also variable depending on the date that warm spring temperatures begin and the date spring soil moisture becomes depleted. Thus, precipitation controls the beginning and end of the whole growing season while temperature controls the end of the fall and beginning of the spring growing season.

The winter annual growth habit of California's annual rangeland appears to be an ideal system for explaining forage productivity based on accumulated degree-days (ADD), which integrates season length and temperature. Equations derived from degree-days to estimate or predict phenological stage or growth rate have been criticized (Wang 1960) but Bauer et al. (1984) concluded that the precision of ADD is equal to alternative methods and practical because air temperature is readily available from weather stations. This paper presents the simple correlations of seasonal herbage and resultant livestock yield with ADD at 5 annual range locations in California.

Materials and Methods

A 3-year field study of seasonal range herbage yield on 2 sites in Yuba and Butte Counties (Fig. 1) suggested a strong relationship between seasonal yield and ADD. To further verify this relationship, existing published and unpublished weather data and seasonal herbage yield data from the San Joaquin Experimental Range and University of California Hopland Field Station (Murphy et al. 1986) and seasonal cattle gain data from the University of California, Sierra Foothill Range Field Station (Raguse et al. 1986), were analyzed (Table 2). Weather data were acquired from the research stations and from the University of California Integrated Pest Management Data Base for Durham, California. The Durham data are more representative of the valley and adjacent terrace weather at the Butte County site than nearer weather stations at higher elevations in the foothills.

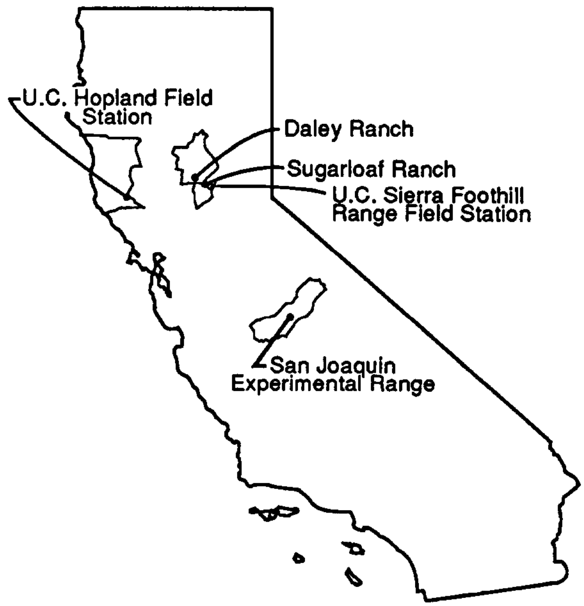

Fig. 1. *Location of 5 annual rangeland sampling sites in 4 California counties.*

Cages were used in the phytomass estimation procedures on the grazed sample sites Y1, B1, and H1-4 (Table 2). The grazed areas (SJ1 and SJ3) were split into 2 pastures that were alternately grazed and ungrazed during successive growing seasons. Seasonal yield was estimated in the ungrazed pasture each year. The ungrazed pasture was grazed following the growing season. Ungrazed standing crop was estimated in permanent livestock exclosures (SJ2 and SJ4).

Senior, second, and third authors are extension specialist, professor, and extension specialist, Agronomy and Range Sci. Dep., Univ. of California, Davis 95616. Fourth, fifth, and sixth authors are farm advisors, Yuba, Butte, and Madera Counties, Univ. of Calif. Coop. Ext., Berkeley 94720. Seventh author is director, San Joaquin Exp. Range, California State Univ. Fresno 93710. Eighth author is superintendent (retired), Univ. of California Hopland Field Sta., Hopland 95449.

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Table 1. Site descriptions and sampling conditions for 11 sample areas.

Site Description			Sample Description				
Soil series and family	Location (elevation)	Weather station (distance)	Area	Conditions	Size and unit	Dates	Years
Auburn loamy, mixed thermic Ruptic-Lithic Xerocrept	Sugarloaf Ranch, Yuba County (290 m)	Sierra Foothill Range Field Station (13 km)	Y1	grazed, caged exclosures	mean of 16 0.09 m² plots	4 dates each year October–May	1982–85
Corning fine, mixed thermic Typic Palexeralf	Daley Ranch, Butte County (40 m)	Durham, Butte County (33 km)	B1	grazed, caged exclosures	mean of 16 0.09 m² plots	4 dates each year October–May	1982–85
Ahwahnee Series coarse-loamy, mixed thermic Mollic Haploxeralf	San Joaquin Experimental Range (360 m)	Station (1.5 km)	SJ1	grazed at end of growing season	mean of five 0.09 m² plots	4 to 6 dates October–July depending on length of growing season	1980–85
Ahwahnee Series coarse-loamy, mixed thermic Mollic Haploxeralf			SJ2	ungrazed permanent exclosures	mean of five 0.09 m² plots	4 to 6 dates October–July depending on length of growing season	1980–85
Visalia Series coarse-loamy, mixed thermic Pachic Haploxeralf			SJ3	grazed at end of growing season	mean of five 0.09 m² plots	4 to 6 dates October–July depending on length of growing season	1980–85
Visalia Series coarse-loamy, mixed thermic Pachic Haploxeralf			SJ4	ungrazed permanent exclosures	mean of five 0.09 m² plots	4 to 6 dates October–July depending on length of growing season	1980–85
Mixture of Laughlin and Sutherlin Series Laughlin fine-loamy, mixed, mesic Typic Xeroxchrept Sutherlin fine, mixed mesic Aquic Haploxeralf	Hopland Field Station (350 m)	Station (1 km)	H1	grazed, caged exclosures	mean of 20 0.09 m² plots	Early February and late April to early May	1962–82
			H2	grazed, caged exclosures	mean of 20 0.09 m² plots	Early February and late April to early May	1962–82
			H3	grazed, caged exclosures	mean of 20 0.09 m² plots	Early February and late April to early May	1962–67
			H4	grazed, caged exclosures	mean of 20 0.09 m² plots	Early February and late April to early May	1962–72
Sobrante-Las Posas fine-loamy or fine mixed thermic Mollic Haploxeralfs	Sierra Foothill Range Field Station (330 m)	Station (1 km)	SF1	8–12 calves (200–400 kg) per pasture	mean of 4 pastures (14 ha each)	Weighed every three or four weeks from December to June	1982–85

The weight gain data were gathered from stocker cattle (200 to 230 kg) at the Sierra Foothill Range Field Station (SF1) which began grazing in November or early December. Initial stocking rates were 3.3, 2.2, and 1.7 ha per animal, respectively, each year. Stocking rates increased as herbage levels increased, attaining 1.1, 0.86, and 0.54 ha per animal for the corresponding years. Each year grazing was terminated in May or June when average daily gain began to decline, based on an every 21-day weigh schedule.

Accumulated degree-day values were determined using the sine function method described by Logan and Boyland (1983). Negative values were equated to zero. Negative values are infrequent because the mean daily temperature is seldom less than 5° C in the mild winters of California's Mediterranean climate. The base temperature used in this study was 5° C. Temperatures at or near 5° C have been used as the base temperatures or minimum temperatures for growth for many cool-season plants (Chang 1968, Bootsma 1983, Fitzpatrick and Nix 1970, and Bentley and Talbot 1951). Several annual range plants have minimum germination temperatures near a daily average temperature of 5° C (Young et al. 1973, 1975a, 1975b).

Degree-day accumulations were initiated on the estimated date that fall germination began, using Bentley and Talbot's (1951) criterion that annual plants start to germinate after the first rains of 12 to 25 mm. For this study the start of germination was defined as the day after 25 mm of precipitation occurred in 1 week. Days and degree-days were accumulated to each sampling or animal weigh date.

Linear correlation was used to determine the degree of association between accumulated days (AD) or ADD and herbage yield or livestock gains (Y). Accumulated degree-days integrates the 2 variables AD and temperature. The "extra sums of squares principle" (Draper and Smith 1981) was used to determine if the linear model using ADD as the independent variable was an improvement over a linear model using AD as the independent variable.

Table 2. Regression equations for accumulated degree-days (ADD) and forage yield or stocker cattle gains, R^2 or ADD accumulated days (AD) and their differences.

Sample Area	ADD a	b	SEŷ	R^2	AD R^2	Differ. R^2
			Forage Yield			
Y1	-120	5.2	424	0.95	.86	.09
B1	14	4.4	396	0.91	.83	.09
SJ1	- 90	3.8	632	0.85	.77	.18
SJ2	-141	3.1	570	0.82	.64	.18
SJ3	- 54	3.9	1052	0.77	.74	.04
SJ4	-280	4.9	925	0.88	.75	.13
H1	77	2.2	469	0.74	.83	-.09
H2	138	2.8	580	0.76	.83	-.07
H3	96	4.1	439	0.91	.84	.07
H4	82	2.7	591	0.74	.77	-.03
			Cattle Gain			
SF1	2.9	0.1	8.81	0.94	.86	.08

Table 3. Regression coefficients and maximum productivity under favorable weather conditions for six range soils.

Soil Series	Regression Coefficient	Maximum Yield
	(b)	(kg/ha)
Laughlin	2.7	2500[1]
Ahwahnee	3.1	3200[2]
Sutherlin	4.1	3500[1]
Corning	4.4	3600[3]
Visalia	4.9	5000[1]
Auburn	5.2	5700[3]

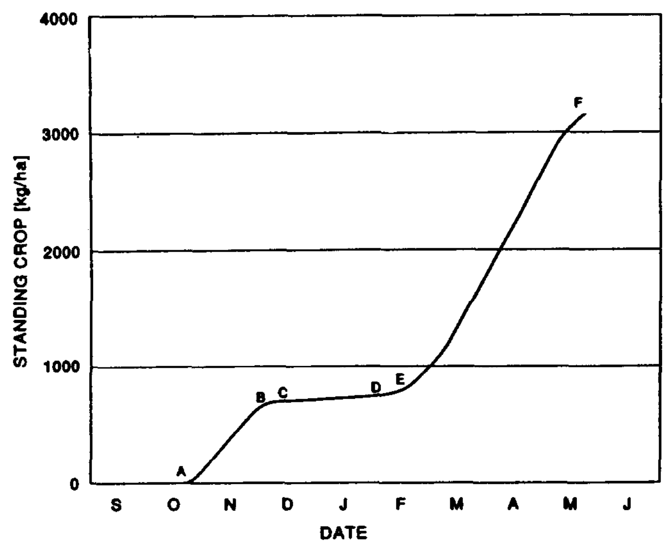
[1]George, M.R. and E.A. Jacobsen 1987.
[2]Clawson, W.J. 1986. unpublished.
[3]George, M.R. et al. 1987

Results and Discussion

The regression of herbage yield on ADD for the Yuba (Y1) and Butte (B1) sites indicated a strong relationship between these 2 variables (R^2>0.9) (Table 2). Analysis of larger data sets from other locations indicated that ADD accounted for 74 to 91% of the variation in seasonal herbage yield. It also accounted for 94% of the variation in seasonal weight gains of stocker cattle. Significant regression coefficients were obtained for ADD on seasonal yield regressions for all sites in the study.

Regression (slope) coefficients for the regression of herbage yield on ADD at areas SJ1-4 were 3.8 and 3.1, respectively, for the grazed and ungrazed Ahwahnee soil series and 3.9 and 4.9, respectively, for the more productive Visalia series (Table 3). Accumulated degree-days accounted for a greater proportion of variation (R^2=0.77 to 0.88) in seasonal herbage yield than AD (R^2=0.64 to 0.77) at SJER. The SEŷ was greatest on the Visalia series where yields are potentially quite high under favorable growing conditions and can be quite low under poor conditions. The associated Ahwahnee series has a lower potential under favorable weather conditions.

Regression coefficients for areas H1-4 were 2.2, 2.8, 4.1, and 2.7. The data set for H3 covered fewer years than areas H1, H2, and H4. For the 1962–67 period H3 had a higher herbage yield than the other 3 areas (Murphy et al. 1986). Accumulated days accounted for a greater proportion of the variation in seasonal herbage yield than did ADD in 3 of 4 pastures (Table 1). Unlike the data from the other sites, the Hopland data do not include an early winter yield estimate (C in Fig. 2). Without an early winter yield estimate, the relationship between AD and yield may be stronger than the relationship between ADD and yield. Addition of an early winter



A. emergence of new seedlings
B. beginning of winter
C. early winter herbage yield estimate
D. late winter herbage yield estimate
E. end of winter
F. end of growing season (peak standing crop) herbage yield estimate

Fig. 2. *Seasonal herbage production profile for annual rangelands.*

yield estimate tends to make the relationship between ADD and yield stronger than the relationship between AD and yield.

The results of this study using widely separated locations support the notion that ADD is a useful index to growing conditions on annual rangeland, where season length and temperatures are highly variable. Strong relationships between ADD and standing crop or yield have been shown for several forages including alfalfa (Selirio and Brown 1978) and barley (Chakravarty et al. 1984). This study applies degree-day concepts to a community of mixed vegetation dominated by cool-season annual species that have similar minimum temperature requirements for germination (Young et al. 1973, 1975a, 1975b), grow slowly during the winter, and grow rapidly during spring (Pendleton et al. 1983). Degree-day concepts assume every degree of temperature is physiologically equivalent. Since this assumption is only an approximation, we are dealing with a concept of indexing rather than a precise cause-effect relationship. However, the information developed in this study provides the basic relations from which we can approximate annual range herbage yield during the growing season on like soils and under like climatic variation to that of the study sites.

Regression (slope) coefficients appear to be related to site productivity as indicated in Table 3. If further study confirms this relationship over a wider array of sites, we would have the basis for an index to site productivity based on past climatic records.

The relationship between ADD and herbage yield can only be strong if soil moisture is not limiting. Droughts causing high plant mortality are normally rare in the middle of the growing season because the soil moisture recharge is adequate to keep plants alive during the winter when potential evapotranspiration is very low. Droughts within the growing season may be more important at more southerly locations than those in this study. If this is the case the regression coefficients may not be correlated with site productivity.

Applications and Conclusions

Accumulated degree-days can be used to normalize seasonal yield data to produce seasonal production curves described by George et al. (1985) (Fig. 2). They describe 3 phases of herbage production simulated by ELMAGE (Pendleton et al. 1983). These growth phases are:

1. Break of season in fall (A) beginning after the first fall rains which exceed 25 mm of rainfall. This fall growth period (A–B) is usually 2 to 3 weeks in length but can be longer with early rains or late onset of cold temperatures. Fall growth may not occur if germinating rains occur after the onset of cold temperatures.
2. Winter growth period (B–E) occurs at the end of the fall growing season and is the result of cooling temperatures, shorter days, and low solar radiation levels.
3. Rapid spring growth (E–F) begins with the onset of warming spring temperatures, longer days, and high solar radiation. Peak standing crop and soil moisture depletion occur at the end of this period marking the beginning of the dry season.

The following procedure estimates points A, C, D, and F using field observations and 3 clipping dates. Degree-day accumulations are used to estimate the inflection points at the beginning (B) and end (E) of winter.

1. Record the growing season starting date (A). This can be the date of the first observed seedling emergence or it can be estimated from daily precipitation records following 25 mm precipitation in 1 week.
2. Determine the beginning of the winter growth period (B). This is defined as the first cold day (degree-days <2.78) in a 7-day period that averages less than 2.78 degree-days per day (2.78 degree-days is derived from a minimum temperature of 5° C, a maximum temperature of 10.5° C, and a base temperature of 5° C).
3. Estimate herbage standing crop at the beginning of the winter growth period (C) to establish forage yield between the beginning of the growing season and the start of the cold winter season. Forage should be estimated as soon as possible after the onset of cold weather (B).
4. Late in the cold winter season (usually before mid-February), a second standing crop estimate will define herbage production during the winter growth period (D).
5. Determine the first day of the spring growing season (E) which is defined as the first warm day (degree-days >2.78) in the first 14 day period that averages more than 2.78 degree-days per day.
6. Finally, a herbage standing crop estimate at the end of the growing season (F) will define spring production as well as total growing season production. Proper timing of the peak standing crop estimate is not specified in the literature, but common practice is to sample when the annual grasses such as soft chess *(Bromus mollis)* are between the soft and hard dough stage of maturity. Waiting too long will result in loss of delicate herbage, especially some forbs which shatter quickly on drying.

A difference of several days between the beginning of winter (B) and the actual sampling date (C) or the end of winter (E) and sampling date (D) is inherent in this procedure. However, the rate of growth during the winter period is less than 5 kg/ha/day (Jones 1967, Pendleton et al. 1983, George et al. 1987) and this difference is unlikely to be of statistical significance. George et al. (1987) report that the differences between early and late-winter standing crop estimates, a period of 60 to 90 days, were not significantly different at the Yuba and Butte locations used in this study.

In practice, most studies only report treatment effects on peak standing crop (F), missing important information about treatment response in fall and winter. Fall and winter forage yield is important because that is the period when forage need exceeds forage supply in foothill livestock operations. A few researchers have reported 2 or 3 seasonal measures of standing crop, but their timing has not followed that proposed here. For example, Pitt and Heady (1978) used March standing crop to estimate fall and winter production. In years where spring starts in early-to-mid February, 2 or more weeks of rapid spring growth may be included in the fall and winter estimate, giving an inflated estimate of fall-winter production.

Growth analysis techniques (Russelle et al. 1984) that compare productivity on a yield per degree-day basis rather than yield per day could be used to remove differences in observed experimental or site productivities due to season length and temperature. Differences in results from experiments conducted on similar sites but in different years have resulted in wide variation in yield response to seeding and fertilization. Although data from control treatments can be used to show yield differences due to treatment, they do not account for yield differences due to weather variation between locations or years which are often more influential than the treatments themselves.

Because of the strong relationship between ADD and herbage yield at several locations and under a variety of sampling regimes, ADD shows promise as an estimator of herbage yield in California's winter annual ranges. In future monitoring efforts, collection of weather data on-site and sampling as proposed in this paper should allow testing and improvement in the strength of this relationship.

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Factors influencing infiltrability of semiarid mountain slopes

BRADFORD P. WILCOX, M. KARL WOOD, AND JOHN M. TROMBLE

Abstract

The objective of this research was to determine the effects of selected vegetation, soil, rock, and slope variables on infiltration of semiarid rangelands with slope gradients ranging from 0–70%. Analyses were made on 2 sets of data collected a year apart in the Guadalupe Mountains of New Mexico and consisted of Pearson and partial correlation analysis of the dependent infiltration variables and independent site variables. In addition, infiltration was regressed against uncorrelated factors produced by factor analysis. Vegetal cover and biomass strongly influenced infiltration. The relative importance of grasses, shrubs or litter was dependent on their respective abundance, especially grass. Soil depth also limited infiltration especially as soil water storage became satisfied. Infiltrability was negatively correlated with rock cover and the smallest rock size fragments were the most negatively related. When the effects of vegetal cover and slope were removed (using partial correlation analysis) however, the median sized rock fragments (26–150 mm) were positively related to infiltrability, and the smallest rock fragements (2–12 mm) were negatively related. Partial correlation analysis also suggested a positive correlation between infiltrability and slope gradient.

Key Words: soil water, infiltration, rangeland hydrology

An understanding of basic hydrologic processes on rangeland is critical for effective range watershed management. The infiltration process fundamentally influences rangeland hydrology; thus, knowledge of factors that influence infiltration is important. Many studies have assessed the influence of soil and vegetation factors on rangeland infiltration. Few, however, have evaluated semiarid rangelands and none to our knowledge have included very steep slopes in their study. Results of these studies have been variable depending on the characteristics of the study area (Branson et al. 1981).

Authors are assistant professor, Department of Earth Resources, Colorado State University, Fort Collins 80523; associate professor, Department of Animal and Range Sciences, New Mexico State University, Las Cruces, New Mexico 88003; range hydrologist, USDA/ARS Jornada Experiment Station, New Mexico State University, Las Cruces 88003.

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Hillel (1971, 1982) has pointed out the shortcomings of the term "infiltration capacity" and has proposed the term "infiltrability" in its place to "designate the infiltration flux resulting when water at atmospheric pressure is made freely available at the soil surface" (Hillel 1982 p. 212). We concur that "infiltrability" is a more appropriate term and have used it throughout this article.

Smith and Leopold (1941) concluded that vegetal cover and initial soil moisture had the greatest influence on infiltrability in the Pecos River watershed in New Mexico. The importance of vegetal cover has been shown by many others (Woodward 1943, Dyksterhuis and Schmutz 1947, Duley and Domingo 1949, Rauzi 1960, Johnson 1962). In western Colorado infiltrability was more highly correlated with bare soil than it was with plant cover (Branson and Owen 1970). Blackburn (1975) reported that soil morphological characteristics (organic matter, clay content) had the greatest influence on infiltrability in Nevada. Tromble et al. (1974) evaluated infiltrability on 3 range sites in Arizona and found vegetal cover and litter biomass to be most positively related, whereas gravel cover was negatively related. Meeuwig (1970) and Dortignac and Love (1961) also found litter cover to be important. In the Rolling Plains of Texas, infiltrability was most strongly correlated with aggregate stability (Wood and Blackburn 1981). Generally, as the size of the bare ground area increases, influence of plant cover decreases (Wright et al. 1982). Soil macroporosity can also have a tremendous influence on infiltrability (Beven and Germann 1982). A complete review of the influence of soil and vegetation factors to rangeland infiltration is given by Branson et al. (1981).

The influence of slope on infiltrability has received less attention. Agronomic studies have shown little relationship between slope and infiltrability, especially on slope gradients greater than 4% (Duley and Hays 1932, Neal 1938, Duley and Kelley 1939). Slope gradients in these studies did not exceed 20%. Few rangeland studies have addressed the influence of slope gradient on infiltration. Meeuwig (1970) found little correlation between slope gradient and infiltrability of Utah rangelands. The range of slope gradients included in his study was not reported. Mean slope gradient was 20%. In northern Utah, runoff from sagebrush-grass covered plots (22.1 × 1.8 m) was the same for 10 and 32% gradients

(Hart 1984). Assuming comparable evaporation losses, infiltrability on both slope gradients should have been the same as well. Others have found infiltrability to be positively related to slope angle (Wilcock and Essery 1984, McCord 1985).

The objectives of this study were two fold. One was to determine the effects of selected site variables on infiltrability of semiarid slopes with slope gradients ranging from 0–70%. This study is unique in that steep slope gradients have been sampled as well as the more gentle ones. The second objective was to determine when in the infiltration process each variable was most important. In other words, does the correlation between infiltrability and the respective variable increase, decrease, or stay the same with time?

Study Area

The study was conducted in the northern Guadalupe Mountains of southeastern New Mexico. The Guadalupe Mountains are a dissected plateau of moderate to high relief (King 1948, Hayes 1964). The plateau runs northwestwardly, and is about 64 km long and 5 to 19 km wide. Plateau width increases towards the south. The western edge is defined by a great fault scarp known as the Guadalupe Rim. Field work was conducted on and adjacent to the Guadalupe Rim. Elevation of the study area ranges from about 1,200 to 2,000 m. The climate is semiarid and is characterized by relatively mild winters and warm temperatures throughout the year. Average annual precipitation is about 50 cm per year. Approximately 80% of the precipitation comes from May to October (Gehlbach 1967).

Most soils in the study area developed from limestone or dolomite residuum and are shallow. Underlying bedrock begins at depths of 10 to 50 cm. Textures are gravelly loams and gravelly clay loams. Soils are classified as loamy-skeletal, carbonatic, mesic Lithic Calciustolls (Deama series) or clayey, mixed mesic Lithic Argiustolls (Encierro series). Deeper soils occur on alluvial valleys and fans. They are classified as Aridic Haplustalfs (Montecito series). Soils are well drained with moderate permeability (USDA 1981). Rock outcrops are common on steep slopes.

Succulent desert and evergreen woodland formations are present in the study area (Gehlbach 1967). Common shrub and tree species are one-seed juniper (*Juniperus monosperma* [Engelm.] Sarg.), three-leaf sumac (*Rhus aromatica* Ait. var. *flabelliformis* Shinners), mountain mahogany (*Cercocarpus montanus* Raf.), skeleton-leaf goldeneye (*Viguiera stenoloba* Blake), and wavy-leaf oak (*Quercus undulata* Torr.). Smooth-leaf sotol (*Dasylirion leiophyllum* Engelm.), lechuguilla agave (*Agave lechugilla* Torr.), and walkingstick cholla (*Opuntia imbricata* [Haworth] DC.) are common succulents. Major grasses are blue grama (*Bouteloua gracilis*), sideoats grama (*Bouteloua curtipendula* [Michx.] Torrey), slim tridens (*Tridens muticus* [Torr.] Nash), curlyleaf muhly (*Muhlenbergia setifolia* Vasey), needle and thread (*Stipa comata* Trin. and Rupr.), and cliff muhly (*Muhlenbergia polycaulis* Schrilon). The area is seasonally grazed by sheep and cattle at moderate stocking levels (up to 2 ha per animal unit). Mule deer are also abundant in the area.

Methods

A hand-portable rainfall simulator (Wilcox et al. 1986) was used to apply rainfall to flexible plots about 1 m² in size. The rainfall simulator employed a single stationary nozzle that was placed 2.0 m above the plot. Rainfall application rate was 10.3 cm hr^{-1}. Drops varied from 0.8 to 2.0 mm in size. Median drop size was 1.2 mm. Plots constructed from sheet metal strips 10 cm wide and 355 cm long were lightly tamped into the soil. The lower inside borders were sealed with soil to prevent leakage. The soil seal was covered with a mulch layer to protect it from raindrop impact and subsequent soil particle detachment. Plot area was measured at each location using a grid construction from 1.27 cm wire mesh.

Water was applied twice at each plot location. Application times were separated by about 16–24 h. Water was applied for 45 minutes during the first application (dry run) and 35 minutes during the second (wet run). These times were selected to attain steady state infiltrability. Dry and wet runs were included in the analysis to increase the range in soil moisture conditions and to approximate field capacity conditions as well as dry or antecedent conditions. Immediately after the dry run the plot was covered with a plastic sheet to prevent evaporation loss.

Infiltrability was considered to be application rate minus runoff rate from the plot. Other components of the water budget (surface water storage, interception storage, evaporation) were not accounted for in determining infiltration since they represented minor losses to the system and would have been difficult to determine for each plot. Runoff was determined at 5-min intervals.

Data were collected for 2 consecutive field seasons (June–August). In year 1 (1983) infiltrability was determined at 72 locations on the face of the Guadalupe Rim. Plot slope gradients varied from 16–70%. In year 2 (1984) infiltrability was determined on 80 plots of which 34 were located on lower slope gradients (<10%) above the Guadalupe Rim and 46 were located on steep slopes of the Guadalupe Rim. Soils on and above the Guadalupe Rim were similar to one another (shallow, silty clay loams) with the exception of the deep soils on the alluvial valley bottoms (Montecito series). Six plots were located on alluvial soils in year 2 but not year 1. A productive grass community dominated by *Stipa comata* and *Bouteloua gracilis* was sampled (16 plots) in year 1 but not year 2. Plant communities sampled appear in Table 1.

Standing biomass (g m^{-2}) was determined for shrubs, grasses, and forbs by clipping to a 1.5 cm height. Plant litter was also collected. All plant material was dried for 48 h at 60–70° C before weighing.

Aerial and basal cover were estimated by species using a point sampling method (Pieper 1978). One-hundred points were read per plot for both aerial and basal cover estimates using a 100 cm wide 20-pin point frame. Aerial cover was estimated before the plot was clipped, and basal cover was estimated afterward. Bare ground and rock cover was also noted. Rocky were recorded by size classes (2-12, 13-25, 26-75, 76-150, >150 mm) in year 2. Rock cover was estimated before the vegetation was removed by clipping.

Antecedent soil moisture was estimated for the surface 5 cm by the gravimetric method. Samples were collected adjacent to the runoff plot before the first rain application. Soils were assumed to be at or near field capacity before the wet run. After the wet run, soil samples were taken within the plot at a depth of 0–5 cm for particle size and organic carbon analysis. Particle size distribution

Table 1. Steady state infiltrability and associated standard deviations of the plant communities sampled.

Vegetation types labelled by dominant Species	Slope	Infiltrability (cm/hr) Year 1 Dry	Year 1 Wet	Year 2 Dry	Year 2 Wet
Muhlenbergia setifolia-Bouteloua curtipendula	Steep	6.9 (2.1)	4.1 (2.0)	7.4 (1.9)	5.5 (2.2)
Muhlenbergia palycaulis-Quercus undulata	Steep	9.1 (1.0)	7.6 (1.8)	6.8 (2.4)	5.7 (2.8)
Bouteloua gracilis-Juniperous monosperma	Low			6.3 (2.7)	4.3 (2.5)
Muhlenbergia richardsonis-Opuntia imbricata	Low			9.4 (0.8)	7.3 (2.1)
Stipa comata-Bouteloua gracilis	Steep	9.1 (1.2)	7.6 (2.7)		

was estimated using the hydrometer method (Bouyoucos 1962). Organic carbon percentage was determined by the Walkly-Black method (Allison 1965). Surface bulk density was determined for each plot by the core method (Blake 1965). In some cases, soil was too rocky within the plot, so samples were taken adjacent to the plots where the core sample could be tamped into the soil. Depth to bedrock was determined 3 times in each plot by probing with an iron bar. Slope gradient was determined in each plot as the maximum difference in elevation of a given length (0.9 m) divided by that length.

Pearson and partial correlation coefficients were computed between independent variables (soil, vegetation, rock slope) and the dependent infiltration variables (infiltrability at 5-minute increments). Partial correlation analysis was employed to reduce multicollinearity among the independent variables. This analysis allows the linear effect of one or more variables to be removed when examining the relationship between another pair of variables (Thorndike 1976).

Factor analysis was also used to reduce or account for multicollinearity. Principal component analysis (PCA) with a Varimax rotation extracted new uncorrelated factors from the independent variables. These factors were then regressed against the dependent variables (Afifi and Clark 1984). Analyses were performed separately on the 2 sets of data. Principal component analysis can be used to effectively overcome multicollinearity of the data by transforming the original independent variables into new uncorrelated variables or principal components (Afifi and Clark 1984). As many factors are produced as the number of original variables but the new factors are arranged in order of decreasing variance. Thus, most of the variance of the original data is accounted for by fewer variables. Interpretability of the principal components is often difficult and can be simplified by using a rotation technique. The most accepted method and the one used here is the Varimax rotation (Thorndike 1976). The new factors are easier to interpret than the principal components and are still uncorrelated with one another.

Results and Discussion

Correlation Analysis

Vegetation

Both years of data indicate a strong relationship between infil-

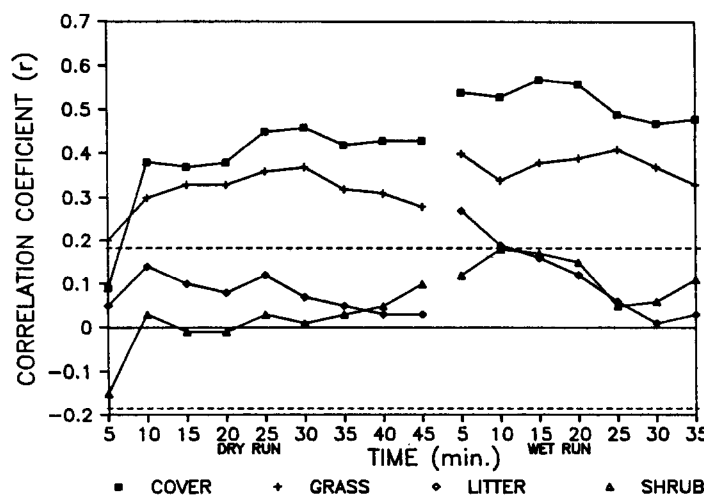

Fig. 1. *Year 1 correlations between vegetal cover and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant (p≤0.05).*

trability and total vegetal cover (Figs. 1 and 2). Coefficients were generally higher for year 2 than year 1. After the first 5 minutes coefficients remained steady throughout the dry run and increased slightly during the wet run. In year 2 (Fig. 2) wet run coefficients

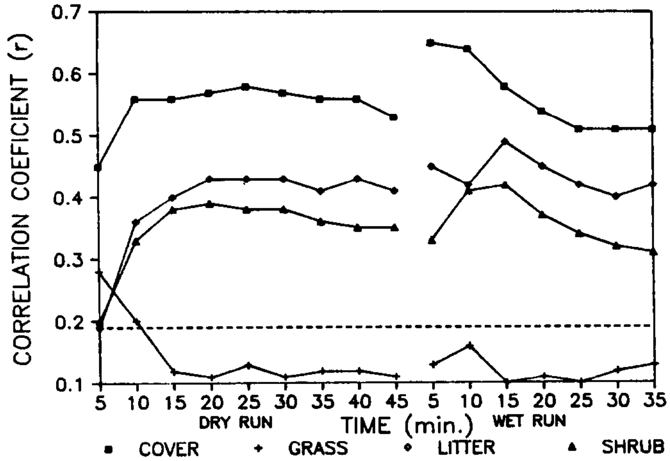

Fig. 2. *Year 2 correlations between vegetal cover and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value the which correlations are significant (p≤0.05).*

between total vegetal cover and infiltrability decreased with time. Correlation coefficients were also computed between the components of vegetal cover (grasses, forbs, shrubs, litter) and infiltrability. In year 1 grass cover was the dominant factor while shrub and litter cover were nonsignificant. In year 2 shrub and litter cover were dominant and grass cover was nonsignificant. Site differences account for some of this incongruity. Recall that the productive *Stipa comata-Bouteloua gracilis* community (high grass cover and production, low shrub-litter cover and production) were sampled in year 1 but not year 2. When these plots were removed and the data analyzed again correlations between infiltrability and shrub, litter, and grass cover were about the same for both years.

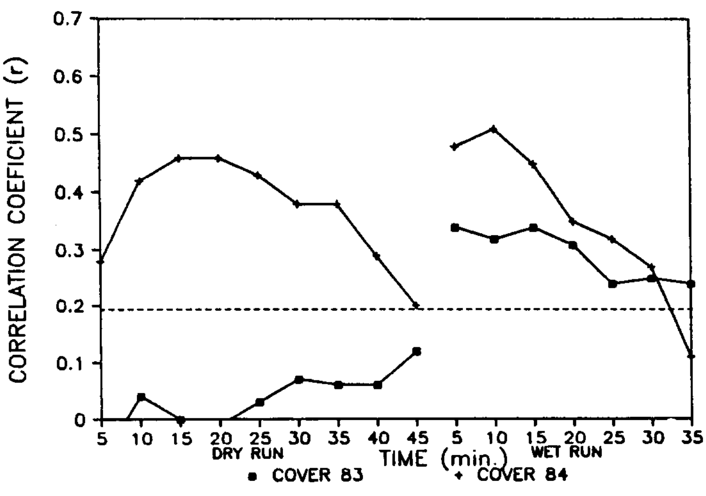

Fig. 3. *Partial correlations (effect of rock cover and slope gradient removed) between total vegetal cover and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant (p≤0.05).*

Partial correlation analysis was used to examine the relationship between infiltrability and vegetal cover with the effect of slope gradient and rock cover removed (Fig. 3). Both variables (slope gradient, rock cover) were highly correlated with vegetal cover. The resulting correlation coefficients were much reduced, especially in year 1. In year 2 a marked decline with time was evident in both the dry and wet run. These graphs also indicate that in year 1 (1983) infiltrability was more correlated with vegetal cover during the wet run. In year 2, however, little difference existed between coefficients of the dry and wet runs. The removal of only slope gradient had little effect on the correlation between infiltrability and vegetal cover. When only rock cover was removed, the resulting coefficients were very similar to Figure 3, suggesting that rock cover has a positive impact on infiltrability. In a semiarid environment rock cover should increase as vegetal cover decreases (assuming rocks are in the soil) because with lower vegetal cover raindrop impact and overland flow remove the finer particles, leaving the coarse particles behind (Cooke and Warren 1973). The effect of rock cover will be discussed in more detail later.

Basal vegetal cover was a poorer indicator of site infiltrability than aerial cover. In general, correlations between infiltrability and basal cover were nonsignificant. Kincaid et al. (1964) also found basal cover a poor indicator of infiltrability.

Results of the correlation analysis of infiltrability and vegetal biomass to some extent mirrors the results of the correlation between infiltrability and vegetal cover. Both cover and biomass are a reflection of vegetation abundance. Coefficients were higher during the wet run for both years. In year 1 (Fig. 4) grass was the

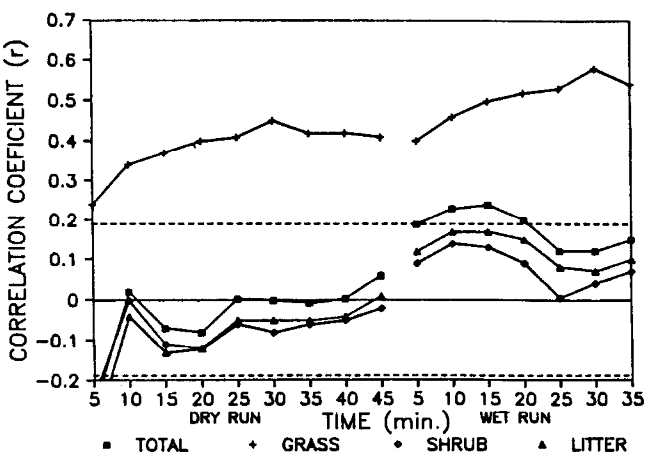

Fig. 4. *Year 1 correlation between vegetal biomass and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant (p≤0.05).*

only biomass component significantly correlated with infiltrability. Even total vegetal biomass (which is most heavily weighted by shrub biomass) was nonsignificant. In year 2 results were quite the opposite with significant correlations between infiltrability and total, shrub and litter biomass and low correlation for grass biomass (Fig. 5). Again it was thought that site differences caused these observed differences between year 1 and year 2. However, when the *Stipa comata-Bouteloua gracilis* plots were removed from the year 1 data, results were not much different. Grass biomass was higher in year 1 than in year 2 (Table 2) even when the productive grass stands were removed. These data suggest a threshold value of grass biomass must be surpassed before grass biomass has a large impact on infiltrability. Blackburn et al. (1980) noted that infiltration is higher under bunch grasses (high biomass) than sod-forming grass (low biomass) with all other conditions being equal. Most research however (Lyford and Qashu 1969, Tromble et al. 1974, Wood and Blackburn 1981, Brock et al. 1982, Thurow et al. 1986), with the exception of Box (1961), has demonstrated higher infiltrability under shrub canopy than in the interspace zone. Box (1961) measured higher infiltrability on some grassland communities than under mesquite canopies. Shrubs usually enhance infiltrability by providing protection from raindrop impact and preventing formation of a soil crust. The copious litter supply, besides reducing raindrop impact, also adds organic matter to the soil. Organic matter increases soil porosity by encouraging aggragation and reducing soil bulk densities.

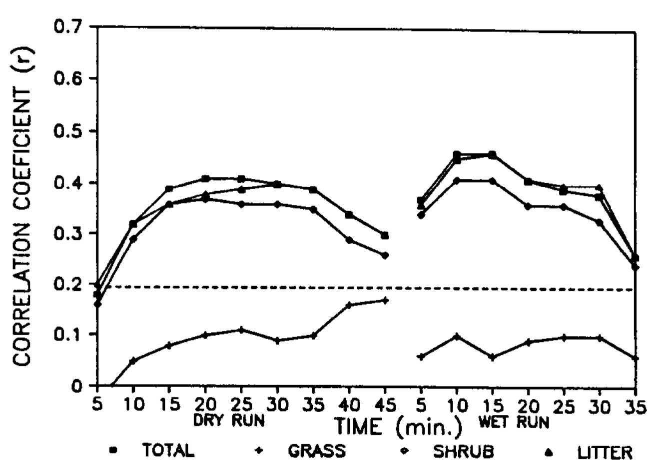

Fig. 5. *Year 2 correlations between vegetal biomass and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant (p≤0.05).*

The positive impact of vegetation on infiltrability is borne out by these data. Vegetation, in general, influences surface hydrological properties by decreasing velocity of overland flow, increasing surface roughness, enhancing soil infiltrability by root activity and addition of organic matter (Selby 1982). Vegetal cover also reduces impact energy of raindrops (Osborn 1954, Smith and Wischmeier 1957), substantially reducing rain splash erosion and formation of less permeable soil crusts.

Soil

Of all the soil variables measured infiltrability was most correlated with soil depth (depth to bedrock) (Fig. 6). Soils in the study

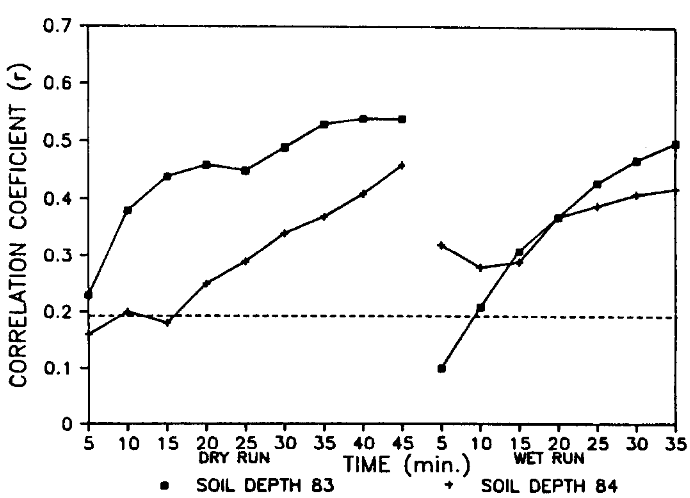

Fig. 6. *Correlations between soil depth and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant (p≤0.05).*

area tended to be very shallow (underlain by limestone or dolomite bedrock) with the exception of the alluvial soils. Note that soil depth became more correlated with time. Soil depth limits soil water storage capacity and as storage capacity is reached, infiltrability slows. Others have also noted that infiltrability is limited by soil storage capacity (Dunne and Leopold 1978).

Infiltrability was slightly correlated with soil texture in both years (Fig. 7). It was positively related to percentage of clay sized particles and negatively related to sand and silt sized particles. Blackburn (1975) reported a significant relationship between infiltrability and soil texture in semiarid watersheds of Nevada. He found however, that clay and silt were negatively correlated while sand was positively correlated, just the opposites of these results.

Table 2. Mean values and associated standard deviations for measured plot characteristics.

	Year 1		Year 2			
	Steep Slopes		Flat Slopes		Steep Slopes	
Variable	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
Aerial vegetal cover (%)	38.5	16.0	63.5	18.7	42.3	17.5
Basal vegetal cover (%)	11.5	7.8	30.7	9.8	15.1	8.1
Aerial forb cover (%)	2.3	2.7	1.8	2.5	1.4	1.6
Aerial grass cover (%)	26.9	17.1	38.8	15.1	24.0	13.4
Aerial shrub cover (%)	9.0	14.4	10.0	17.1	10.7	16.9
Litter cover (%)	11.6	11.0	12.9	10.2	6.2	4.7
Bare ground (%)	16.6	10.9	21.8	12.3	20.6	8.6
Basal forb cover (%)	0.2	0.4	0.2	0.6	0.3	0.6
Basal grass cover (%)	11.0	8.0	29.8	10.2	13.7	8.7
Basal shrub cover (%)	0.4	1.0	0.7	1.1	1.2	2.3
Rock cover (%)	33.2	16.8	14.0	14.3	34.5	14.4
Rock 2–12 mm (%)			4.2	4.5	6.5	4.8
Rock 13-25 mm (%)			4.1	4.6	7.8	4.4
Rock 26-75 mm (%)			4.1	4.9	12.2	6.9
Rock 76-150 mm (%)			1.4	1.8	6.1	4.6
Rock 151+ mm (%)			0.1	0.6	1.9	2.7
Grass biomass (g)	132.5	110.5	75.8	43.1	87.5	34.3
Litter biomass (g)	237.0	232.8	133.7	238.6	64.7	106.7
Shrub biomass (g)	185.5	382.8	164.8	413.9	284.4	575.2
Forb biomass (g)	11.2	13.2	7.7	12.8	6.7	7.5
Organic carbon 0-5 cm (%)	6.0	1.7	5.3	2.0	5.3	1.4
Bulk density (g/cm^3)			0.98	0.2	0.98	0.1
Sand 0-5 cm (%)	25.7	5.3	22.0	3.7	23.1	4.0
Clay 0-5 cm (%)	33.9	5.6	33.5	6.5	35.3	4.8
Slope gradient (%)	41.0	13.1	5.7	4.5	51.1	8.0
Soil depth (cm)	23.1	13.6	34.9	21.3	26.5	7.5
Steady state dry run infiltrability (cm/hr)	8.0	2.0	6.8	2.7	7.3	2.0
Steady state wet run infiltrability (cm/hr)	6.0	2.5	4.8	2.6	5.6	2.3

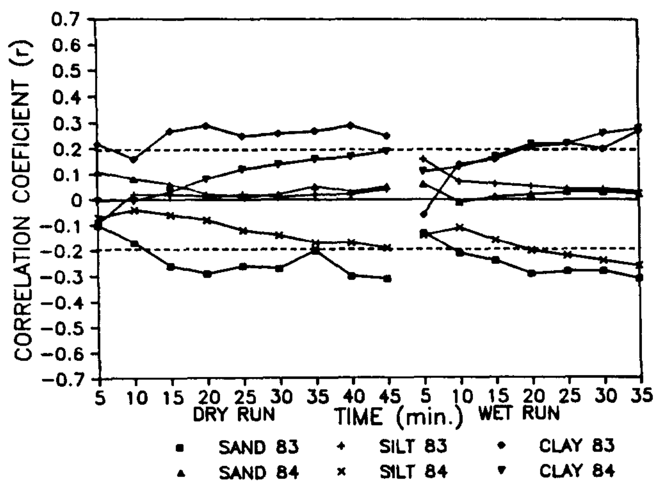

Fig. 7. *Correlations between soil texture and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant* ($p \leq 0.05$).

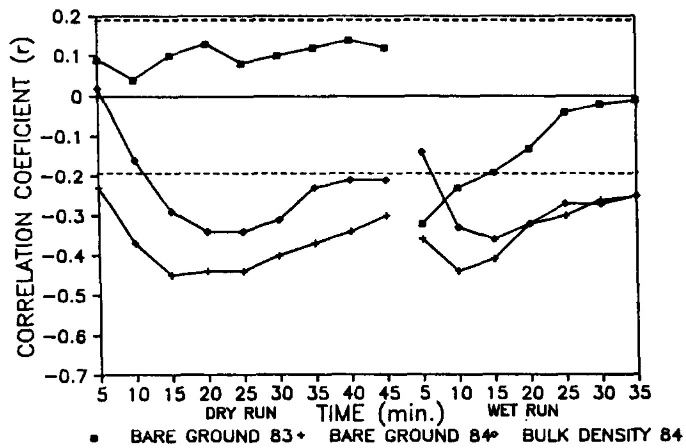

Fig. 8. *Correlations between bulk density and bare ground and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant* ($p \leq 0.05$).

Indeed one would expect coarse size particles to enhance infiltrability rather than inhibit it. The surface soil textural range however was quite narrow (clay loam-silty clay loam). In this range it is conceivable that clay increases could increase infiltrability since clay enhances soil aggregation (Baver et al. 1972).

Bulk density was measured only in year 2. As expected, infiltrability was negatively correlated with bulk density (Fig. 8). Highest coefficients were observed in the middle of the infiltration event. The shape of the bulk density correlation curve was quite similar to the bare ground correlation curve of year 2. Both variables influence soil porosity. As more bare ground becomes exposed, raindrop impact has a greater compacting effect. The more extreme microenvironment of exposed soil also contributes to soil compaction (Satterlund 1972). Infiltrability however, was poorly correlated with bare ground in year 1. Significant negative correlations occurred only in the beginning of the wet run. Average bareground was lower in year 1 than year 2 (Table 1).

The positive influence of organic matter on infiltrability is well established. Organic matter encourages soil aggregation and increases water holding capacity of the soil (Brady 1974). The year 2 data reflects this but the year 1 data do not (Fig. 9). In fact there was actually a negative relationship for the 1983 data set. One reason for this was that organic carbon was negatively correlated

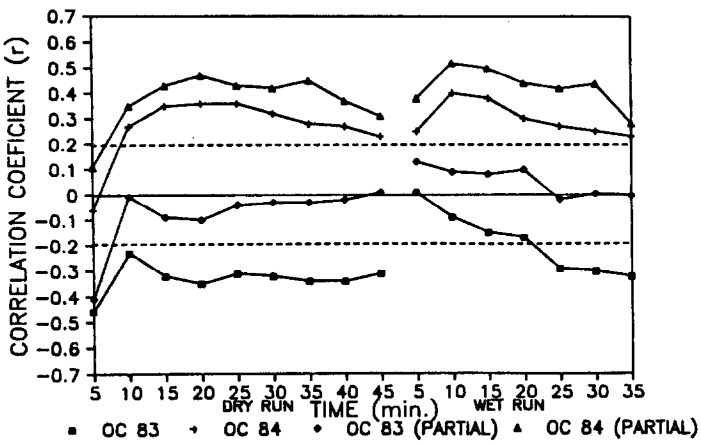

Fig. 9. *Correlations and partial correlations (effect of soil depth removed) between organic carbon and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant (p≤0.05).*

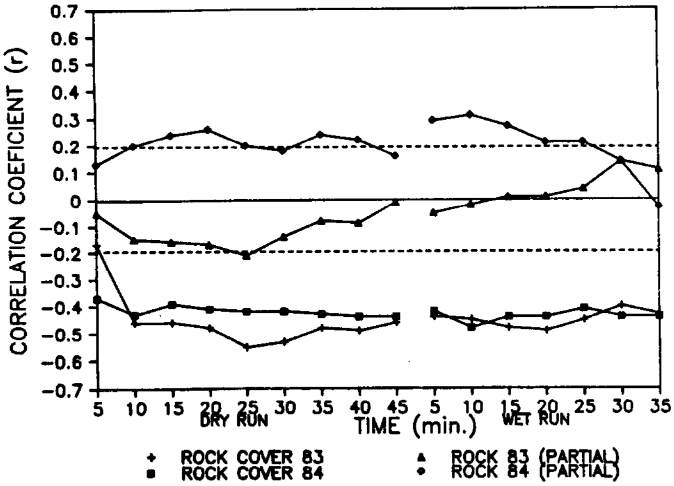

Fig. 10. *Correlations and partial correlations (effect of vegetation and slope removed) between rock cover and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant (p≤0.05).*

with soil depth. Very shallow soils had the highest amounts of organic carbon. When the effect of soil depth was removed, the relationship was nonsignificant in year 1 and made more positive for year 2. Another reason for the weak correlation in year 1 was that organic carbon was lower in the *Stipa comata - Bouteloua gracilis* community soils, which had high infiltrabilities.

Rock Cover

Infiltrability was negatively correlated with rock cover for both sets of data (Fig. 10). The key question is does rock cover on semiarid mountain slopes contribute to lower infiltrability and increased runoff or is it simply an indicator of low infiltrability? Thornes (1980, p. 162) states that "development of a stone carapace while protecting the soil from raindrop impact tends to inhibit infiltration and increase surface runoff though it may occasionally have the reverse effect." Research by Yair and Lavee (1976) on talus mantled slopes in Israel showed that rock cover contributed to runoff by concentrating and delivering water. Tromble et al. (1974) also found infiltrability to be negatively correlated with gravel (<10 mm) cover in semiarid rangeland of Arizona. Conversely, others have noted that under laboratory conditions a stone cover enhances infiltration by protecting the soil from raindrop impact and subsequent surface crusting (Grant and Struchtemeyer

Table 3. Communalities and factor loadings produced by the PCA with Varimax rotation on the 1983 data set.

Factor	Variable	Communality	Factor Loadings 1	2	3	4	5	6	7
	Shrub biomass	.85	.88	0	-.23	.16	-.03	-.03	.04
	Shrub cover	.89	.86	.03	-.32	.17	.04	-.07	.09
1	Total biomass	.92	.85	.21	-.19	.34	-.07	-.01	0
	Basal shrub cover	.74	.77	-.18	.10	-.06	.15	.19	-.19
	Litter biomass	.84	.73	.15	-.10	.52	-.03	.03	-.09
	Rock cover	.85	-.31	-.80	-.19	-.18	-.10	.15	.07
	Total cover	.89	.42	.78	.14	.15	-.11	.22	.07
2	Grass biomass	.66	-.14	.73	.04	-.04	-.28	.10	.16
	Grass cover	.90	-.29	.71	.45	.01	-.24	.23	-.03
	Soil depth	.82	-.12	.58	-.28	-.41	.26	-.33	-.18
	Total basal cover	.87	-.20	.41	.81	-.03	-.04	.06	-.04
3	Basal grass cover	.88	-.28	.43	.78	-.05	-.05	.03	-.03
	Slope gradient	.65	.16	.21	-.69	.07	.28	-.09	-.10
	Litter cover	.83	.15	.17	-.04	.85	.06	-.18	-.11
4	Bareground	.72	-.29	-.01	.08	-.69	.22	-.33	-.07
	Organic carbon (0-5 cm)	.78	.37	-.31	.01	.52	.06	.47	-.23
	Forb cover	.83	-.22	-.19	-.19	.02	.84	.04	.07
5	Forb biomass	.76	.11	-.10	-.35	-.04	.73	-.15	.25
	Ante. Moisture	.62	.35	.02	.40	-.08	.56	.10	.01
6	Silt (0-5 cm)	.84	0	.13	.12	-.02	-.02	.90	-.06
	Clay (0-5 cm)	.91	-.12	0	-.01	-.14	.13	-.43	.82
7	Sand (0-5 cm)	.90	.10	-.16	-.11	.06	-.11	-.48	-.78
	Basal forb cover	.29	.13	-.05	-.06	.34	.07	-.07	.36
	Eigenvalue		5.7	4.3	2.5	1.8	1.5	1.2	1.2
	% variance		25	19	11	8	7	5	5
	Cumulative %		25	44	55	63	70	75	80

1959, Jung 1960, Dadkhah and Gifford 1981). In Arizona, Simanton et al. (1984) demonstrated that if the erosion pavement is removed, erosion will increase, presumably because the soil surface is less protected. After root plowing and pitting semiarid rangeland, Tromble (1976) found that infiltrability was positively related to rock and gravel cover.

The apparent conflict in the literature can be readily explained. Under laboratory or even cultivated conditions, surface rock cover represents additional protection to the otherwise bare soil surface and will reduce raindrop impact and soil crusting. Under natural conditions in an arid or semiarid environment, a stone pavement has evolved and exists because of the lack of vegetal cover (Cooke and Warren 1973). In areas not protected by vegetation, more erosion will occur, resulting in removal of fine soil particles and organic matter and a lowering of the surface, leaving coarse fragments or a stone pavement behind. Exposure of the soil surface accelerates decomposition of organic matter and compaction of the soil by raindrop impact (Satterlund 1972) resulting in a more impermeable surface. Infiltrability of stone pavements is low, therefore, not because of the rock cover per se, but because of the soil crusting and compaction that has resulted from raindrop impact. This is supported by partial correlation analysis (Fig. 10) showing that when the effects of vegetal cover and slope are removed, rock cover was much less significant in year 1 and was positively related to infiltrability in year 2. This supports the laboratory research showing that rock cover enhances infiltrability.

A very interesting feature of the data was the relationship between the rock size classes and infiltrability (Fig. 11). The

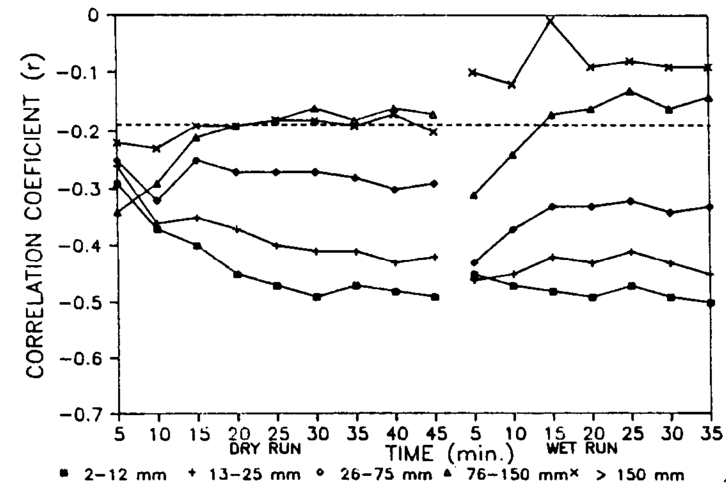

Fig. 11. *Year 2 correlations between rock cover by size class and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant ($p \leq 0.05$).*

smaller the rock size the more significant and negative the relationship. Each succeedingly smaller rock size class became more strongly correlated with infiltrability. Yair and Lavee (1976) found the opposite relationship between rock size and infiltrability on talus mantled slopes in arid Israel. They concluded that runoff was positively correlated with rock size class. In their study area, however, rocks were larger and covered a greater surface area. In general, conditions were quite different from those in the Guadalupe mountains. The questions remains as to why low infiltrability was associated with cover by small rocks rather than larger ones? The most obvious answer is that the erosion pavement (from which sediment production was high) was composed mostly of the smaller sized rock fragments incorporated in the soil. The larger rock fragments mostly originated from weathered limestone cliffs faces which commonly protrude from the Guadalupe Rim, and do not represent erosional pavement.

When the effects of vegetal cover and slope gradient were removed, infiltrability was only negatively correlated with the very smallest size class of rocks and was positively correlated with the intermediate size classes (26–75 mm, 76–150 mm) (Fig. 12). Correlations were nonsignificant for the 13–25 mm and >150 mm size classes. These data indicate that if rock cover inhibits infiltration, it

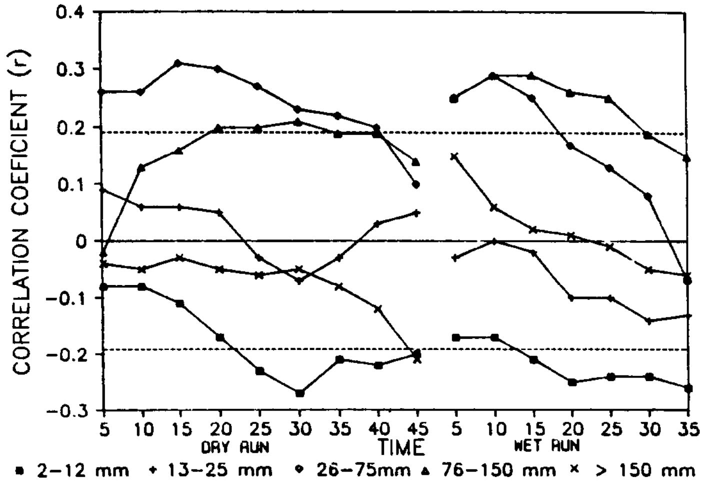

Fig. 12. *Year 2 partial correlations (effect of vegetal cover and slope removed) between rock cover by size class and infiltrability. Dashed lines represent the value at which correlations are significant. ($p \leq 0.05$).*

is most likely when smallest rocks dominate. Infiltration is encouraged by larger sized rock cover. Perhaps soil coverage by small rocks does not afford the same degree of protection as an equal coverage by larger sized rock fragments. The largest rock class was nonsignificant because of its low overall cover (Table 2). Similarly, Tromble et al. (1974) found that infiltrability was negatively correlated with gravel (<10 mm), but was positively correlated (not significantly) to the larger rock size fragments.

Slope Gradient

Infiltrability was positively related to slope gradient in year 1, although not significantly (Fig. 13). It was negatively related in year 2, with significant coefficients occurring at the beginning of the rainfall event. In other words in year 2, on the steep slopes infiltrability was initially lower than on the low ones, but after a

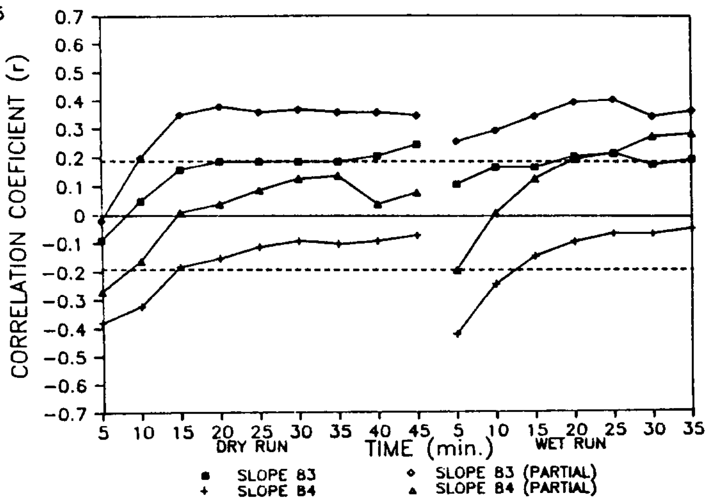

Fig. 13. *Correlations between slope and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant ($p \leq 0.05$).*

few minutes differences were minimal. Rock and vegetal cover were significantly correlated with slope and when the effect of these variables were removed (by partial correlation analysis), the correlation was mostly positive. Partial correlation coefficients were most significant for year 1. These data support the work of Wilcock and Essery (1984), who found a strongly positive correlation (r = .78) between infiltrability and slope, and McCord (1985), who argued that slope positively influences infiltrability because of its influence on subsurface flow. One possible reason for the positive correlation between slope gradient and infiltrability is that interflow rates are increased with slope gradient, particularly if a shallow subsurface impeding horizon is present (Whipkey and Kirkby 1978).

Factor Analysis

Factor analyses were performed on each set of data. Seven factors were produced from year 1 (Table 3) and 6 from year 2 (Table 4). Each factor has an eigenvalue >1, and thus accounted for more variation than an individual, original variable. Factor loadings and communalities appear in Tables 3 and 4. Communalities are assigned to each variable and are the percentage of the respective variable variance accounted for by the factors. For example, the 7 factors retained for year 1 accounted for 85% of the variance of shrub biomass (Table 3). The factor loadings are the correlation between the respective variables and factors.

The factors produced from both sets of data were quite similar and interpretation was straight forward. In each set there was a factor representing (1) vegetal and rock cover (2) vegetal biomass (3) forb cover and biomass (4) soil texture (each data set has 2 factors representing soil texture) and (5) soil surface condition (bare ground organic carbon, litter cover).

The factors produced were satisfactory but not ideal. The basal cover-slope gradient factor (year 1) was generally uninformative because slope gradient and basal cover counteracted one another. Basal cover was negatively correlated with slope gradient (r = –.44); thus as slope increased, basal cover tended to decrease. Pearson and partial correlation analysis has indicated that both are positively related to infiltrability. In year 2, slope was buried in the cover factor. The year 1 cover factor was heavily weighted by grass biomass and grass biomass contributed little to the biomass factor. The 2 soil textural factors produced from each data set also differ. In year 1, clay and sand were combined and silt occurred as a single factor, while in year 2 clay and silt were combined and sand accounted for an individual factor. Vegetal cover was positively related and rock cover was negatively related to the year 1 cover factor. The opposite relationship occurred for year 2.

The cover factor easily accounted for the most variation in year 1 (Fig. 14 and 15). Rock cover and total vegetal cover were the major variables loaded into this factor, but grass biomass was included as well (Table 3). The cover factor curves for the dry and wet run were quite similar. Infiltrability was generally poorly correlated to the biomass factor (minus grass biomass) in year 1. The only other factor with which infiltrability was significantly correlated was the clay/sand factor (Fig. 14). Note the gradual increase in correlation with time during both the dry and wet runs. This factor was positively weighted by clay and negatively weighted by sand (Table 3). The silt factor was nonsignificant. The soil surface factor and forb factor were nonsignificant.

In year 2 the cover, biomass and soil surface factors (Figs. 16 and 17) were most significant. Infiltrability was most correlated with

Table 4. Communalities and factor loadings produced by the PCA with Varimax rotation on the 1984 data set.

			Factor Loadings					
Factor	Variable	Communality	1	2	3	4	5	6
	Total rock cover	.97	.91	–.28	.19	.09	–.01	.10
	Total cover	.94	–.85	.36	–.09	.30	–.02	–.02
	Rock cover 26–75mm	.78	.84	–.20	.13	.11	.01	–.03
	Slope gradient	.84	.76	.37	–.30	.18	–.08	–.04
1	Rock cover 76-150mm	.97	.72	–.07	.04	.05	–.11	–.20
	Rock cover 13-25mm	.72	.71	–.32	.23	.03	0	.26
	Litter cover	.70	–.69	.20	.06	.33	–.06	–.27
	Basal grass cover	.82	–.66	–.51	.12	.18	–.04	.28
	Rock cover 2-12mm	.72	.51	–.37	.24	.09	.04	.37
	Shrub cover	.93	–.21	.93	.13	.06	.04	.02
	Shrub biomass	.88	–.16	.90	.01	.22	.03	.06
2	Total biomass	.88	–.24	.86	.03	.28	0	.05
	Basal shrub cover	.62	–.03	.78	.02	–.06	–.09	.02
	Litter biomass	.63	–.42	.57	.16	.30	–.05	.01
	Clay (0-5 cm)	.80	–.10	–.05	–.87	.09	0	–.16
	Silt (0-5 cm)	.84	.03	.02	.84	–.03	.06	–.37
3	Silt (5-10 cm)	.82	.08	.02	.72	.35	–.17	–.39
	Clay (5-10 cm)	.65	–.06	–.07	–.67	–.34	.24	.11
	Organic carbon (5-10 cm)	.71	.12	.05	.52	.49	.43	–.06
	Bare ground	.70	0	–.26	–.17	–.76	.08	–.13
	Organic carbon (0-5 cm)	.75	–.08	.35	.42	.55	.27	–.26
4	Bulk density	.46	.02	–.21	–.09	–.50	–.11	.37
	Grass biomass	.55	.03	–.25	–.33	.48	–.36	–.14
	Forb cover	.77	–.10	.06	–.02	–.03	.86	–.16
5	Forb biomass	.75	–.11	.06	–.11	.03	.85	–.02
	Basal forb cover	.43	.14	–.19	.01	–.01	.61	–.04
	Sand (0-5 cm)	.72	.10	.04	–.12	–.08	–.09	.82
6	Sand (5-10 cm)	.51	–.08	.10	–.19	–.06	–.12	.66
	Soil depth	.76	–.46	–.10	–.43	–.30	–.23	–.46
	Eigenvalue		7.0	5.0	3.1	2.4	2.0	1.5
	% variance		24	17	11	8	7	5
	Cumulative %		24	41	52	60	67	72

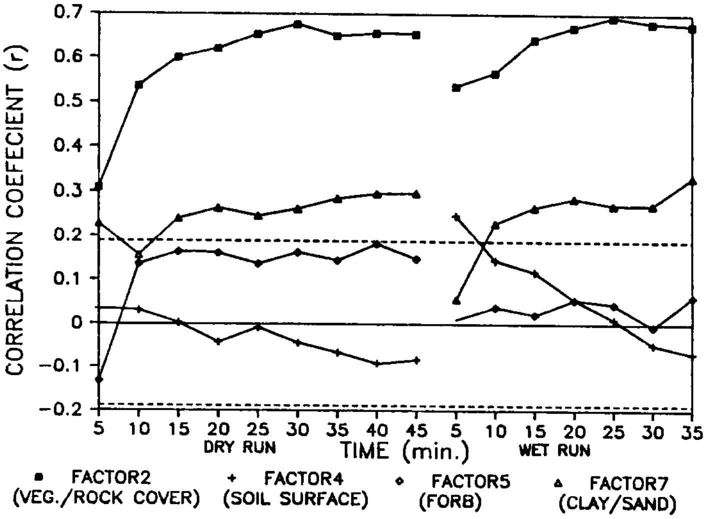

Fig. 14. *Positive correlations between the year 1 PCA factors and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant* ($p \leq 0.05$).

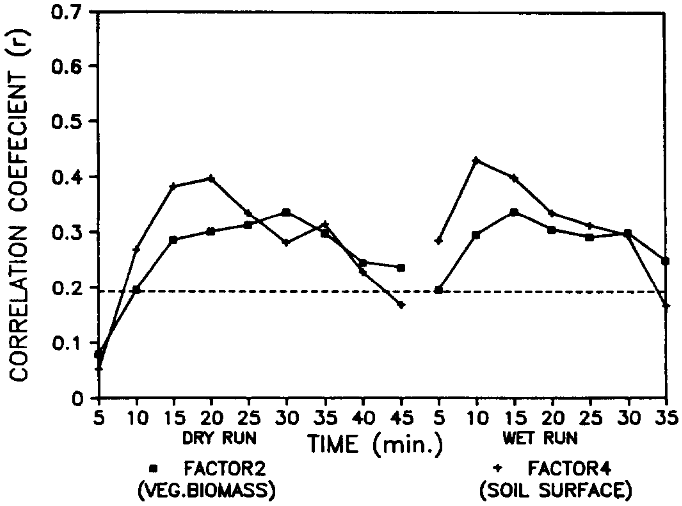

Fig. 16. *Positive correlations between the year 2 PCA factors and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant* ($p \leq 0.05$).

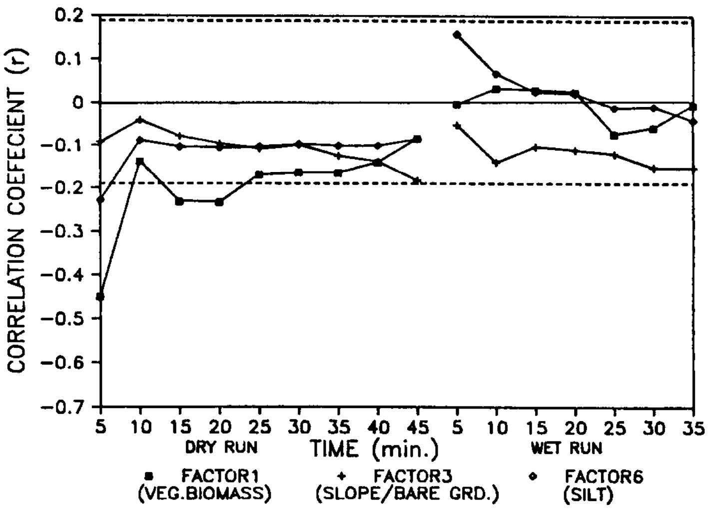

Fig. 15. *Negative correlations between the year 1 PCS factors and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant* ($p \leq 0.05$).

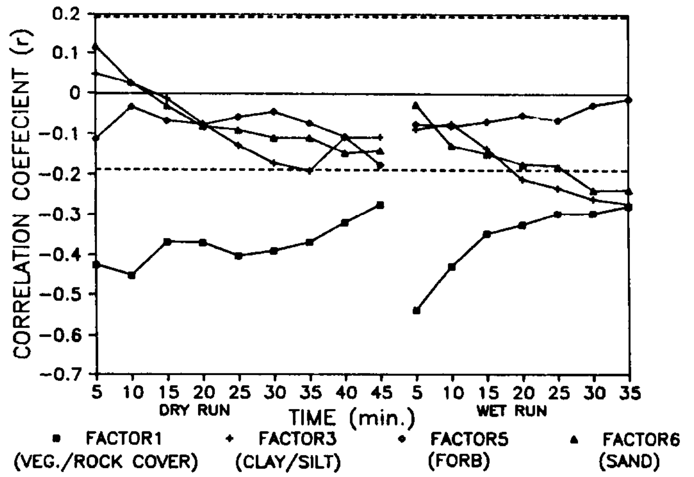

Fig. 17. *Negative correlations between the year 2 PCA factors and infiltrability at 5-minute intervals for the dry and wet runs. Dashed lines represent the value at which correlations are significant* ($p \leq 0.05$).

the cover factor, however, the coefficient decreased (absolute value) with time. (Infiltrability was negatively correlated with the cover factor because the factor was negatively weighted by vegetal cover and positively weighted by rock cover (Table 4)). Recall that vegetal cover (year 2) also decreased in significance in the wet run (Fig. 2). Similar phenomena were not observed in year 1 (Fig. 14). The soil surface and biomass factors correlation curves (Fig. 16) were very similar in shape (highest correlations occurred in the middle of the infiltration runs). This is the same general shape of the vegetal biomass, organic carbon, bareground and bulk density correlation curves produced for year 2 (Figs. 5, 8, and 9). This relationship to infiltrability was not evident for any of these variables or factors for year 1.

Conclusions

Analysis of 2 years of infiltration data collected with a small plot rainfall simulator on semiarid slopes indicated the following.

(1) Vegetation has a major effect on soil infiltrability. This conclusion is nothing new and has been shown by numerous previous research. Previous research, however, has generally ignored steep slopes. The relative importance of grasses, shrubs, and litter is dependent on their respective productivity, especially of grasses. Infiltrability was generally better correlated with vegetal cover than biomass. Aerial cover was a much better indicator of infiltrability than was basal cover.

(2) For shallow soils small changes in soil depth have a large impact on infiltrability. The impacts of soil depth to infiltrability become more acute as infiltration progresses.

(3) Increases in clay within the clay loam-silty clay loam textural classes increases infiltrability; possibly because of increased aggregation.

(4) Rock cover is negatively associated with infiltrability because generally low vegetal cover accompanies high rock cover. Some protection however is offered by rock cover, especially if fragments

are larger than 25 mm in length. In other words, infiltrability is higher if rock cover is protecting the soil surface than if the soil surface is bare.

(5) Infiltrability is positively related to slope gradient; possibly because interflow increases with increases in slope.

Factor analysis supported the conclusions drawn from the Pearson correlation analysis. Partial correlation analysis proved especially valuable in separating out the effects of one or more variables from another variable. Results of the 2 years of data were not always in complete agreement, sometimes making it more difficult to draw general conclusions, but well illustrating the potential danger of interpreting relationships based upon 1 year of data.

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Effects of temperature, water potential, and sodium chloride on Indiangrass germination

TIMOTHY E. FULBRIGHT

Abstract

Indiangrass [*Sorghastrum nutans* (L.) Nash] is widely used in range seeding. Objectives of this study were to determine the effects of temperature, water potential, and sodium chloride on germination of 'Lometa', 'Cheyenne', 'Llano', 'Oto', and 'Tejas' Indiangrass. Seeds were germinated at 6 alternating temperatures ranging from 5–15 to 30–40° C (12 hours–12 hours). Lometa, Cheyenne, and Tejas seeds were germinated in polyethylene glycol (mol. wt. = 8,000) solutions mixed to approximate water potentials of 0, -0.4, -0.8, -1.2, and -1.6 MPa and in 0, 0.06, 0.12, 0.18, and 0.24 mol liter^{-1} sodium chloride solutions. Optimum temperatures for percent germination were 10–20 to 25–35, 10–20 to 20–30, and 15–25 and 20–30° C for Cheyenne and Tejas, Llano and Oto, and Lometa seeds, respectively. Percent germination of Cheyenne and Lometa seeds was reduced at water potentials of -0.8 MPa and lower, while Tejas seeds exhibited lower percent germination than controls at -1.2 and -1.8 MPa. Percent germination of Cheyenne and Lometa seeds was reduced by sodium chloride concentrations of 0.12 mol liter^{-1} and greater. Germination of Tejas seeds was reduced at 0.18 and 0.24 mol liter^{-1}. Indiangrass varieties appear to germinate within a similar range of temperatures but vary in germination response to low water potentials.

Key Words: ***Sorghastrum nutans*, range seeding, ecophysiology, seed ecology, salinity**

Indiangrass [*Sorghastrum nutans* (L.) Nash] is a native warm-season bunchgrass widely used in range seeding. 'Lometa' Indiangrass is a variety developed by the USDA Soil Conservation Service at Knox City, Texas, for use in central and southern Texas (Lorenz and Heizer 1982). Lometa is drought tolerant and produces forage yields almost twice that of 'Cheyenne' and 'Tejas' Indiangrass, 2 other varieties commonly planted in Texas, but has been difficult to establish in experimental plantings at the South Texas Plant Materials Center at Kingsville, Texas (Richard Heizer, SCS State Plant Materials Specialist, pers. commun.).

Success in artificial range seeding requires knowledge of many parameters, including optimum temperature and moisture conditions for germination (Sabo et al. 1979). Hsu et al. (1985) found that chilled 'IG-2C-F1' Indiangrass seeds germinated best at constant temperatures of 20 to 35° C, while highest germination of unchilled seeds occurred between 12 and 15° C. The Association of Official Seed Analysts (1970) recommends testing Indiangrass seeds at 20–30° C (16 hours–8 hours).

Germination is also affected by soil salinity. Soluble salts such as sodium chloride may reduce or prevent germination by direct ion effects or by lowering the osmotic potential of the soil solution (Young et al. 1983).

My objective was to determine the effects of 6 alternating temperature regimes, reduced water potentials, and sodium chloride on germination of Lometa Indiangrass. A second objective was to compare germination of Lometa with that of 4 other Indiangrass varieties commonly planted in the Southern Great Plains.

Author is associate professor, College of Agriculture and Home Economics, Campus Box 156, Texas A&I University, Kingsville, Texas 78363.

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Materials and Methods

General Methods

Lometa Indiangrass seeds were obtained from the USDA-SCS Plant Materials Center at Knox City, Texas. Seeds used in temperature experiments were harvested in 1978 and those used in other experiments were harvested in 1981. Cheyenne (harvested in 1981), 'Llano' (harvest date unknown), 'Oto' (harvest date unknown), and Tejas (harvest date unknown) seeds were obtained from commercial sources. Seed viability was determined by soaking seeds in a 0.1% 2,3,5-triphenyltetrazolium chloride solution at 30° C for 3 hours (Grabe 1970). Viability of Lometa seeds was 84% for seeds harvested in 1978 and 52% for seeds harvested in 1981. Viability of Cheyenne, Llano, Oto, and Tejas seeds was 32, 83, 68, and 62%, respectively. Until used in experiments, seeds were stored in cloth bags at 15° C and 40% relative humidity. Temperature experiments were conducted in 1983 and other experiments were conducted in 1985.

Seeds were germinated on blotter paper (temperature experiments) or 2 layers of filter paper underlain by a layer of creped cellulose placed within 13.0 by 13.5 by 3.5 cm plastic boxes with tightly fitting lids. Seeds were treated with thiram [bis(dimethylthiocarbamoyl)disulfide] to minimize fungal growth.

Four plastic boxes arranged within controlled environment chambers in a randomized complete-block design were used as experimental units for each treatment and each experiment was repeated twice. Chambers were illuminated for 12 hours daily with cool-white fluorescent lights (photosynthetic photon flux density averaged 24 μmol m^{-2} s^{-1}).

Seeds were considered germinated when radicles and shoots were >4 mm long. Germinated seeds were counted daily for 28 days in the temperature experiments and at 5-day intervals for 20 days in other experiments. Germination rate (GR) was calculated by the equation of Maguire (1962). Corrected germination rate index (CGRI) was obtained by dividing GR by the final germination percentage and multiplying by 100 (Hsu et al. 1985).

Temperature Effects

Effects of temperature on germination of the 5 varieties of Indiangrass were determined by germinating seeds at 5–15, 10–20, 15–25, 20–30, 25–35, and 30–40° C (12 hours of darkness–12 hours in light). Each plastic box contained 100 seeds and the substrata were moistened with 100 ml of tap water.

Response curve analyses were used to determine the relationship between temperature and germination (Snedecor and Cochran 1967). Percent germination data were arcsine transformed before analysis, but untransformed data are reported in tables. Optimum temperatures for percent germination were defined as those temperatures for which mean percent germination was within the 95% confidence interval of the maximum mean percent germination (Young et al. 1981). Optimum temperatures for CGRI were defined similarly.

Water Potential and Sodium Chloride Effects

Seeds of Lometa, Cheyenne, and Tejas Indiangrass were germinated at 15–25° C (12 hours light–12 hours dark) on substrata moistened with 100 ml polyethylene glycol (PEG) 8000 solutions mixed according to Michel (1983) to give water potentials of 0,

-0.4, -0.8, -1.2, and -1.6 MPa. Since the water potential of PEG solutions may vary between PEG lots (Berkat and Briske 1982), samples of the solutions were sent to Dr. D. Kreig, Texas Tech University, for verification. Thermocouple psychrometer values for -0.4, -0.8, -1.2, and -1.6 MPa solutions were -0.44 ± 0.05, -0.88 ± 0.17, -1.17 ± 0.01, and -1.59 ± 0.11 MPa ($\bar{x}$ ± SD, n = 6). The pH of the PEG solutions ranged from 7.0 to 7.9, and the pH of distilled water averaged 6.0.

Seeds of the 3 Indiangrass varieties were also germinated on substrata moistened with sodium chloride (NaCl) solutions of 0, 0.06, 0.12, 0.18, and 0.24 mol $liter^{-1}$. The pH of these solutions ranged from 5.8 to 6.4

In PEG and NaCl experiments, plastic boxes contained 50 seeds each and were sealed in plastic bags to inhibit evaporation. Radicle and shoot lengths of 2 randomly selected seedlings in each box were measured at the end of each experiment.

Response curve analyses were used to determine the relationship between water potential or NaCl concentration and percent germination, CGRI, radicle length, and shoot length (Snedecor and Cochran 1967). Percent germination data were arcsine transformed before analysis. Untransformed data are reported in tables. Fisher's protected LSDs were used to determine if germination at various levels of PEG or NaCl were significantly (P<0.05) different from controls (distilled water). This test is appropriate when comparing each treatment mean with the control (Petersen 1985).

Results

Temperature Effects

Germination of each of the 5 Indiangrass varieties exhibited a quadratic response to temperature (Table 1). Optimum temperatures for percent germination were 10-20 to 25-35° C for Cheyenne and Tejas, 10-20 to 20-30° C for Llano and Oto, and 15-25 and 20-30° C for Lometa seeds.

Table 1. Means and standard deviations (in parentheses) for the effects of 6 alternating temperatures (° C) on percent germination of 5 varieties of Indiangrass. Underlined means are within the 95% confidence interval of the maximum germination percentage for a variety.

Temperature	Cheyenne	Llano	Lometa	Oto	Tejas
	%				
5-15	11(8)	7(6)	24(18)	17(13)	16(9)
10-20	33(5)	65(5)	70(4)	53(8)	52(6)
15-25	33(5)	66(6)	75(3)	53(4)	53(6)
20-30	32(7)	62(2)	74(5)	49(4)	49(4)
25-35	30(4)	54(8)	60(3)	39(3)	47(7)
30-40	21(4)	40(3)	45(9)	30(6)	34(7)
Response curve relationship	Quadratic	Quadratic	Quadratic	Quadratic	Quadratic
R^2	0.58**	0.78**	0.68**	0.61**	0.65**

**Significant at P<0.01.

Corrected germination rate index of the 5 Indiangrass varieties increased quadratically with increasing temperature (Table 2). Highest CGRI of Cheyenne and Oto seeds occurred at 30-40° C. Optimum temperatures for CGRI were 25-35 and 30-40° C for Llano and Tejas seeds and 20-30 to 30-40° C for Lometa seeds.

Water Potential and Sodium Chloride Effects

Percent germination of Cheyenne, Lometa, and Tejas seeds decreased quadratically with decreasing (more negative) water potential (Table 3). Germination of Tejas seeds was lower at water potentials of -1.2 and -1.6 MPa than in distilled water. Percent germination of Cheyenne and Lometa seeds was significantly (P<0.05) lower than that of controls at -0.8 MPa and more negative water potentials.

Table 2. Means and standard deviations (in parentheses) for the effects of 6 alternating temperatures (° C) on corrected germination rate index (CGRI) of 5 varieties of Indiangrass. Underlined means are within the 95% confidence interval of the maximum CGRI for a variety.

Temperature	Cheyenne	Llano	Lometa	Oto	Tejas
	%				
5-15	3.6(0.1)	3.6(0.2)	3.8(0.1)	3.7(0.2)	3.9(0.3)
10-20	7.1(0.8)	6.5(0.5)	6.4(0.2)	6.6(0.4)	7.1(0.4)
15-25	10.5(1.0)	9.6(0.7)	9.8(0.9)	10.1(1.0)	11.1(0.8)
20-30	12.2(0.9)	12.7(1.0)	13.4(0.6)	12.3(0.6)	12.9(0.5)
25-35	12.7(0.6)	13.3(0.3)	12.7(0.5)	12.4(0.4)	13.4(0.4)
30-40	13.7(0.7)	13.4(0.5)	13.3(0.3)	13.5(0.8)	13.7(0.6)
Response curve relationship	Quadratic	Quadratic	Quadratic	Quadratic	Quadratic
R^2	0.95**	0.97**	0.95**	0.96**	0.97**

**Significant at P<0.01.

Table 3. Means and standards deviations (in parentheses) for the effect of reduced water potentials (MPa) on percent germination, corrected germination rate index (CGRI), root length (mm), and shoot length (mm) of 3 varieties of Indiangrass at 15-25° C (12 hours light-12 hours dark). Underlined means are not significantly different (P>0.05) from controls (0 MPa) according to Fisher's protected LSD.

Variety and water potential	% Germination	CGRI	Root length	Shoot length
	%		mm	mm
Cheyenne				
0	31(4)	12.5(1.9)	43(16)	47(15)
-0.4	30(6)	9.0(0.8)	29(21)	30(15)
-0.8	24(8)	6.2(0.4)	18(13)	20(13)
-1.2	5(5)	5.1(0.2)	14(7)	10(5)
-1.6	0	—	—	—
Response curve relationship	Quadratic	Quadratic	Linear	Linear
R^2	0.62**	0.87**	0.33**	0.48**
Lometa				
0	44(5)	10.8(1.2)	54(15)	53(10)
-0.4	38(8)	9.1(0.4)	36(16)	35(21)
-0.8	27(14)	6.0(0.3)	21(9)	20(13)
-1.2	5(6)	5.1(0.3)	12(6)	10(6)
-1.6	0	—	—	—
Response curve relationship	Quadratic	Linear	Linear	Linear
R^2	0.68**	0.88**	0.61**	0.55**
Tejas				
0	46(9)	13.7(1.8)	48(10)	52(19)
-0.4	47(6)	10.9(0.6)	44(19)	42(20)
-0.8	40(9)	7.8(0.8)	29(9)	38(11)
-1.2	17(10)	5.4(0.3)	15(9)	18(11)
-1.6	0	—	—	—
Response curve relationship	Quadratic	Linear	Linear	Linear
R^2	0.67**	0.91**	0.52**	0.37**

**Significant at P<0.01.

Corrected germination rate index of Cheyenne decreased quadratically with decreasing water potential and decreased linearly with decreasing water potential for seeds of the Lometa and Tejas varieties (Table 3). CGRI of all 3 varieties at –0.4 MPa and lower water potentials was lower than that of controls.

Root and shoot length of each variety decreased linearly with decreasing water potential (Table 3). Tejas appeared better adapted for seedling development at low water potentials than Cheyenne and Lometa Indiangrass. Root length of Tejas seedlings was similar to that of controls at –0.4 MPa. Tejas shoot length was similar to that of controls at –0.4 and –0.8 MPa. Roots and shoots of Cheyenne and Lometa seedlings were shorter than those of controls at –0.4 MPa and lower water potentials.

Cheyenne and Tejas seeds exhibited a quadatic decrease in percent germination with increasing NaCl concentration, while percent germination of Lometa seeds decreased linearly (Table 4).

Table 4. Means and standard deviations (in parentheses) for the effect of sodium chloride concentration (mol liter^{-1} on percent germination, corrected germination rate index (CGRI), root length (mm), and shoot length (mm) of 3 varieties of Indiangrass at 15–25° C (12 hours light–12 hours dark). Underlined means are not significantly different (P>0.05) from controls (0 MPa) according to Fisher's protected LSD.

Variety and sodium chloride level	Characteristic			
	% Germination	CGRI	Root length	Shoot length
	—%—		–mm–	–mm–
Cheyenne				
0	33(5)	14.3(1.7)	32(9)	46(15)
0.06	31(6)	11.5(2.8)	46(10)	51(13)
0.12	25(7)	9.1(0.6)	32(7)	35(8)
0.18	18(7)	6.6(0.7)	21(6)	20(8)
0.24	5(3)	5.5(0.8)	11(4)	7(3)
Response curve relationship	Quadratic	Linear	Quadratic	Quadratic
R^2	0.78**	0.81**	0.62**	0.71**
Lometa				
0	37(11)	12.1(3.0)	44(11)	47(12)
0.06	30(4)	9.3(0.9)	44(6)	41(10)
0.12	19(5)	7.3(0.4)	40(8)	32(8)
0.18	5(4)	6.0(0.8)	17(10)	17(10)
0.24	1(1)	5.0(0)	5(2)	6(3)
Response curve Relationship	Linear	Linear	Quadratic	Linear
R^2	0.81**	0.69**	0.68**	0.64**
Tejas				
0	47(7)	14.8(1.4)	42(11)	69(16)
0.06	42(8)	13.3(1.9)	40(6)	57(12)
0.12	44(10)	10.4(1.3)	35(6)	40(14)
0.18	31(9)	7.0(0.7)	29(7)	24(4)
0.24	11(6)	5.7(0.6)	13(5)	13(6)
Response curve relationship	Quadratic	Linear	Quadratic	Linear
R^2	0.74**	0.88**	0.69**	0.79**

**Significant at P<0.01.

Percent germination of Cheyenne and Lometa seeds was lower than that of controls at 0.12 mol liter^{-1} and greater concentrations. Percent germination of Tejas seeds was reduced at 0.18 and 0.24 mol liter^{-1}.

Corrected germination rate index of all varieties decreased linearly with increasing NaCl concentration (Table 4). CGRI of all varieties was lower than controls at all NaCl concentrations.

Root lengths of all varieties responded quadratically to increasing NaCl concentrations (Table 4). Cheyenne and Lometa roots were shorter than those of controls at concentrations of 0.18 and 0.24 mol liter^{-1}. Roots of Tejas seedlings were shorter than those of controls at all concentrations greater than 0.06 mol liter^{-1}.

Shoot length of Cheyenne seedlings responded quadratically to increasing NaCl concentration and shoots of Lometa and Tejas seedlings decreased linearly with increasing concentration (Table 4). Shoot length of Cheyenne and Lometa seedlings was reduced by NaCl concentrations of 0.12 mol liter^{-1} or more compared to controls. Shoot length of Tejas was reduced by all NaCl concentrations.

Discussion

The optimum temperatures for percent germination of Indiangrass were similar to those reported for little bluestem [*Schizachyrium scoparium* (Michx.) Nash], a species with which Indiangrass often grows in association. The optimum temperature for percent germination of little bluestem is 16.5–27° C (16 hours–8 hours) (Sabo et al. 1979). The optimum temperature for percent germination was lower than that of brownseed paspalum (*Paspalum plicatulum* Michx.), a species that commonly grows in association with Indiangrass in southern Texas. The optimum temperatures for percent germination of brownseed paspalum sources from south Texas range from 20–30 to 30–40° C (12 hours–12 hours) (Flenniken and Fulbright 1987).

Monthly average daily minimum and maximum air temperatures in the optimum temperature range for percent germination of Lometa occur most frequently in southern coastal Texas in March, April, May, and October (NOAA 1972). Optimum temperatures for CGRI of Lometa occur from April to October. Planting in April or May would possibly favor percent germination and germination rate of Lometa. Spring planting might also be desirable because May is a period of relatively high rainfall.

Tejas seeds appeared to be better adapted for germination and seedling development at low water potentials than Cheyenne or Lometa seeds. Tejas seeds also appeared better adapted for germination in the range of salt concentrations tested than the other varieties. Although Tejas seeds appeared adapted for optimum germination at higher salt concentrations than the other varieties, Lometa and Cheyenne seedlings produced greater root and shoot growth at higher salt concentrations than Tejas.

The osmotic potential of a 0.18 mol liter^{-1} solution of NaCl is about 0.81 MPa. Effects of the NaCl solutions on Cheyenne and Tejas seeds were possibly more related to osmotic effects than toxic effects of NaCl because germination percentages and rates were similar for the 0.18 mol liter^{-1} NaCl solution and the 0.8 MPa PEG solution. Percent germination of Lometa Indiangrass was lower in NaCl solutions than in PEG solutions with similar water potential, indicating possible toxic effects of the salt.

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Irrigation water for vegetation establishment

R.E. RIES, F.M. SANDOVAL, AND J.F. POWER

Abstract

This research project was conducted to evaluate the use of irrigation water to supplement precipitation during establishment of perennial forage plant communities on surface mined lands in the northern Great Plains. The treatments included precipitation and 9 combinations of various quantities of medium and low quality water applied to a clay loam topsoil replaced over a loam minespoil. We measured the response to the added water of a seeded forage species mixture, volunteer weeds, and changes in salinity and sodicity of the soil/spoil profile. All levels of irrigation, regardless of water quality, increased seeded species production, but decreased weed dry matter. One season of irrigation with medium or low quality water produced minimal changes in soil salinity and sodicity. Some increase in soil salinity and sodicity was observed when low quality water was added during the second season. Therefore, low quality water can be used beneficially to supplement precipitation for 1 or 2 seasons during the establishment of perennial plant communities on moderately permeable soil/spoil areas.

Key Words: irrigation, grass/legume, sodicity, salinity, revegetation, reclamation, perennial forages

Prompt reestablishment of vegetation on disturbed lands is important to protect replaced soil materials from excessive soil erosion. Successful revegetation in the semiarid and arid West (Ries and Day 1978) is dependent on amount and distribution of precipitation. Irrigation to supplement natural precipitation during stand establishment of perennial plant communities is often beneficial, especially when precipitation is limited (Ries 1980).

Within the lignite fields of North Dakota, most ground waters (Croft 1974) and surface impounded waters (Gilley et al. 1976) are of marginal quality for irrigation. Because these waters usually have to be disposed of during mining, there has been interest in using them for irrigation during perennial plant community establishment. Recent studies have shown the usability of poor quality water, even sea water, for crop production with carefully managed irrigation practices (Epstein and Norlyn 1977, Thomas et al. 1981). Other research using blowdown water (a highly saline water resulting from power plant cooling towers) has shown similar usability (Zartman et al. 1980, Jury et al. 1980).

The research reported in this paper was conducted to evaluate the use of marginal quality water to supplement precipitation during establishment of perennial forage plant communities on surface mined lands. Results could also be applied to grass establishment on undisturbed lands.

Study Area and Methods

This research was conducted in southwestern North Dakota, near Gascoyne about 46° N, 103° W, on land that had been surface mined for lignite. Soil in the area before mining was Shambo loam (fine-loamy, mixed *Typic Haploboroll*) on nearly level to gentle slopes. Climate is continental, with frequent and rapid temperature changes throughout the year. Average annual temperature is 6.1° C and the highly variable precipitation averages 380 mm annually. Seventy percent of the long-term average precipitation falls from May through September with June being the wettest month (almost 100 mm). Droughts are common and may last for months or years. Potential evapotranspiration is about twice average precipitation.

After mining, mine spoils were leveled to less than 1% grade, disked, and an average thickness of 210 mm of topsoil spread over the plot area. The plot area was fertilized with 18 kg N and 35 kg P/ha, disked and harrowed. A total of 30 plots, 120 by 180 cm, were established on the plot area in 3 blocks.

Soil and spoil samples were taken from each plot in June of 1977, prior to seeding, to characterize soil and spoil on the plot area. Topsoil was sampled in depth increments of 0 to 100 to 210 mm. Spoil was sampled in 150-mm increments from 210 through 810 mm, and in 300-mm increments from 810 to 1,710 mm. Each sample was composed of 2 separate cores, 36 mm diameter, composited by depth increment. Laboratory procedures are described in Handbook 60 (USDA 1954) and Handbook 525 (Sandoval and Power 1977). The soil and spoil pH was determined on a saturation paste and electrical conductivity (EC) on paste extract. Atomic absorption spectrophotometry was used to determine calcium, magnesium, and sodium concentrations in the saturation extract. Sodium adsorption ratio (SAR) was calculated for each soil and spoil sample to evaluate sodicity. Texture (% sand, silt and clay) was determined by the hydrometer method. The same procedures for sampling and analysis of the soil and spoil were repeated each fall after harvest in 1977, 1978, and 1979.

Calcium carbonate and gypsum concentrations were determined because some acid pH values were encountered in lower depths of the spoil. The low pH was probably caused by an excess of hydrogen ions from the lignite contained in the spoil materials. However, low pH should be a transitory condition because of the high levels of calcium reserve in these materials. Soil and spoil characteristics on the research plots at the start of the study are given in Table 1.

Authors are range scientist and soil scientists, respectively, USDA-ARS, Northern Great Plains Research Laboratory, P.O. Box 459, Mandan, ND 58554. J.F. Power is now with the USDA-ARS, Soil and Water Conservation Research Unit, University of Nebraska, Lincoln 68583. F.M. Sandoval, retired, 4685 Clearview Rd., Belgrade, Mont. 59714.

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Each plot was broadcast seeded June 30, 1977, at a rate of 13.4 kg/ha pure live seed (pls) of a grass-legume mixture [23% western wheatgrass (*Agropyron smithii* Rydb.); 11% slender wheatgrass [*A. trachycaulum* (Link) Malte.]; 17% green needlegrass (*Stipa viridula* Trin.); 42% annual rye (*Secale cereale* L.); and 7% yellow sweetclover (*Melilotus officinalis* (L.) Lam.)]. The plots were raked by hand to cover the seed.

Precipitation was measured on site during each growing season with a standard recording rain gauge. Pan evaporation, air temperatures, and wind speed were measured with standard U.S. Weather Bureau equipment (Table 2 and 3).

Medium and low quality waters were used in this study to supplement precipitation. The medium quality water came from the Missouri River and a well near the Gascoyne mine. The low

Table 1. Soil and spoil characteristics.

Depth	pH	CaCO3 Equiv.	Gypsum	Sand	Silt	Clay	Texture[1]	EC[2]	SAR[3]
(mm)			M mol/kg^{-1}		%			dS m^{-1}	
Topsoil									
0-100	7.4[4]	8.3	0.8	36	36	28	CL	4.9	5.5
100-210	7.4	7.8	0.5	36	36	28	CL	5.5	7.2
Spoil									
210-360	6.3	4.2	2.7	35	41	24	L	6.2	4.5
360-510	6.1	2.9	3.3	35	41	24	L	5.7	3.6
510-660	6.0	2.4	3.7	35	41	24	L	5.7	3.6
660-810	5.9	2.5	3.6	36	41	23	L	5.7	3.6
810-1110	5.8	2.8	2.6	36	41	23	L	5.8	3.7
1110-1410	5.9	3.0	2.8	39	40	21	L	5.9	3.7
1410-1710	5.6	2.4	2.3	39	40	21	L	5.4	3.5

[1]CL, clay loam; L, loam.
[2]Salinity as measured by electrical conductivity (EC).
[3]Sodium adsorption ration = SAR = $Na/[(Ca + Mg)/2]^{1/2}$ soluble cation concentrations expressed in meq./L for calculation.
[4]Each value represents the means of 30 samples.

Table 2. Precipitation and free water evaporation data collected at Knife River Mine near Gascoyne, North Dakota.

Month	Precipitation				Evaporation		
	1977	1978	1979	LTA[1]	1977	1978	1979
	mm				mm		
June	108	78	51	97	326	284	287
July	41	85	77	56	351	314	276
August	74	38	80	45	280	242	275
September	133	67	31	35	162	208	234
Growing season Total	356	268	239	233			

[1]Long term average (30+ years) from U.S. Weather Bureau records, Bowman, ND., 22 km W. of mine.

Table 3. Temperature and wind speed data collected at Knife River Mine near Gascoyne, North Dakota.

Month	Average Temperature				Average Wind		
	1977	1978	1979	LTA[1]	1977	1978	1979
	° C				m s^{-1}		
June	19.7	17.4	19.3	16.6	3.4	2.8	3.6
July	21.6	20.9	20.6	21.1	3.6	2.4	2.5
August	17.8	20.7	19.3	20.5	2.8	2.1	2.7
September	15.1	16.1	17.4	14.0	3.3	2.4	2.7

[1]Long term average (30+ years) from U.S. Weather Bureau records, Bowman, ND., 22 km W. of mine.

Table 4. Quality parameters of water used for irrigation.

Water	Year	EC[1]	Tconc.[2]	SAR[3]	Hazard[4] Class	Salinity	Sodicity
		dS m^{-1}	meq./l.				
Medium Quality[5]	1977	1.0	14.5	6.5	C3-S2	High Medium	
Low Quality	1977	3.2	36.4	11.6	C4-S3	Very High	High
	1978	3.8	43.8	18.2	C4-S4	Very High	Very High

[1]Salinity as measured by electrical conductivity (EC).
[2]Tconc. = total concentration
[3]Sodium adsoprtion ratio = SAR = $Na/[(Ca+Mg)/2]^{1/2}$; concentration of cations used in calculation are expressed in meq./L.
[4](U.S. Salinity Laboratory Staff 1954) p. 80.
[5]"Medium" and "low" are relative terms arbitrarily chosen and do not imply water classification.

quality water was ground water intercepted by mining and pumped from the pit. Samples of both waters were analyzed for EC, calcium, magnesium, and sodium concentrations and SAR was calculated (Table 4).
from the pit. Samples of both waters were analyzed for EC, calcium, magnesium, and sodium concentrations and SAR was calculated (Table 4).

Ten water treatments were evaluated. These treatments are listed in Table 5 along with actual amounts of water applied during the study. Besides the precipitation control plots, there were 3 levels of total water applied (precipitation plus irrigation) per season for each water quality (medium and low). Level 1 received 193 mm of water during the season (about 75% expected average precipitation). Level 2 approximated mean free water evaporation of 628 mm during the 3-month season. Level 3 was arbitrarily set at 915 mm during the season.

Water treatments were randomly assigned to each of the 10 plots in each block. Water was applied to each plot by dripping through a 120 by 180 cm galvanized pan with 0.8 mm holes in the bottom, at the rate of about 25 mm per hour. Each plot had a soil border (76 mm high) around it to prevent runon and runoff. Irrigation to supplement natural precipitation was applied during the months of July, August, and September of 1977 and 1978. Medium quality water was applied for one year and low quality water (worst case) was applied for 2 years. The total water required per season was divided by the number of weeks irrigation was applied to obtain weekly application amounts. Any precipitation received was subtracted from the weekly application amounts. If water was needed above precipitation, it was applied to the appropriate plot. Because precipitation occasionally exceeded the weekly rate, actual quantities of water received (Table 5) were slightly higher than planned. No irrigation was applied during the 1979 growing season.

Soil water in each plot was measured periodically with a neutron meter by 300-mm increments to a depth of 2,400 mm. Available soil water (total soil water minus 1.5 MPa soil water) is shown at the beginning of the study in June of 1977 and in May of both 1978 and 1979 in Table 6.

Vegetation yield, used as an indirect measure of establishment, was measured in late summer each year by clipping at ground level, two 929-cm^2 areas from each plot. The vegetation was separated

Table 6. Available soil water at the start of season.

Water Treatments	Available Soil Water[1] Jun '77	May '78	May '79
	mm H_2O/910mm		Soil/Spoil
1. Natural Pptn.[2]	1	48	4
2. Pptn. + MQW[3] 193 mm; 1 yr.	4	11	11
3. Pptn. + MQW 628 mm; 1 yr.	8	69	14
4. Pptn. + MQW 915 mm; 1 yr.	8	100	34
5. Pptn. + LQW[4] 193 mm; 1 yr.	4	18	11
6. Pptn + LQW 628 mm; 1 yr.	0	74	14
7. Pptn. + LQW 915 mm; 1 yr.	0	104	9
8. Pptn. + LQW 193 mm; 2 yr.	0	24	3
9. Pptn. + LQW 628 mm; 2 yr.	4	75	21
10. Pptn. + LQW 915 mm; 2 yr.	1	79	44

[1]Available soil water = Total soil water minus 1.5 MPa soil water.
[2]Pptn. = Precipitation
[3]MQW = Medium Quality Water
[4]LQW = Low Quality Water

into seeded forage species and weeds, oven-dried at 60° C for 48 h, and weighed.

Data were analyzed as a randomized complete block analysis of variance. The significance of differences between means for vegetation yield was determined by a Fisher's protected least significant difference (LSD) test at $P \leq .05$ (Steel and Torrie 1980). The relationships of total yield of seeded and weed species to total water applied by irrigation were evaluated by correlation analysis.

Mean changes in soil/spoil salinity and sodicity were calculated by subtracting the ending (Fall 1979) EC and SAR from the baseline (Spring 1977) EC and SAR level by each soil depth. Comparisons of the quantity of change under the various water

Table 5. Precipitation and water added by irrigation to 10 water treatments during the 3 year period.

Water Treatments	Precipitation, Water Added by Irrigation (Jul – Sep) 1977 Precip.	1977 Irr.	1977 Total	1978 Precip.	1978 Irr.	1978 Total	Total Added by Irrigation 1977-78	1979 Precip.
	mm							
1. Natural Pptn.[1]	248	0	248	190	0	190	0	188
2. Pptn. + MQW[2] 193 mm; 1 yr.	248	47	295	190	0	190	47	188
3. Pptn. + MQW 628 mm; 1 yr.	248	382	630	190	0	190	382	188
4. Pptn. + MQW 915 mm; 1 yr.	248	697	945	190	0	190	697	188
5. Pptn. + LQW[3] 193 mm; 1 yr.	248	47	295	190	0	190	47	188
6. Pptn. + LQW 628 mm; 1 yr.	248	382	630	190	0	190	382	188
7. Pptn. + LQW 915 mm; 1 yr.	248	697	945	190	0	190	697	188
8. Pptn. + LQW 193 mm; 2 yr.	248	47	295	190	34	224	81	188
9. Pptn. + LQW 628 mm; 2 yr.	248	382	630	190	391	581	773	188
10. Pptn. + LQW 915 mm; 2 yr.	248	697	945	190	728	918	1425	188

[1]Pptn. = Precipitation
[2]MQW = Medium Quality Water
[3]LQW = Low Quality Water

Table 7. Yield of seeded forage species.

Water Treatment	Seeded Forage Yield (g m^{-2}) Years 1977	1978	1979	Total 1977-79
	LSD .05 Years = 85			
1. Pptn.[1]	4	302	51	357
2. Pptn. + MQW[2] 193 mm; 1 yr.	7	268	59	334
3. Pptn. + MQW 628 mm; 1 yr.	130	425	65	620
4. Pptn. + MQW 915 mm; 1 yr.	192	495	96	783
5. Pptn. + LQW[3] 193 mm; 1 yr.	12	373	69	454
6. Pptn. + LQW 628 mm; 1 yr.	125	522	127	774
7. Pptn. + LQW 915 mm; 1 yr.	199	557	108	864
8. Pptn. + LQW 193 mm; 2 yr.	12	400	61	473
9. Pptn. + LQW 628 mm; 2 yr.	150	663	163	976
10. Pptn. + LQW 915 mm; 2 yr	136	701	212	1049
LSD .05	101	246	66	321

[1]Pptn. = Precipitation
[2]MQW = Medium Quality Water
[3]LQW = Low Quality Water

treatments was accomplished by a Fisher's protected LSD test at $P \leq .05$ (Steel and Torrie 1980).

Results and Discussion

Vegetation Yield

In 1977, forage yields were greater than the control on plots that received 382 or 697 mm of irrigation (water treatments 3, 6, 9 and 4, 7, 10, respectively, Table 7). No significant ($P \leq .05$) effect of water quality was observed (treatments 3 vs 6 and 9, and 4 vs 7 and 10). Vegetation yield was greatest for the year 1978. In 1978, yield was greater on plots that received 697 mm (treatment 7) of low quality water during 1977 and 391 and 728 mm (treatments 9 and 10) of low quality water during 1978 compared to the control. In 1979, the growing season when no irrigation was applied, forage yield was greater than the control on plots that received 773 and 1,425 mm of low quality irrigation water for 2 years (treatments 9 and 10, respectively). Forage yield was also greater than the control in 1979 on plots that had received 382 mm (treatment 6) of low quality water during 1977.

In 1977, stand composition, based on dry matter weight, consisted of 27% wheatgrasses, a trace of green needlegrass, 49% annual rye, 21% clover, and 3% weedy species. Composition changed in favor of the wheatgrasses (72%) in 1978. Green needlegrass was still present in trace amounts, while annual rye, clover, and weedy species were present at compositions of 5, 3, and 20%, respectively. By 1979, no green needlegrass was present in the stands. Wheatgrasses composed 59% of the stands, while weedy species composed 41%. Kochia (*Kochia scoparia* L.) was the dominant weed, making up 97% of the weedy species composition.

Total forage yield for 1977-79 was correlated with the 1977 and 1978 irrigation water applied. Yield differences between plots receiving the same quantity of medium and low quality water for one season were not significant ($P \leq .05$, Table 7). Figure 1 shows the relationship of total forage yield to total irrigation water added (r=0.93, significant @$P \leq .01$). This is important because the more water added resulted in better stand establishment as shown by increased production of seeded forage species.

The relationship of 1979 forage and weed yields with total water added by irrigation in 1977 and 1978 is shown in Figure 2. Both the

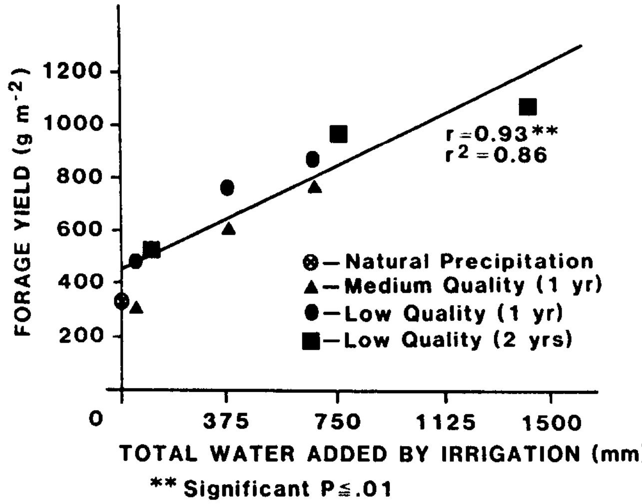

Fig. 1. *Relationship of total seeded forage yield (1977-79) to total water added by irrigation during 1977 and 1978.*

seeded forage species and weed yields were significantly related to total water added by irrigation (r=0.91 and r=0.77 @$P \leq .01$, respectively). The relationship was positive for the forage species and negative for the weeds. Therefore, during 1979, both forage and weed yields still reflected water added above natural precipitation during 1977 and 1978. Stands receiving added water increased in yield of forage species and had fewer weeds. These data further show that the seeded forage species established more competitive stands when supplied with irrigation water, regardless of water quality. The annual weedy species were unable to compete with these more vigorous perennial forage species and thus showed a decrease in dry matter with increased irrigation water.

Soil/Spoil Changes

Water penetration on the precipitation only treatment was observed to a depth of 1,800 mm while on irrigated plots soil water movement was observed to a depth of 2,100 mm. This indicates that the soil/spoil profile was moderately permeable. Soil/spoil changes in salinity and sodicity from baseline conditions (Table 1,

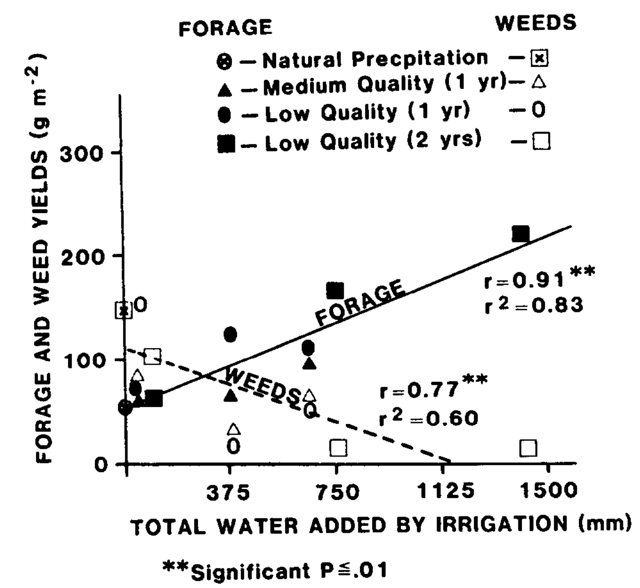

Fig. 2. *Relationship of 1979 forage and weed yields with total water added by irrigation during 1977 and 1978.*

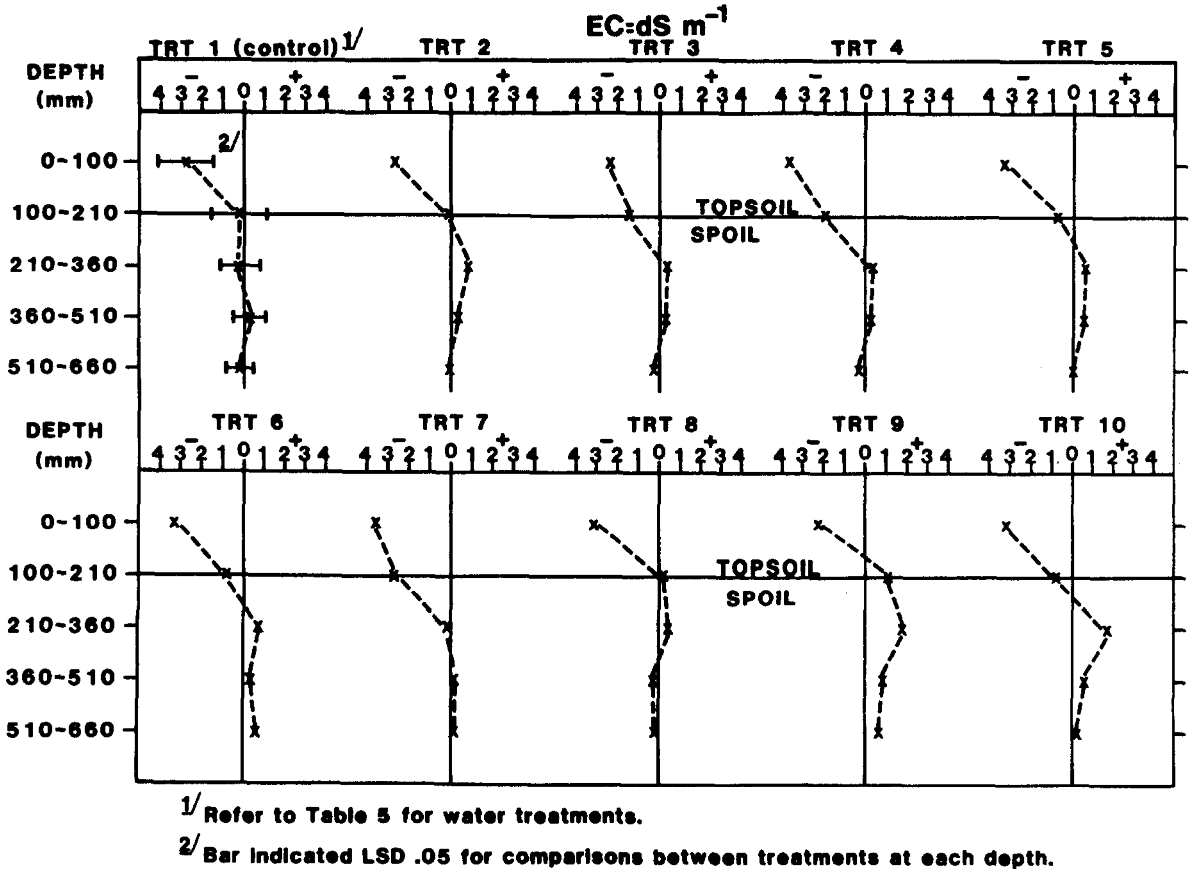

Fig. 3. *Changes in salinity (EC) level of soil/spoil profiles from beginning of study (Spring 1977) to end of study (Fall 1979).*

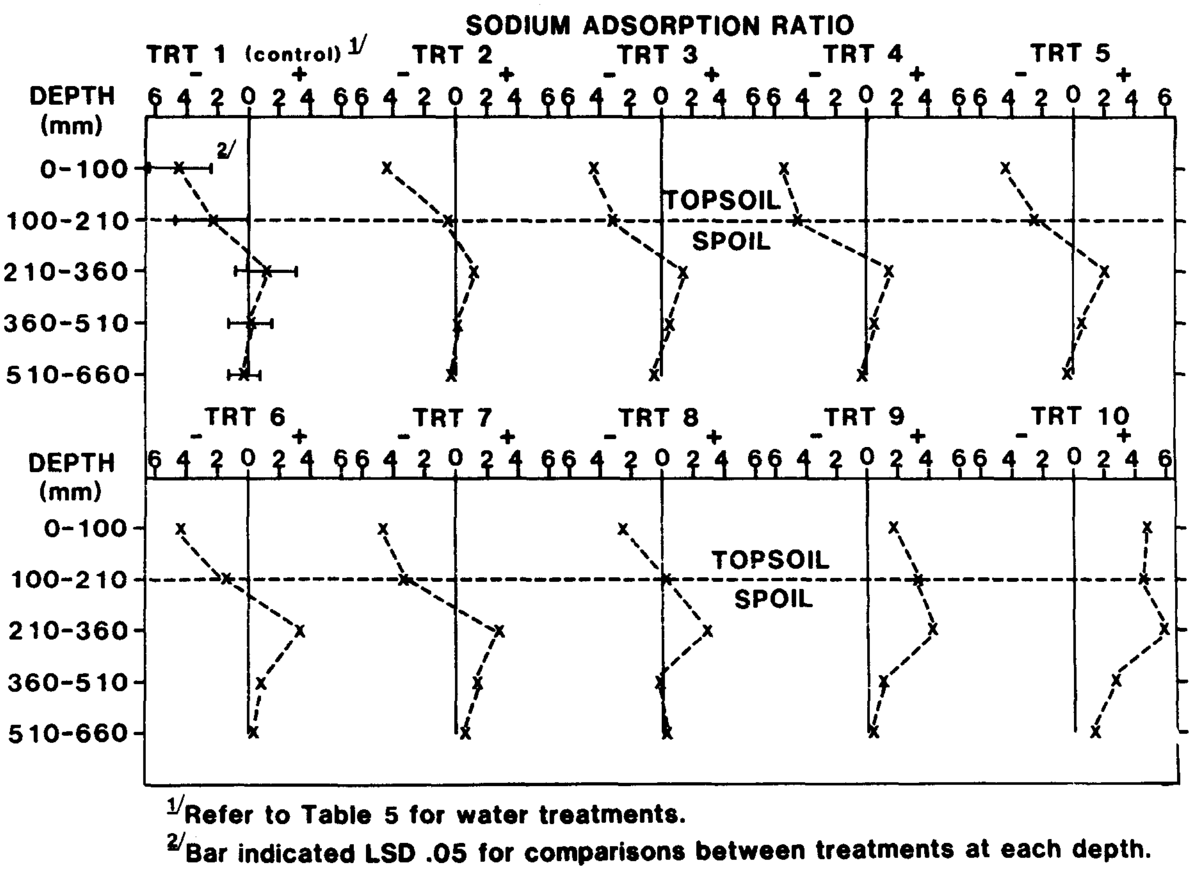

Fig. 4. *Change in sodium adsorption ratio (SAR) of the soil/spoil profile from beginning of study (Spring 1977) to end of study (Fall 1979).*

Spring 1977) to the end of the study (Fall 1979) were used to assess the salinity and sodicity effect of different qualities and quantities of irrigation water. Significant changes ($P\leq.05$) in salinity and sodicity during the study were observed only to a depth of 660 mm. Compared to the control treatment, significant ($P\leq.05$) decreases in EC were observed at the 100 to 210 mm depth in plots receiving 697 mm (treatment 4 and 7) of either medium or low quality water added during 1977, but a significant ($P\leq.05$) increase in EC was observed at the 510 to 660 mm depth when 382 mm low quality water (treatment 6) was added during 1977 (Fig. 3). With a total of 773 mm low quality water (treatment 9) added in 1977 and 1978, a significant ($P\leq.05$) increase in EC over the control plots was observed at the 210 to 360 and 510 to 660 mm depths (Fig. 3). When 1,425 mm low quality water (treatment 10) were added in 1977 and 1978, a significant ($P\leq.05$) increase in EC was observed at the 210 to 360 mm depth (Fig. 3).

Compared to the control, SAR increased at the 210 to 360 mm depth from 382 mm low quality water (treatment 6) added in 1977 (Fig. 4). Increases in SAR were observed when low quality water was applied for 2 years. The plots that received 81 mm (treatment 8) showed decreased SAR at the 0 to 100 mm depth, and plots receiving 773 mm (treatment 9) showed increased SAR in the 0 to 360 mm soil/spoil zone (Fig. 4). The 1,425 mm low quality water (treatment 10) added in 1977 and 1978 increased SAR throughout the whole 0 to 660 mm soil/spoil profile (Fig. 4).

The findings are consistent with those reported by Zartman et al. (1980) and Jury et al. (1980) from the use of blowdown water for irrigation. Changes in EC in our study are considered slight. The SAR increase was more pronounced than salinity increase and appeared to be primarily related to the low quality water applied in 1978.

Conclusion

Irrigation with low quality water improved perennial plant establishment as measured by production. In the growing season after irrigation was terminated, seeded forage yield was increased and weed dry matter decreased within stands established with supplemental irrigation compared to the stand established with precipitation only. Water quality had no effect on forage yield.

When low quality water was used for 1 year to supplement precipitation, changes in salinity and sodicity, evaluated by EC and SAR, were minor. When a total of at least 773 mm of low quality water was added over 2 growing seasons, EC increases were observed at the 210 to 360 mm depth and SAR increases at the 0 to 360 mm zone. Sodicity increased in the zone of 0 to 660 mm when 1,425 mm of low quality water were added over 2 years.

Results from this study indicate that, in well-drained spoils, low quality irrigation can be used to supplement precipitation for 1 to 2 seasons to establish forage stands. This appears to be an acceptable revegetation technique for disturbed areas of medium textures with moderately permeable soil profiles.

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Planting depth and soil texture effects on emergence and production of three alkali sacaton accessions

ABRAHAM DE ALBA-AVILA AND JERRY R. COX

Abstract

Pure stands of alkali sacaton *(Sporobolus airoides)* once grew on playas and lowland alluvial flood plains, as well as on surrounding hills and terraces in semiarid areas of North America. Stands have all but disappeared on hills and terraces in the past 100 years. The purpose of this research was to evaluate the establishment and initial production characteristics of 3 alkali sacaton accessions when seeds were sown at various depths in 3 soils where soluble salts and exchangeable sodium do not accumulate. 'Saltalk', 'NM-184' and 'DU-82' accessions were sown at 5 depths in Pima fine-silty, Sonoita coarse-loam, and Comoro coarse-loam soils in a greenhouse. Seedling emergence from seed sown at 5 mm was greater than for seed sown at 0, 10, 15, and 20 mm in Comoro (sandy), but was equal at all depths in the cracking Pima soil. Above- and below-ground biomass were greatest in Comoro, intermediate in Pima, and lowest in Sonoita soils, but differences were not always significant. The 3 accessions responded similarly to planting depth within a soil, although initial emergence counts indicate differences among accessions.

Key Words: Sporobolus airoides, soils, planting depths, emergence, growth and production, Chihuahuan and Sonoran Deserts

Alkali sacaton *(Sporobolus airoides)*, a perennial warm-season bunchgrass is distributed from North Dakota to eastern Washington (USA) and from Zacatecas to southern Sinaloa (Mexico) in North America (Gould 1975, Hitchcock 1950). One hundred years ago, this grass could be found growing in soils on playas and flood plains, and in soils on hills and terraces. Today the species is found growing only in soils on playas and low alluvial flood planes where water and excessive concentrations of either soluble salts or exchangeable sodium, or both, accumulate (Hickey and Springfield 1966, Knipe and Springfield 1972).

Because alkali sacaton persisted only where water and either soluble salts or exchangeable sodium accumulated, it has been assumed that the species is adapted only to these soil environments (McFarland et al. 1987, School and Miyamoto 1984). Therefore, attempts to reestablish this grass from seed have been limited to mesic, salty soils (Cox et al. 1982).

The seed of 25 alkali sacaton accessions were sown in 3 soils where soluble salts and exchangeable sodium concentrations were either high or low, and we measured seedling emergence and forage production (unpublished data, USDA-ARS and USDA-SCS, Tucson, Ariz.). The seedling emergence and forage production of 23 accessions averaged 10% and 25 g/plant, respectively, and neither measure changed as salt or sodium concentrations varied. For 2 accessions, 'Saltalk' and 'NM-184', emergence increased from 15 to 30% and forage production from 55 to 85 g/plant as salt and sodium concentrations decreased. 'Saltalk' emergence appeared to increase when seed were sown in fine textured soils, while 'NM'-184' emergence appeared to increase when seed were sown in loam textured soils.

Authors are ecologist and former graduate student, Instituto Nacional de Agricolas del Norte Centrol (CEDEC), Apartado 69, Jalpo, ZAC., 99690, Mexico; and range scientist USDA-Agricultural Research Service, 2000 E. Allen Road, Tucson, Arizona 85719. Reprint requests should be sent to J.R. Cox.

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'Saltalk' and 'NM-184' were selected because they were easy to establish (unpublished data, USDA-SCS, Beltsville, Maryland). Both have been widely seeded in the western United States on fine textured soils where salts and sodium accumulate, but neither is widely used because seedlings are difficult to establish (Cox et al. 1982). This study was initiated to determine the emergence and forage production potential of 'Saltalk' and 'NM-184'. Both accessions are commercially unavailable in Mexico. Therefore, seed collected at Mapimi Biosphere Reserve, Durango, Mexico ('DU-82') was included for comparative purposes. To determine soil textural affects on seedling emergence and forage production, we collected soils at 3 sites where soluble salts and exchangeable sodium had not accumulated in high concentrations.

Methods and Materials

In preliminary laboratory studies we found that seed germination among the 3 alkali sacaton accessions varied from 5 to 20%, and variability was great among replicates of the same accession. Seed lots were separated on 26, 28, 30, 32, 34, 36, and 38 mm screens, and seed of each size class were germinated on moist filter paper in plastic petri dishes at 30 °C. Mean germination of seed collected from the 32-mm screen varied from 30 to 35% among the 3 accessions, and the variability among replicates was less than 10% of the mean.

Soils with textural characteristics common to the desert regions of the southwestern United States and northern Mexico, where alkali sacaton grasslands once occurred, were collected at 0 to 30 cm depths in the summer of 1984. Comoro soil (Table 1) was collected in the foothills near the Santa Rita Mountains, Sonoita soil on a secondary terrace above the Santa Cruz river, and Pima soil on a primary terrace within the Santa Cruz flood plain. Soluble salts and exchangeable sodium do not accumulate in high concentrations in these soils (Richardson et al. 1979). The clay fraction in both the Comoro and Sonoita soils is predominantly kaolinite, while in Pima the dominant fraction is montmorillionite (Gelderman 1972).

Table 1. Textural characteristics and classification of 3 soils commonly found in the Chihuahuan and Sonoran Deserts of North America.

Soil Series	Texture Sand	Silt	Clay	Soil family classification[1]
		%		
Comoro	65	25	10	Coarse-loamy, mixed thermic Typic Torrifluvent
Sonoita	50	25	25	Coarse-loamy, mixed, thermic Typic Haplargid
Pima	30	30	40	Fine-silty, mixed (calcareous), thermic Typic Torrifluvent

[1]Classification follows Soil Survey Staff 1975.

Soils were screened to 1 cm to remove rocks, and added to 203 cc tapered plastic plots at 130, 125, 120, 115, and 110 mm depths above the pot base. To obtain 25 germinable alkali sacaton seed, either 83 ('DU-82') or 71 ('Saltalk' and 'NM-184') seeds from each

Table 2. Probability levels (*=0.05, **=0.01, *=0.001, NS=non-significant) of orthogonal polynomials used to evaluate differences among 3 alkali sacaton accessions; when seed were sown at 5 depths in 3 soils.**

	Days after planting							
	Emergence			Shoot lengths			Above-ground biomass	Below-ground biomass
	10	20	30	10	20	30		
	%			mm			g/pot	
Accession (A)	NS	***	***	***	***	***	NS	NS
Soil (S)	***	***	***	***	***	***	***	***
Depth (D)	***	***	***	***	***	**	**	**
Linear	***	***	NS	***	***	***	***	*
Quadratic	NS	***	***	NS	NS	NS	NS	***
A × S	NS	**	**	NS	NS	NS	NS	NS
A × D	***	***	***	NS	NS	NS	NS	NS
Linear	***	***	***	NS	NS	NS	NS	NS
Quadratic	**	**	*	NS	NS	NS	NS	NS
S × D	***	***	***	***	*	*	**	*
Linear	NS	***	***	***	*	**	*	*
Quadratic	***	**	**	NS	NS	NS	NS	*
A × S × D	NS	NS	NS	NS	NS	NS	NS	NS

accession were sown on the soil surface in separate pots. Soils were added to 130 mm depths in all pots; thus, seeds were planted at 0, 5, 10, 15, and 20 mm depths. Pots were subirrigated with distilled water continuously for 7 days, and thereafter for 8 h on days 10, 15, 20, and 25. Sub-irrigation was used to minimize soil disturbance and seed movement.

Greenhouse relative humidity varied from 58 to 80%, and temperatures ranged from 27 to 32 °C. Day length was 10.5 h, and no supplemental light or fertilizer was added.

Seedling emergence was considered complete when the first leaf was 15 mm above the soil surface and the seedling radicle had penetrated the soil surface in pots where seed were surface sown. Shoot lengths, the distance from the soil surface to the extended leaf tips, of the 3 tallest plants in each pot and emergence were measured 10, 20, and 30 days after the experiment began. After seedlings were counted and leaves were measured on the 30th day, shoots were harvested at the soil surface, and roots were washed from soil. Plant material was dried at 40 °C for 48 h in a forced-draft oven and weighed.

Pots were arranged in a randomized complete block design, with a 3 × 3 × 5 factorial arrangement. There were 6 blocks and each contained 3 soils, 3 accessions, and 5 planting depths. Data were arcsin transformed and subjected, by date, to analyses of variance (ANOVA). ANOVA included orthogonal and polynomial decomposition of depth effects into linear and quadratic components and the identification of significant main effects and interactions (Table 2). Cubic and quartic components were not included because depth degrees of freedom (4) were limited. When the accession by soil interaction was significant ($P \leq 0.05$), means were separated by Tukey's HSD test (Sokal and Rohlf 1981).

Results

Seed of the 3 alkali sacaton accessions sown on the 3 soil surfaces began to germinate on day 5 and ranged from 75 to 95% on day 10. 'Saltalk' and 'NM-184' seedlings grew more rapidly than 'DU-82', and 60% or more of their viable seeds had produced seedlings which exceeded 15 mm on day 10 (Fig. 1A). 'DU-82' densities were as numerous and appeared to be as healthy as 'Saltalk' and 'NM-184', but seedlings were smaller.

Seminal roots of seed sown on Comoro soil quickly penetrated the soil surface, but approximately 50% of the roots from seed of each accession grew horizontally along the Sonoita and Pima soil surfaces for 24 to 36 h. Seminal roots of most seedlings penetrated the Sonoita and Pima soils within 24 to 36 h, but leaves were elevated and a portion of the root exposed to air. Seedlings not penetrating the soil surfaces died after 7 days when sub-irrigation was discontinued and soil surfaces dried. Seedling emergence declined with planting depth in Sonoita and Pima soils on day 10, but increased when seed were sown at 5 and 10 mm depths in Comoro soil (Fig. 2A).

'DU-82' seedlings from surface-sown seed with exposed seminal roots died as surface soils dried between sub-irrigations on days 10 and 15. 'DU-82' emergence increased by 10% between 10 and 20 days, while 'Saltalk' and 'NM-84' emergence increased 40% (Fig. 1B). Accession emergence from 5 mm planting depths either equalled or exceeded emergence from surface sown seed by day 20, and declined with depth.

As soils dried following sub-irrigation, cracks 30 mm deep appeared in the Pima soils. Seedlings emerged from these cracks between 10 and 15 days (Fig. 2B). Seedlings from seed sown in the non-expanding Sonoita soil emerged more slowly.

The pure live seed estimates, based on standard laboratory testing techniques, did not correspond with seedling emergence once seed had been placed in soil. Hence, estimates from laboratory techniques may underestimate germination when seed are planted in soil. 'Saltalk' emergence from 0–15 mm, 'NM-184' from 0–10 mm and 'DU-82' from 10 mm depths exceeded 100% of the pure live seed on day 30 (Fig. 1C) and the majority of the seedlings emerged from 5 and 10 mm depths in the 3 soils (Fig. 2C). 'Saltalk' emergence by day 30 was 12% more than the mean emergence of 'NM-184' and 'DU-82' on Comoro soil, and 'Saltalk' and 'NM-184' were superior to 'DU-82' on Sonoita and Pima soils (Table 3).

Seedling shoot length, in this instance used as a measure of plant vigor, was greatest for seedlings developing from surface sown seed and declined with planting depth at days 10 and 20 (Fig. 3A and B).

Table 3. Emergence of 3 alkali sacaton accessions from 3 soils 20 and 30 days after planting seed.

Days after planting[1]	Accessions	Soils: Comoro	Sonoita	Pima
		%		
20	Saltalk	96a	79b	101a
	NM-184	87b	95a	96a
	DU-82	83b	71b	79b
30	Saltalk	97a	116a	119a
	NM-184	87b	116a	112a
	DU-82	84b	93b	80b

[1]Means within dates and soils followed by the same letters are not significantly different ($P \leq 0.05$).

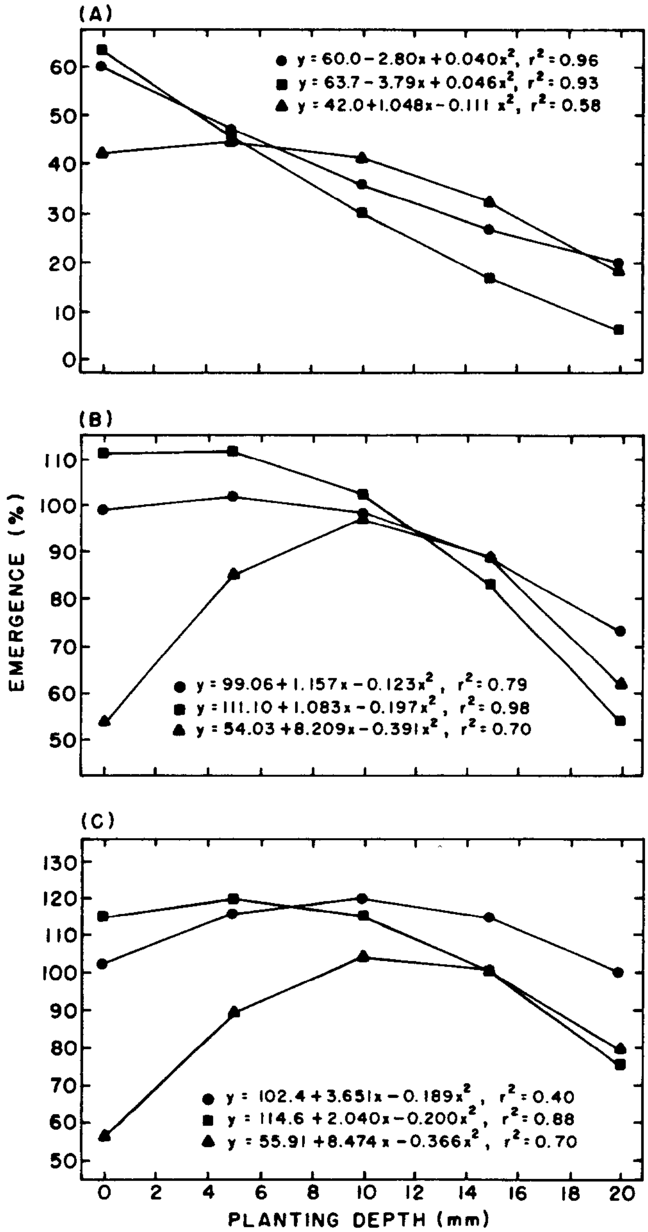

Fig. 1. *Predicted emergence of Saltalk (●), NM-184 (■) and DU-82 (▲) alkali sacaton accessions from seed sown at 5 depths 10 (A), 20 (B), and 30 (C) days after planting in 3 soils.*

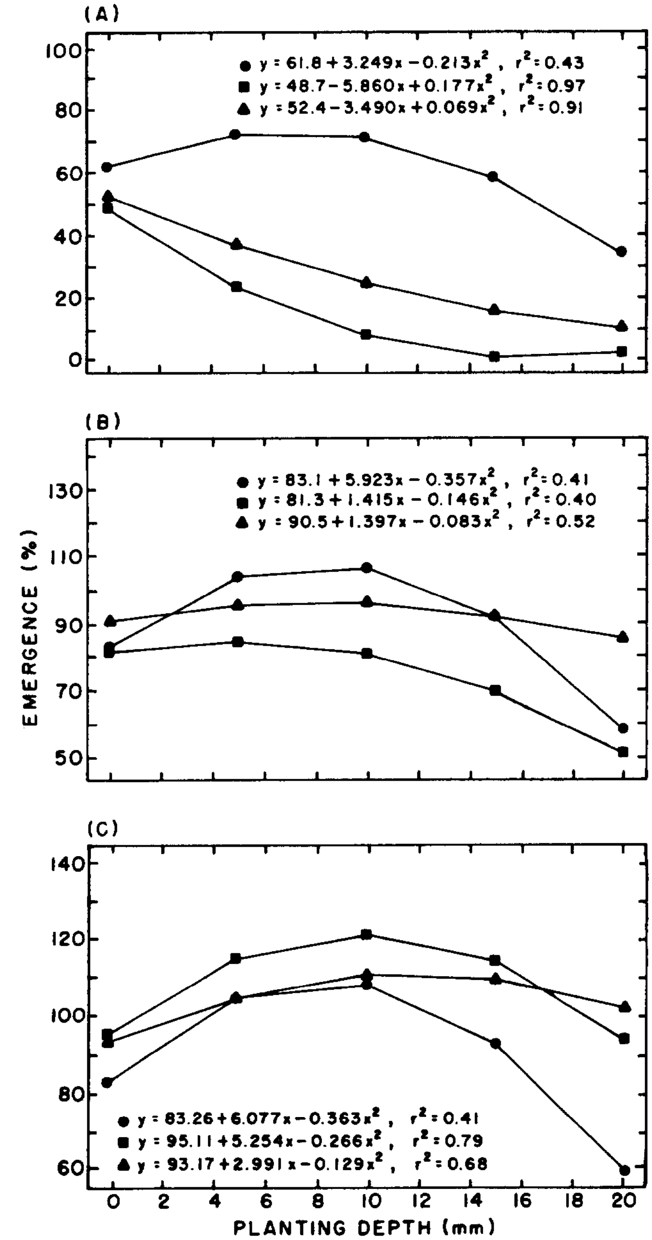

Fig. 2. *Predicted emergence of 3 alkali sacaton accessions from seed sown at 5 depths in Comoro (●), Sonoita (■), and Pima ▲) soils 10 (A), 20 (B), and 30 (C) days after planting.*

Differences among accessions did not occur, but seedlings in Comoro soil grew faster than seedlings in Sonoita and Pima soils. At the conclusions of the study (day 30, Fig. 3C) shoot lengths varied from 34 to 36 cm in Comoro and from 28 to 30 cm in Pima soil, and were unchanged among the 5 planting depths. In Sonoita soil, however, shoot lengths varied from 12 to 23 cm and declined with depth.

The amounts of above-ground biomass that accumulated were similar for the 3 accessions at 30 days (Table 2) but differed among soils and planting depths (Fig. 4A). Above-ground biomass was greatest when seedlings grew in Comoro soil, intermediate in Pima soil, and lowest in Sonoita soil. Above-ground biomass declined with planting depth in Comoro and Sonoita soils and was not influenced by planting depth in the cracking Pima soil.

Below-ground biomass was greatest in Comoro, intermediate in Pima, and least in Sonoita soil (Fig. 4B). Root biomass was higher when seed had been sown at 5 mm in the 3 soils, but differences among depths were not always significant.

Emergence differed among accessions, soils and depths but plant production was similar among accessions and differed among soils and planting depths. Accession emergence, shoot length, and production were greatest when seeds were sown in a coarse-textured soil where percent sand equalled 65 (Table 1), and in a fine-textured soil that cracked as the surface dried. Plant emergence, vigor, and production declined when seed were sown in a coarse soil, where fine particles (clay plus silt) equalled 50% and the soil did not crack upon drying.

Accession shoot growth and above-ground production were either unaffected or declined by day 30 as planting depth increased in the 3 soils (Fig. 3C and Fig. 4A). However, emergence and root biomass by day 30 peaked when seed were sown at 5 and 10 mm depths and declined when seed were sown above or below.

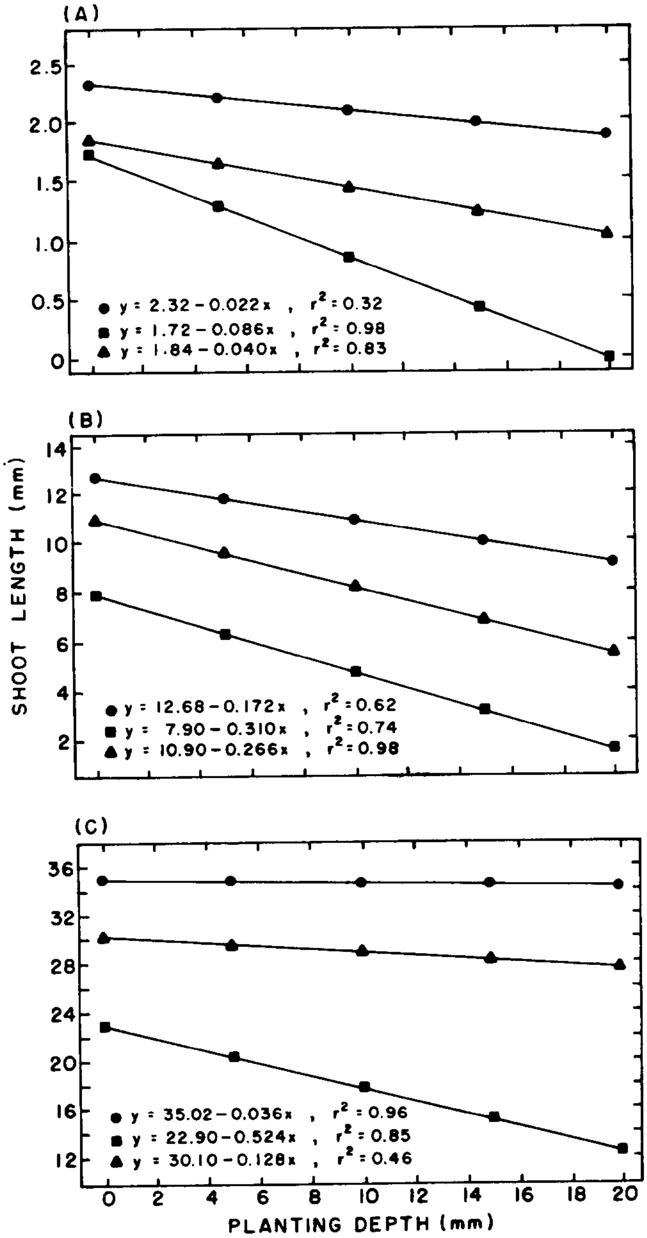

Fig. 3. *Predicted shoot lengths of 3 alkali sacaton accessions from seed sown at 5 depths in Comoro (●), Sonoita (■), and Pima (▲) soils 10 (A), 20 (B), and 30 (C) days after planting.*

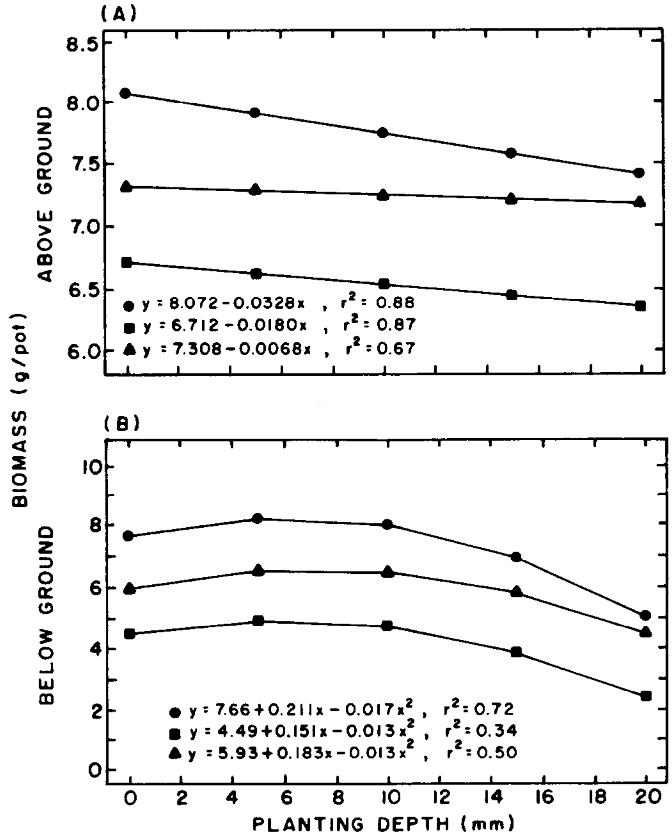

Fig. 4. *Predicted accumulations of above- (A) and below (B) ground biomass of 3 alkali sacaton accessions from seed sown at 5 depths in Comoro (●), Sonoita (■), and Pima (▲) soils 30 days after planting.*

Discussion

In the western United States and northern Mexico, living alkali sacaton plants are found where water accumulates in alluvial flood plains or in alkaline playas. Observations by the authors at more than 40 sites in the southwestern United States and Mexico tend to support the prevailing opinion that the species is only adapted to land areas were water accumulates, and where soils remain moist for extended periods. Logically, we might conclude that reseeding efforts should be confined to lowland areas where water accumulates.

Scattered alkali sacaton plants as well as dead crowns have been observed on hillsides and secondary terraces above flood plains (Hickey and Springfield 1966, Valentine and Norris 1964). These observations and the superior growth of the accessions in Comoro soil (Figs. 2, 3, and 4) support Dortignac's (1960) hypothesis that at one time the species grew throughout the Chihuahuan and Sonoran Deserts, regardless of soil texture.

Because of overgrazing (Humphrey 1958) and possibly competition from other grasses and shrubs better adapted to non-saline and non-alkaline conditions (Hubbell and Gardner 1950), alkali sacaton currently survives only under ideal conditions, found in alluvial lowlands where runoff accumulates and soils crack. Heavily grazed plants may only be able to produce sufficient seed to maintain existing standings under ideal growing conditions (Knipe and Springfield 1972, Hickey and Springfield 1966). On hillsides and secondary terraces, where loam surface soils are commonly found (Richardson et al. 1979), stands may have died due to either insufficient seed or heavy grazing. Because alkali sacaton stands presently persist on fine textured soils where water and often exchangeable sodium and soluable salts accumulate, revegetation specialists have assumed that the species is adapted only to such sites (Scholl and Miyamoto 1984, McFarland et al. 1987). This study does not support that assumption.

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Root systems of two Patagonian shrubs: A quantitative description using a geometrical method

ROBERT J. FERNÁNDEZ A. AND JOSÉ M. PARUELO

Abstract

A method for mapping coarse root distribution suitable for stony soils was developed. Each root is considered as a broken line, whose segments are fairly straight root portions. The spatial location of end points of these segments is recorded in the field through 3 coordinates: its distance from plant vertical axis, its depth, and its distance to the foregoing point on the same root. With these data the roots' spatial arrangement is reproduced using a computer program including simple geometrical relationships. The main advantages of the method are: (a) it does not require sample harvesting and handling; (b) it considers root length instead of root biomass; and (c) its quantitative character allows statistically valid comparisons. Two species living in the Patagonian semidesert were studied: neneo *(Mulinum spinosum, Umbeliferae)* and mata mora *(Senecio filaginoides, Compositae)*. In both shrubs, roots extend laterally more than 2 m and root length decreases exponentially as the distance from the canopy edge increases. Neneo was found to have its maximal root density at a depth of 0.4 m, whereas mata mora has most of its roots close to the soil surface. An interpretation of the differential response of these shrubs to grazing derives from these results.

Key Words: ***Mulinum spinosum, Senecio filaginoides,*** **stony soil, Argentina**

The paucity of knowledge of root systems relative to its importance is well known. In the case of plants growing in stony soils, as in the Patagonian arid steppe, the usual methodological difficulties are even greater. Previous studies of root systems in this environment referred to the root distribution of forbs (Golluscio and Sala 1985) and grasses (Soriano et al. 1987). For shrubs, only brief, qualitative descriptions have been reported (Soriano 1956, Soriano and Sala 1983).

Authors are graduate students at the Departamento de Ecologia, Facultad de Agronomia, Universidad de Buenos Aires. Av. San Martin 4453. (1417) Buenos Aires, Argentina.

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V. Sadras, E. Montecinos U., S.E.B. Hall and Professor A. Soriano offered valuable suggestions at different stages of the preparation f the manuscript. The statistical software used was developed by P.J. Aphalo and R.A. Golluscio.

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Our objective was to quantify the spatial distribution of roots of 2 woody species: neneo *(Mulinum spinosum, Umbeliferae)* and mata mora *(Senecio filaginoides, Compositae)*. These species account for 76% of the woody cover and 19% of the total cover in the west, central Patagonia (R.A. Golluscio, unpublished data), with an estimated density of 1,200 and 1,900 plants/ha respectively (Fernández A. 1986).

To achieve this objective, it was necessary to develop a reliable method suited to the high stone content of the soil. At the same time, the procedure should not need excessive work, in order to allow replication and statistical inference.

Site Description

The study was carried out near the town of Rio Mayo (45°25'S Lat., 70°20'W Long., 500 m, Province of Chubut, Argentina) in a stand representative of the community of coirón amargo *(Stipa speciosa* and *S. humilis)*, mamuel choique *(Adesmia campestris)*, calafate *(Berberis heterophylla)*, and pasto hilo *(Poa lanuginosa)* (Golluscio et al. 1982) which is present on plateaus.

This arid steppe is dominated by 3 shrubs (neneo, mata mora and mamuel choique) and by several tussock grasses (coirón amargo and coirón poa = *Poa ligularis)*. Sheep graze year round on this type of vegetation, except for the summer months on farms with coirón blanco *(Festuca pallescens)* grasslands or wet valleys ("mallines").

Mean annual temperature is 7, 8° C (July: 2° C; January: 14° C). Average precipitation is 142 mm per year, 64% of which falls during the coldest season of April to September. Strong west winds blow during the whole year. The soil is a *Calciorthid* (Golluscio et al. 1982). Gravel (>5 mm) accounts for 47% of its total weight. More detailed information about the environment and the 2 shrubs studied can be found in Soriano (1983) and Soriano and Sala (1983).

Materials and Methods

The variable considered in the development of this method was root length, which is judged to be a better index of root ability for water and nutrient uptake than root biomass (Bóhm 1979). The method used is of a geometrical character. Each root and each ramification is considered as a broken line, whose segments are fairly straight root portions.

For each shrub species, 5 plants of modal size (A.H. Nuñez, pers. comm.) were sampled (Table 1). These individuals are encircled by a ring of tussock grasses (Soriano 1981). The distance between sampled shrubs and the nearest neighbor was not less than 1 m.

Table 1. Size range of the 5 shrubs measured for each species.

	Neneo	Mata mora
MD (cm)	112–136	70–100
md (cm)	74–120	57–78
H (cm)	58–68	44–52

MD: maximum diameter; md: minimum diameter; H: height.

At the side of each plant a trench was dug in such a way that 2 of its walls joined with a 90° solid angle at the vertical axis of the plant. With origin in one of these walls, and with vertex in the center of the plant, a 45° horizontal angle was traced on the surface of the soil, defining an eighth of a cylinder around the plant, which was considered the sampling unit (Fig. 1).

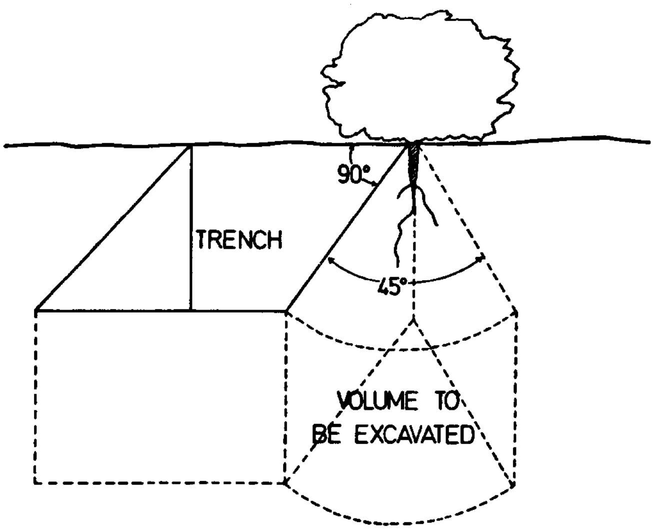

Fig. 1. *Scheme of a sampling unit before root exposure.*

With careful soil removal, the roots were exposed, and the spatial location of end points (Q) of each approximately straight root segment was recorded through 3 coordinates: its distance to the central axis of the shrub (DIST (Q)), its depth (DEPTH (Q)), and it distance to the foregoing point on the same root (LENGTH (P,Q)).

From these data, it was possible to rebuild the 2 dimensional arrangement of roots through a 3-step algorithm (included in a BASIC computer program available from the authors):

a) Calculation of the length of each segment corresponding to each depth interval (VL(i)) (Fig. 2).

b) Calculation of the length of segment included in each horizontal distance interval (HL(j)) (Fig. 3).

c) Combination of the foregoing steps in such a way that the vertical and horizontal position of the segment is obtained. In other words, calculation of the length of the segment RL (i,j) located in each cell (i,j) of a 10 cm × 10 cm grid, re-building the 2 dimensional arrangement of the roots. (The horizontal origin of the pair of coordinates used as a reference is located at the center of the plant, and the vertical origin at the soil surface level.) This third step was considered necessary to avoid losing the interactions

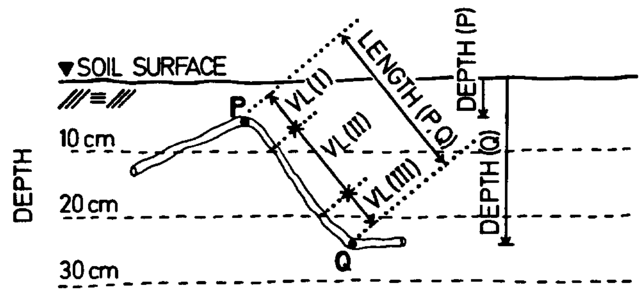

Fig. 2. *Model used to estimate vertical distribution of roots. P and Q: points of a root between which it can be considered a straight segment.*
Data: DEPTH(P), DEPTH(Q) and LENGTH(P,Q).
Unknowns: length of segment PQ included in each stratum (VL(i)).
Solution:
*VL(I) = 10-DEPTH(P) * LENGTH(P,Q)/(DEPTH(Q)-DEPTH(P))*
*VL(II) = 20 - 10 * LENGTH(P,Q)/(DEPTH(Q)-DEPTH(P))*
*VL(III) = DEPTH(Q)-20 * LENGTH(P,Q)/(DEPTH(Q)-DEPTH(P))*

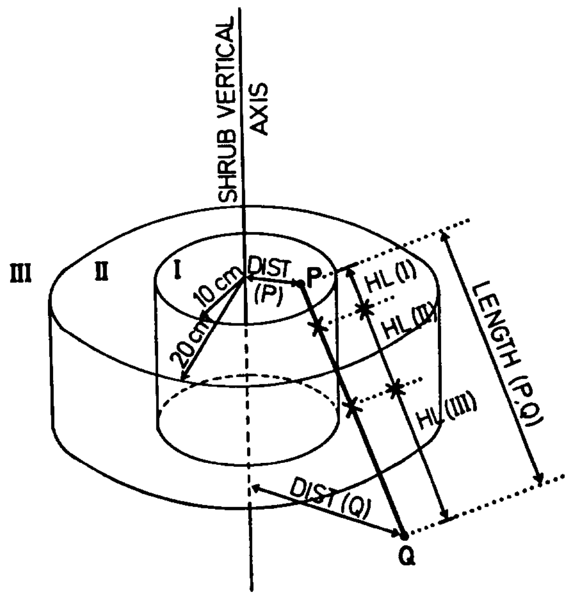

Fig. 3. *Model used to estimate horizontal distribution of roots. P and Q: points of a root between which it can be considered a straight segment.*
Data: DIST(P), DIST(Q) and LENGTH(P,Q).
Unknowns: length of segment PQ included in each range of distances from plant's vertical axis (HL(j)).
Solution:
*HL(I) = 10-DIST(P) * LENGTH(P,Q)/(DIST(Q)-DIST(P))*
*HL(II) = 20 - 10 * LENGTH(P,Q)/(DIST(Q)-DIST(P))*
*HL(III) = DIST(Q)-20 * LENGTH(P,Q)/(DIST(Q)-DIST(P))*

between the 2 dimensions which could be important in the interpretation of the roots' arrangement.

Analysis of covariance was applied to the data with total root length per plant as the covariate. Function adjustment was performed by regression analysis.

Results and Discussion

The method detected differences between the 2 species: two thirds of mata mora's root length was found in the first 40 cm of the soil in a radius of 1.50 m, whereas neneo shows the same proportion of its total root length in the 20–60 cm layer and in a circle of 1.20 m around the plant.

Compared with qualitative descriptions such as photographs or drawings, this method has the advantage of allowing statistical comparisons. Replication was possible since working in the 45°

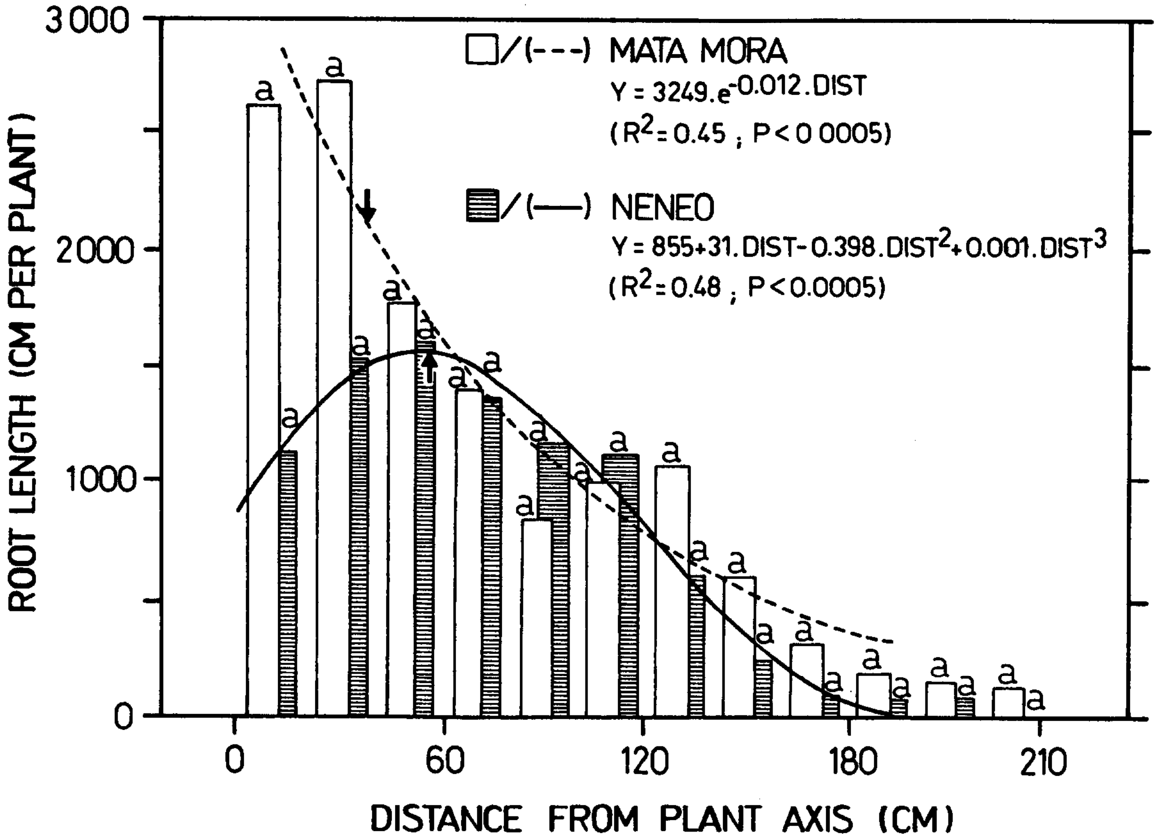

Fig. 4. *Horizontal distribution of roots. Bars show average root length per plant (N=5) found within each 20 cm distance interval. Different letters at the same distance range mean significant differences (P<0.05) between species through ANCOVA (using total root length per plant as independent variable). Arrows indicate the average location of canopy edge for each species.*

sector reduced sampling time to about 6 hours per plant (trench digging excluded).

Maximum and average values of root density obtained here, around 100 and 1.4 cm/dm3 respectively, are lower than those observed by other authors in species from arid environments (e.g., Kummerow et al. 1978). This underestimation derives from the difficulty in detecting roots smaller than 0.5 mm in diameter, which have the greatest length per unit of biomass. However, we expect root spreading not to be affected by fine roots, since they would probably lack secondary growth.

Average root length was greater in mata mora (12,776 cm/plant; CV=32%) than in neneo (8,850 cm/plant; CV=55%); but the difference was not statistically significant. In both species, for each depth, root length followed a similar pattern with distance and, conversely, at each distance range the vertical pattern within a species remained unchanged. So, the analysis of root arrangement was made separately for each dimension.

The analysis of the horizontal distribution of roots revealed that the amount of roots under the projection of the shrub canopy is less than 50% of the total in both species, and that roots reach distances greater than 2m (Fig. 4). Considering that woody individuals in this site average 3 m apart (Soriano et al., unpublished data), root spreading would be enough to allow some degree of overlapping between root systems of adjacent shrubs. Both species demonstrated a similar decrease in the amount of roots as the distance from the canopy edge increased (Fig. 4).

The vertical distribution of roots followed a different pattern in each species: whereas mata mora had most of its roots close to the soil surface, neneo showed its maximum concentration between 30 and 50 cm of depth (Fig. 5). The best fit was obtained with equations of a negative exponential type (Y = 2897.ê(0.019.DEPTH)) and parabolic type (Y=–363++79.DEPTH–0.81.DEPTH2), respectively. Significant differences between species were found in the upper layer (0–30 cm) and in a lower one (50–70 cm) (Fig. 5).

The soil of this community has a calcareous layer at 40 cm depth (Golluscio et al. 1982, Soriano and Sala 1983). Thus, most of mata mora's roots (73%) are between that stratum and the soil surface, and the most of neneo's were found included in the calcareous layer or near it. This would mean reduced overlapping at lower depths with grass roots for neneo than for mata mora, since grasses have a large portion of their underground biomass in the upper 30 cm of the soil (Soriano et al. 1987).

These data allow an interpretation of the differential responses of the 2 shrubs to grazing in the community under study. Whereas mata mora increased its importance when sheep grazing pressure was high (Soriano 1956, Busacca 1981), neneo does not show a clear variation in its cover in response to range use (Busacca 1981). Browsing is minimal in these species (Bonvisuto et al. 1983). As grass biomass decreases under the effect of grazing, it may be expected that water and nutrient consumption by grasses also decreases. In this case, a greater supply of these resources would be available in the upper centimeters of soil, where mata mora has more roots (and supposedly more root activity) than neneo. In this situation, mata mora would be able to increase its biomass per plant or its number of individuals. In addition, the overlap of roots of grasses and mata mora would also have a temporal dimension since neither of them show a dormancy period (Soriano 1983).

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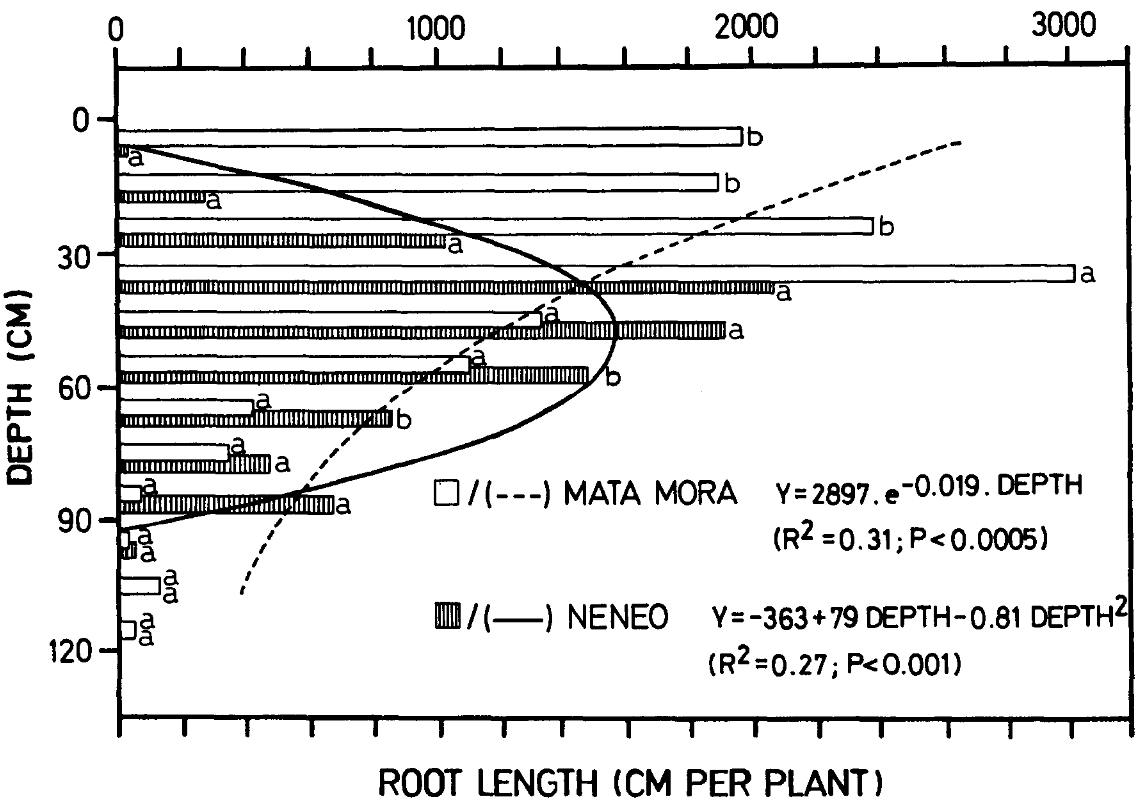

Fig. 5. *Vertical distribution of roots. Bars show average root length per plant (N=5) found within each 10 cm depth interval. Different letters at the same depth mean significant differences ($P<0.05$)* between species through ANCOVA (using total root length per plant as independent variable).

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Levels of a neurotoxic alkaloid in a species of low larkspur

WALTER MAJAK AND MICHAEL ENGELSJORD

Abstract

A survey of the levels of the neurotoxic diterpenoid alkaloid methyllycaconitine (MLA) in low larkspur (*Delphinium nuttallianum* Pritz.) was conducted at 4 diverse rangeland sites in southern British Columbia. Freeze-dried plant samples representing 3 stages of growth over 2 growing seasons were analyzed for MLA by high pressure liquid chromatography. Significant differences were found among experimental sites ($P<0.001$) with higher levels of MLA (>0.2% on a dry weight basis) being associated with sites at higher elevations (900–975 m). At one site, an exceptional level of MLA (>0.3%) was observed during the flower bud stage of growth but in general the alkaloid levels remained fairly constant with advancing stages of growth. Measurement of the MLA concentrations in different plant parts revealed that reproductive parts contained higher levels of MLA than vegetative parts and this may well explain the increased toxicity of the upper portions of the plant.

Key Words: *Delphinium nuttallianum*, diterpenoid alkaloids, methyllycaconitine, livestock poisoning

Plants of the genus *Delphinium,* commonly known as larkspur, are one of the major causes of poisoning in range cattle of North America (Cronin and Nielsen 1978). A particular species of low larkspur, *Delphinium nuttallianum* Pritz., occurs from northern California and Colorado in the U.S. to the interior of British Columbia in Canada (Hitchcock and Cronquist 1964). In B.C., it is generally found on grasslands at elevations up to 1,500 m. Appearing early in spring, often before most of the grasses, it can be palatable but poisonous to cattle (Looman et al. 1983). Recently the toxicity of *D. nuttallianum* (Majak et al. 1987), as well as that of 2 related species, *D. brownii* Rydb. and *D. bicolor* Nutt. (Aiyar et al. 1979, Kulanthaivel et al. 1986), was attributed to the diterpenoid alkaloid, methyllycaconitine (MLA). This alkaloid is a potent neuromuscular blocking agent in cattle (Nation et al. 1982) and it also appears to be a naturally occurring insecticide (Jennings et al. 1986). A method was recently developed to isolate and precisely determine the level of MLA in *D. nuttallianum* by high pressure liquid chromatography (HPLC) (Majak et al. 1987). Before the development of this method, larkspur toxicity was determined by rat or mouse bioassay or estimated by the total alkaloid content of the plant. However the latter method is usually used as a preliminary indicator of toxicity and it may not be strongly correlated to bioassay results (Olsen 1983). The object of the present study was to conduct a survey of the levels of MLA in *D. nuttallianum* growing in different rangeland habitats and thus to determine when and where it could be most hazardous to grazing cattle.

Materials and Methods

Samples were collected from 4 different sites within an 11 km radius of Lac du Bois, near Kamloops, B.C. Sites 1, and 2 and 3 were located in the *Artemisia tridentata, Stipa-Poa* and *Festuca scabrella* grassland zones respectively (van Ryswyk et al. 1966). Site 4 was in a transition zone between the Douglas fir *(Pseudotsuga menziesii)* forest zone and the *Festuca scabrella* upper grassland zone (Tisdale and McLean 1957). Over the last decade, cattle have been excluded from Sites 1 and 2, they have grazed Site 3 in the fall and Site 4 after June 1. The soil classifications and elevations of the 4 sites are as follows: Site 1: Brown Chernozem; fine sandy, mixed, cool, subarid; moderately sloping S, very rocky phases; (Typic Haploboroll); 350 m elevation. Site 2: Dark Brown Chernozem; coarse loamy, mixed, cool, subarid; strongly to very strongly sloping E, very stony phases; (Haploboroll); 350 m elevation. Site 3: Black Chernozem; coarse loamy over compact loamy, mixed, cool, subhumid; strongly sloping SSW, very stony phases; (Udic Haploborall); 900 m elevation. Site 4: Dark Grey Luvisol; loamy, mixed, cool, subhumid; very strongly to very gently sloping S, non-stony phases; (Typic Eutroboralf); 975 m elevation. The systems of the Canada Soil Survey Committee (1978) and, in brackets, the Soil Survey Staff (1975) were used for site classification.

Composite samples (100–200 g fresh weight) representing the 3 sequential stages of growth (flower bud, flower, and pod) were randomly collected at each site during 2 growing seasons (1986 and 1987) and these were stored at –20° C. The samples were collected from the middle of April to the beginning of June and phenology was assigned for each date of collection according to the predominating stage of growth. Samples were usually collected once per week but the number of samples per stage of growth varied with site and year depending on the duration of the phenological stage. When the aerial portions became large enough, they were divided into upper and lower parts of 15–20 cm in length and these were analyzed separately. A number of samples were also separated into specific parts including roots, leaves, stems, flower buds, flowers, pods and seeds. The samples were freeze-dried and ground to pass through a 2-mm screen.

The alkaloids were extracted and analyzed by ion pair HPLC as described previously (Majak et al. 1987). However, the HPLC conditions were slightly modified to permit a larger number of analyses by decreasing the retention time of MLA from 24 min to 12 min. The mobile phase consisted of 4 mM sodium hexane sulfonate in aqueous orthophosphoric acid (0.1%)-acetonitrile (12:88). The flow rate of 0.5 ml/min created a column pressure of 58–62 atmos. The data from 2 years, 4 sites, and 3 stages of growth (n=39) were statistically analyzed using the type II sums of squares for a 3-way analysis of variance in SAS GLM (Freund and Littel, 1981).

Results and Discussion

The analysis of variance revealed that the 4 larkspur sites differed significantly ($P<0.001$) with respect to MLA concentrations in the aerial portions of *D. nuttallianum*. Higher levels of MLA were associated with larkspur sites located at higher elevations. Average levels of MLA at Site 4 (elevation 975 m) for example, could be almost threefold greater than the levels of MLA at Site 1 (elevation 350 m) (Fig. 1 and 2). In general, the average concentration of MLA was slightly lower ($P<0.01$) during the bloom stage ($\bar{x}$ = 0.18%, SE = 0.01%) than during the pod (0.21%) or flower bud (0.21%) stages of growth. This differs from the trends reported for the total alkaloid content of tall larkspurs *(D. barbeyi* and *D. occidentale)* in the U.S. which showed a significant decline with advancing stages of growth (Olsen 1978, 1983). It is interesting to note however, that these species have a much longer growing season than *D. nuttallianum* has in B.C.

The level of MLA at Site 4 during the bud stage of growth was exceptionally high (Fig. 1). This site is known to have a history of

Authors are biochemist and research assistant, Agriculture Canada, Research Station, 3015 Ord Road, Kamloops, B.C. Canada V2B 8A9.

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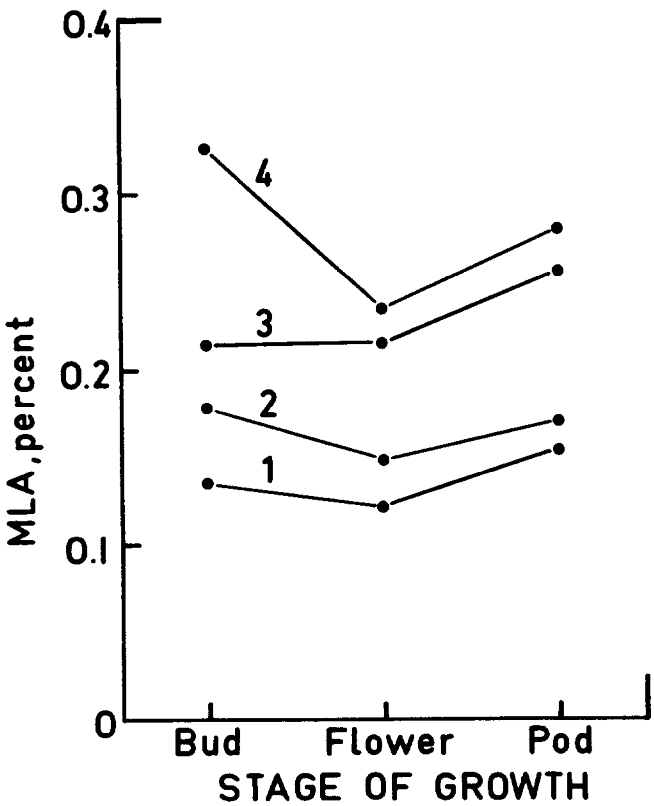

Fig. 1. *Changes in methyllycaconitine (MLA) levels in aerial growth of low larkspur at 4 sites, data averaged over 2 years and expressed on a dry matter basis. Standard errors varied from 0.01 to 0.02 except for the pod stage at site 4 (SE=0.03).*

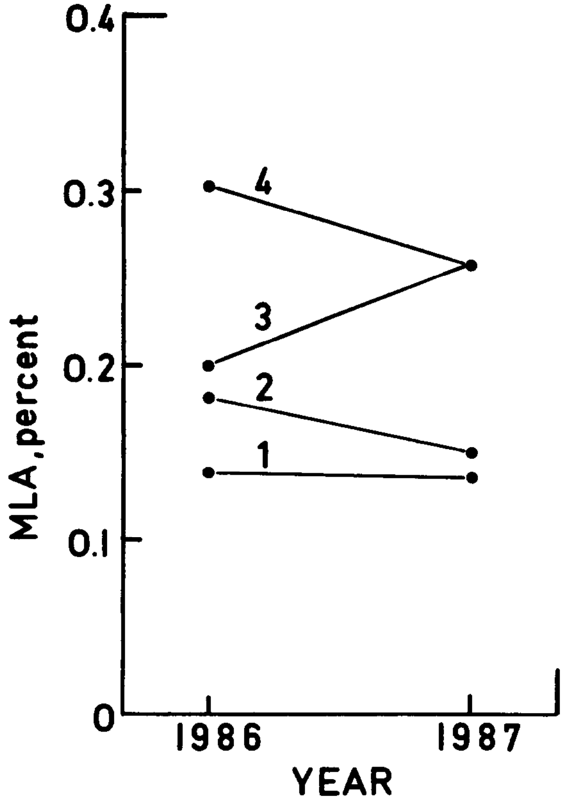

Fig. 2. *Average methyllycaconitine (MLA) levels in aerial growth of low larkspur at 4 sites during 1986 and 1987, data averaged over 3 stages of growth and expressed on a dry matter basis. Standard errors varied from 0.01 to 0.02.*

livestock poisoning (L. Stroesser, personal communication) and our results indicate that it is particularly hazardous at early stages of *D. nuttallianum* growth. In recent memory, the worst outbreak of larkspur poisoning at Site 4 occurred during the spring of 1974 when 8 cows succumbed to the plant and at least 25 others showed signs of poisoning. Outbreaks of larkspur poisoning also occurred in other areas during that spring, which was exceptionally cool and moist (Atmospheric Environment Service 1974). An early, abundant population of larkspur was evident throughout the region and in many areas the larkspur was the predominant green foliage available. During the "green" flower bud stage of growth (with a slight bluish tinge on the bud) the plant appeared to be palatable and it was readily consumed.

There was a significant site × year interaction ($P<0.01$) and this was attributed to the increase in the levels of MLA at Site 3 during 1987. However, the data for Site 3 in 1987 (Fig. 2) should not be misconstrued. Field observations indicated a much lower abundance of larkspur at all sites in 1987 than in 1986, and especially at Site 3, where larkspur abundance was reduced by at least 80%. The grasses predominated in 1987 and the risk of poisoning was reduced because in general, the cattle prefer this forage over larkspur. Therefore the increase in MLA concentrations at Site 3 during 1987 would probably not have a practical consequence. The weather patterns during the spring of 1986 and 1987 differed considerably and this could have affected the emergence and growth of the larkspur. The month of May, which is the major growing period for *D. nuttallianum*, was on average cooler and wetter in 1986 than in 1987. The precipitation during May 1986, which was typical, was approximately twice that of May 1987 (Atmospheric Environment Service 1986, 1987). Since *D. nuttallianum* is a shallow-rooted perennial, the availability of soil moisture could be a critical factor determining the establishment of larkspur seedlings in the spring and the growth of overwintered plants. The drier conditions in 1987 also resulted in a shorter growing season for *D. nuttallianum*. At Site 1 in 1987 for example, the plant progressed from the bud stage of growth to the pod stage in 4 wk. At the same site in 1986, however, the growing season lasted for 7 wk with approximately an equal interval of growth for each phenological stage.

The variations observed with site and stage of growth prompted further analysis of the plant parts. Our preliminary data indicate that vegetative parts (leaves and stems) contain lower levels of MLA than do reproductive parts (flower buds, flowers, and pods). For example, during the bloom stage of growth at Site 3 the MLA content of vegetative parts was 0.05% for leaves and 0.22% for stems. On the other hand, the reproductive parts yielded the following MLA levels: 0.43% (flower buds), 0.37% (flowers), and 0.57% (pods). Similar trends were seen at Sites 1, 2, and 4. The high levels of MLA in pods and pod stage plants can be partly attributed to the development of seeds which contained high levels of MLA (values ranging from 0.28% to 0.49% at Sites 1 and 2, $n=4$). Significantly higher levels of MLA ($P<0.01$) in the upper aerial portions ($\bar{x}=0.14\%$, SE=0.015, n=7) compared with the lower portion ($\bar{x}=0.08\%$) can also be explained by the fact that a greater proportion of the reproductive parts are located in the upper portion of the plant.

Nudicauline, another *Delphinium* diterpenoid alkaloid which is closely related to MLA (Kulanthaivel and Benn 1985), was also found in high levels in the seeds. The toxicity of nudicauline has not been determined but it contains the ester function required for neuromuscular activity (Aiyar et al. 1979, Benn and Jacyno 1983) and it only differs from MLA by having an acetate rather than methoxyl group at C_{14}. Nudicauline was typically present in minor amounts in aerial portions equivalent to 23.6% (SE=1.44, n=39) of

MLA, but in seeds nudicauline occurred at levels equivalent to 82% (SE=15.4, n=4) of MLA. Roots were also similar in this respect. While they contained fairly low levels of MLA (0.07% to 0.17%, n=5) compared with other parts, nudicauline was present at 56.4% (SE=4.93, n=5) of the quantity of MLA. The presence of nudicauline in both seeds and roots was confirmed by using an authentic standard to enhance the nudicauline peak on HPLC. The distribution of MLA and nudicauline in *D. nuttallianum* merits further investigation.

It is apparent that a grazing animal can ingest variable quantities of MLA depending on the part and the quantity of plant material consumed. Observations of cattle grazing low larkspur revealed that in the first pass through a stand, the animals select only the upper growth of the plant (L. Stroesser, personal communication). To evaluate the potential toxicity of the animals' diet, we collected large composite samples (>100 plants) to simulate the ingested part of the larkspur. Two separate samples were collected from Site 4 on the same day when plants were in a transitory stage between flower bud and flower. One sample was composed of the top 10 cm of plants that were predominantly in the bud stage of growth; it gave a MLA level of 0.32%. The other sample was made up of the top 20 cm of plants representing the flowering stage and yielded a MLA level of 0.25%. Another such experiment was carried out at the same site when *D. nuttallianum* was in full bloom. This time the samples were collected 2 days apart but both samples were a composite of flowering plants. The earlier sample consisted of the top 20 cm of plant material giving a MLA level of 0.16%, while the second sample consisted of the top 10 cm and had a MLA level of 0.31%. In future studies, information on the grazing habits of livestock must be integrated with MLA distribution data to assess the potential danger of *D. nuttallianum* to grazing livestock accurately. Studies should also be conducted to determine the effect of seasonal climate on the emergence and growth of *D. nuttallianum*.

In summary, the present studies indicate that indicates that stands of *D. nuttallianum* at higher elevations are more likely to be hazardous to grazing cattle than those at lower elevations. On a dry weight basis, the levels of MLA were fairly constant throughout the growing season, not showing a decrease with advancing stages of growth. However, *D. nuttallianum* may be more hazardous to range cattle at earlier stages of growth when it is more succulent and palatable.

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Some observations from the excavation of honey mesquite root systems

R. K. HEITSCHMIDT, R.J. ANSLEY, S.L. DOWHOWER, P.W. JACOBY, AND D.L. PRICE

Abstract

A single, mature and 12 smaller honey mesquite *(Prosopis glandulosa* Torr. var. *glandulosa)* trees were partially excavated during 1986 to examine root distributional patterns. The mature tree had an extensive lateral root system and a large tap root that subdivided into 3 smaller tap roots at a depth near 1 m. The lateral root system of all trees was concentrated in the upper 0.3 m of the soil profile. Results from the excavations provide evidence in support of honey mesquite's classification as a facultative phreatophyte.

Key Words: *Prosopis glandulosa,* leaf area, biomass, dry weight

Dense stands of honey *(Prosopis glandulosa* Torr. var. *)* and velvet [*P. glandulosa* var. *velutina* (Woot.) Sarg.] mesquite impact extensive areas of rangeland in the southwestern United States (Fisher 1977). Mesquite's persistence following establishment is believed to be related to its facultative phreatophytic strategy (Thomas and Sosebee 1978) which is related to its ability to extract water from a large volume of soil (Fisher et al. 1959, Phillips 1963, Fisher et al. 1973, Ludwig 1977) in a preferential sequence from near the soil surface downward (Haas and Dodd 1972, Easter and Sosebee 1975), while maintaining acute physiological control of transpirational water losses (Mooney et al. 1977, Nilsen et al. 1981).

The objective of this note is to describe the root distributional patterns of partially excavated honey mesquite trees in the Rolling Plains of Texas. Results from 2 studies are described. The first study was undertaken to provide critical information needed to satisfactorily develop dynamic water yield/water use simulations models for honey mesquite infested rangelands. The second study was undertaken to quantify the effect of soil type on the lateral and vertical distribution of roots.

Materials and Methods

Both study sites were located on the eastern edge of the Rolling Plains in north central Texas. Climate is semiarid continental characterized by warm, wet springs and falls, hot summers, and mild winters. Average annual precipitation is about 65 cm. Herbaceous vegetation is a mixture of short and midgrasses. Dominant herbaceous species in this region are buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.], sideoats grama [*Bouteloua curtpendula* Michx.) Torr.], Texas wintergrass (*Stipa leucotricha* Trin. and Rupr.), and Japanese brome (*Bromus japonicus* Thunb.). Honey mesquite is the dominant woody plant.

Study 1

The study site was located on the Wagon Creek Spade ranch in Throckmorton County. A single-stemmed, mature honey mesquite tree growing within a dense (>500 trees/ha) stand of trees was partially excavated during the summer of 1986 (Fig. 1). The tree was located on a nearly level upland site. Soils within the

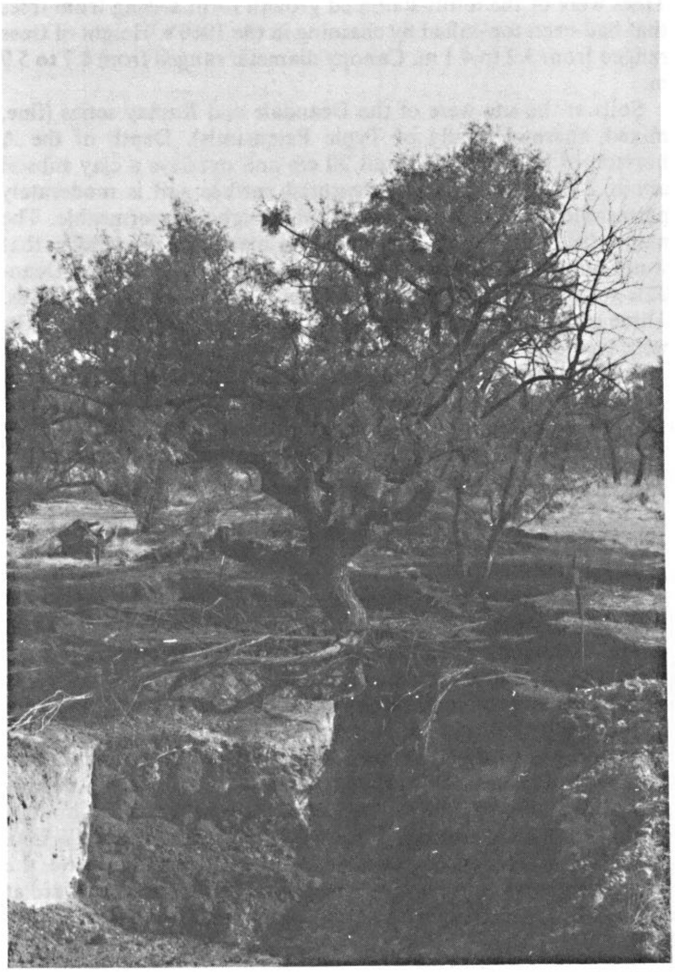

Fig. 1. *Mature honey mesquite tree following partial excavation of root system.*

excavation pit graded from a Nuvalde clay loam (fine-silty, mixed, thermic family of Typic Calciustolls) on the south to a Valera clay loam (fine, montmorillonitic, thermic family of Petrocacic Calciustolls) on the north. Solum depth ranged from about 50 cm on the north to 90 cm on the south. Both soils are moderately permeable and are formed over rather impermeable, cemented calcium carbonated alluvium.

Hand excavation of the 6 m tall tree began in early summer and was completed by mid-August. During excavation, no accelerated leaf abscission was observed. Thus following excavation, all leaves were removed by hand, dried at 60° C to a constant weight and weighed to estimate total leaf biomass. Total leaf area (1 side) was estimated using a linear regression derived from subsample relationships between leaf dry weights and leaf area as estimated using a leaf area meter. Following the abscission of a second set of leaves in late September, the aboveground portion of the tree was harvested by hand and weighed. Dry weight was estimated by drying

Authors are professor, post-doctorate, research associate, and professor, respectively, Texas Agricultural Experiment Station, Box 1658, Vernon 76384; and post-doctorate, Range Science Department, Texas A&M University, College Station 77843.

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subsamples of various size classes of limbs to a constant weight and weighing.

Study 2

The second study site was located approximately 40 km north of the first on the W.T. Waggoner ranch in Wilbarger County. Study was conducted during the excavation and subsequent containerization of 12 honey mesquite trees being prepared for ecophysiology stress studies (Ansley et al. 1988). The site was located on a nearly level upland. Density of trees was about 400 plants/ha. Trees were of the multi-stemmed growth form arising from trees that had been top-killed by chaining in the 1960's. Height of trees ranged from 3.2 to 4.1 m. Canopy diameter ranged from 4.7 to 5.9 m.

Soils at the site were of the Deandale and Kamay series (fine, mixed, thermic family of Typic Paleustolls). Depth of the A horizon of both soils is about 30 cm and overlays a clay subsoil about 2 m thick. The clay textured surface soil is moderately permeable whereas the clay subsoil is highly impermeable. The major difference between the soils is related to micro-relief in that water tends to accumulate on the level to slightly concave Deandale soils and run off the nearly level (1–3% slope) Kamay soils. Three study trees were located on the Deandale soils and 9 trees were located on the Kamay soils.

Following mechanical removal of the soil around the periphery of the trees, numbers of roots (>2 mm in diameter) were counted along the 6 exposed faces of the trend. A 2-m² frame of 0.3-m² grids were utilized to quantify the vertical distribution of roots along each 4-m-wide by 2-m-deep face (Fig. 2).

Results

Study 1

Complete excavation of the tree was not possible because of labor constraints (Fig. 1). However, partial excavation revealed several interesting phenomena. Major lateral roots were located generally in the upper 30 cm of the soil profile (Fig. 3). These roots in turn gave rise to 2 major types of secondary roots. The first were of the small (<5 mm in diameter) fibrous type that extended upward toward the soil surface. These roots were most abundant on the north and east side of the tree and were restricted primarily to the soil under the canopy. The second type were larger (about 20 mm in diameter) and extended downward through the calcified C horizon. A single lateral root was excavated from its origin at the base of the tree to a point about 10 m away from which it turned downward at a right angle. At its origin it was approximately 60 mm in diameter. At the point where it turned downward it was about 8 mm in diameter and about 50 cm below the soil surface. One larger lateral root (about 30 mm in diameter) was found to sequentially turn downward for about 20 cm, upward for about 30 cm, then downward again all within a horizontal distance of about 20 cm.

The vertical root system excavated under the trunk initially consisted of a single tap root (Fig. 4). At a depth near 90 cm, approximately 10 cm below the beginning of the C horizon, the tap root became horizontal before subdividing into 3 roots, 2 extending downward and 1 extending horizontally and then upward. Vertical excavation was halted at a depth near 130 cm.

Harvest of the aboveground portion of the tree yielded a total of 7,377 g (dry weight) of leaves. The linear regression of the leaf area and dry-weight estimates derived from leaf subsamples was LA = −17.1 + 65.0X where LA equaled leaf area (cm²) and X equaled weight (g) ($R^2 = 0.996$, $n = 51$). Total estimated leaf area (1 side) was 47.95 m². Measured ground area of canopy was approximately 43.4 m² yielding a leaf area index of 1.104. Estimated wet weight of aboveground woody tissue was 320 kg. Mean water content ranged from about 40% (twigs) to 28% (trunk) and estimated total woody dry weight was 219 kg.

Study 2

Averaged across soil series, counted root intercepts on faces of the barrier cuts showed 81% of all roots occurred within the top 1 m of the soil profile. The number of roots diminished progressively from 42% of the total in the top 30 cm of the soil profile to 4% at the 2-m depth.

Fig. 2. *Counting number of roots along face of 1 of 6 trenched walls around small honey mesquite tree (see Ansley et al. 1988).*

The effect of soil series on root distributional patterns was expressed in 2 manners (Fig. 5). Firstly, root densities in the top 30 cm of the soil profile were greater in the Deandale (43/m²) than the Kamay (33/m²) soil. Densities at the lower depths were similar. Secondly, there was a greater number of roots on the east-northeast side of the trees growing on the Kamay soils than on the south-southwest side which agreed with the general observations from Study 1. However, no directional pattern was evidenced by the trees growing on the Deandale soil.

Definitive explanations for these differences between soils in root distributional patterns were not readily apparent. It is hypothesized however, that they may be related to differences in soil water dynamics in that water often stands on the Deandale soils as opposed to running off the Kamay soils.

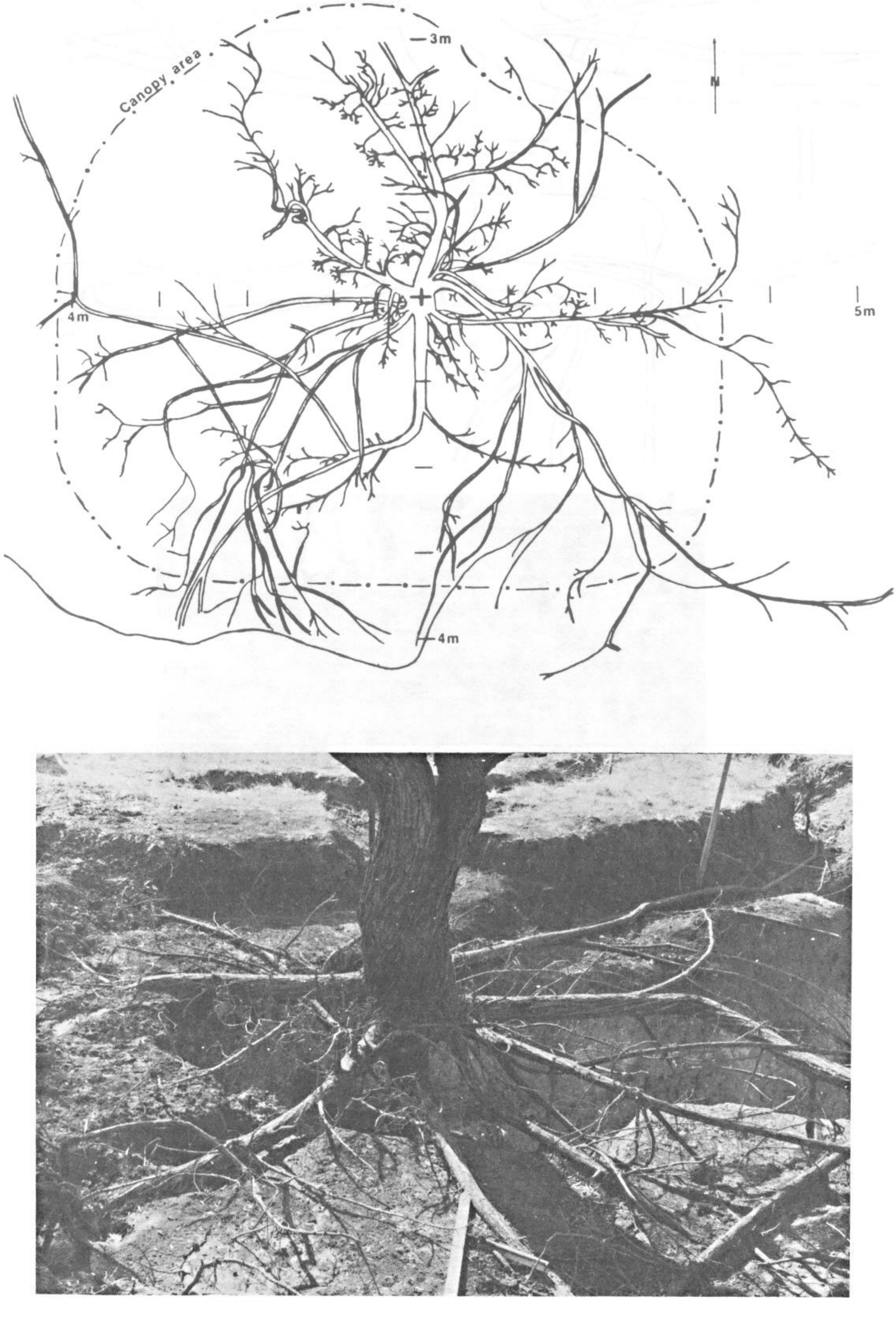
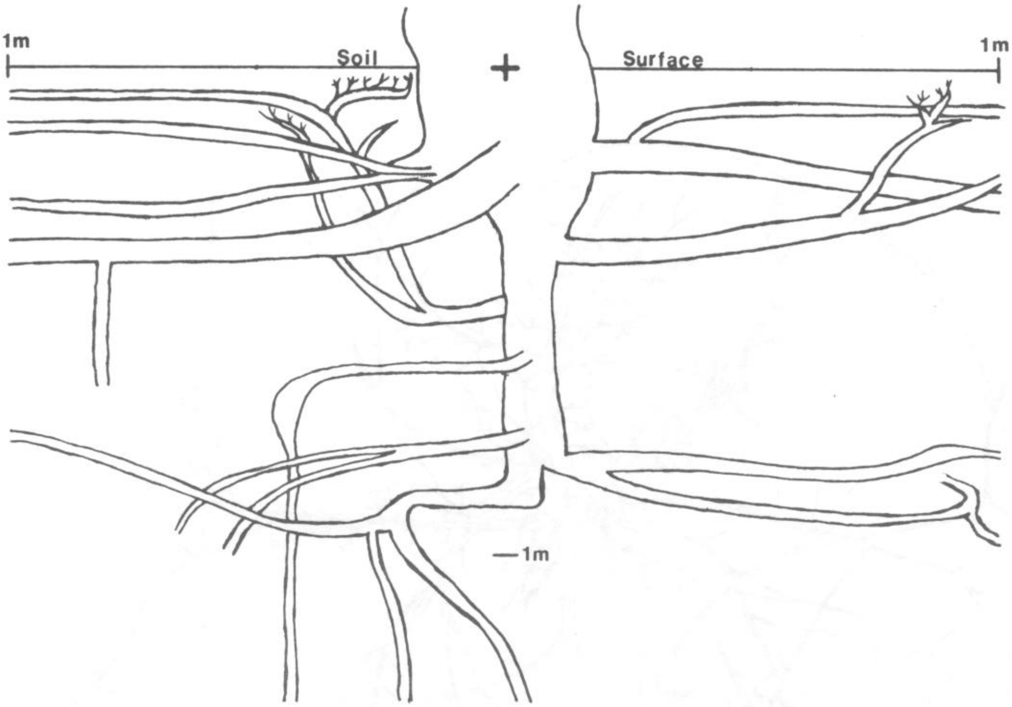


Fig. 3. *Picture and scaled drawing of lateral root system in upper 0.25 m of soil profile of mature honey mesquite tree.*



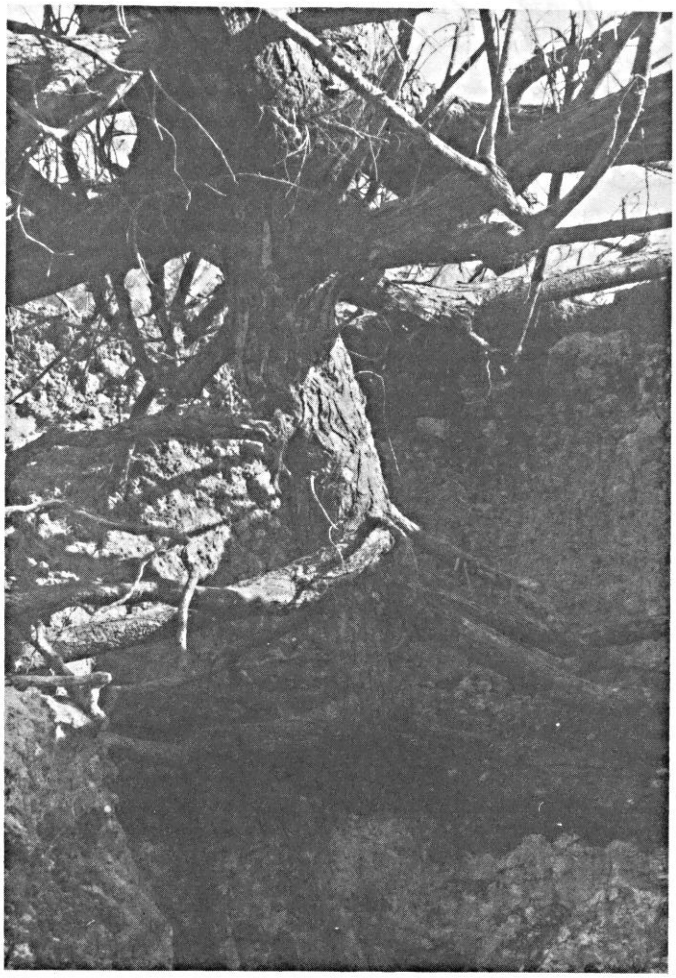


Fig. 4. *Picture and scaled drawing of tap root of mature honey mesquite tree.*

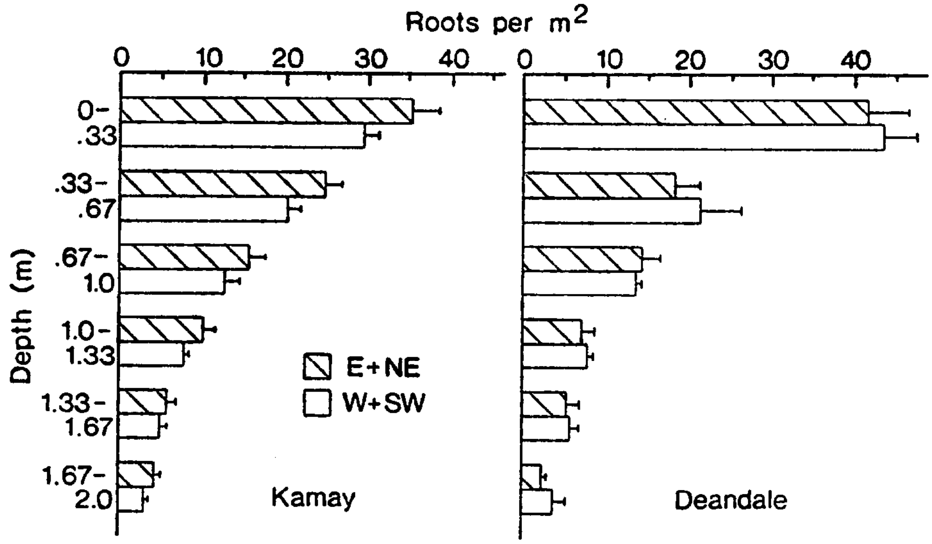


Fig. 5. *Number of roots (m²) at various depths along north-northeast and west-southwest trenched walls of small honey mesquite trees growing in Kamay and Deandale soil series. Vertical lines represent ± S.E. of $\bar{x}$.*

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Effect of burning on seed production of bluebunch wheatgrass, Idaho fescue, and Columbia needlegrass

BOB D. PATTON, M. HIRONAKA, AND STEPHEN C. BUNTING

Abstract

A study was conducted in 1984 to determine the effect of fall prescribed burning on seed production of bluebunch wheatgrass *(Agropyron spicatum)*, Idaho fescue *(Festuca idahoensis)*, and Columbia needlegrass *(Stipa columbiana)* in the sagebrush (*Artemisia* spp.)/grassland region. Plots were located on 7 burns of ages 1 to 5 years, with plots in adjacent unburned areas serving as controls. Seed production (seeds per plant) of bluebunch wheatgrass was greater on 2 of four 1-year-old burns and on one 3-year-old burn than on unburned comparison areas. Idaho fescue seed production was greater on a 5-year old burn than on the control plot, but not statistically different from the controls on 1- or 3-year-old burns. Columbia needlegrass seed production was markedly greater on a 2-year-old burn than on adjacent unburned areas. The percentage of filled florets and the number of seeds per inflorescence tended to be greater on burned plots for all 3 species. Bluebunch wheatgrass showed a variable response in the number of inflorescences produced per plant 1 year after burning, but there were significantly ($P \leq 0.05$) more inflorescences per plant on the 3-year-old burn than the control. Idaho fescue plants produced fewer inflorescences on both 1-year-old burns than on the control plots, but more on the 5-year-old burn than on the control. Columbia needlegrass plants produced more inflorescences on the burn than on the control.

Key Words: fire, *Agropyron spicatum, Festuca idahoensis, Stipa columbiana*

Fire is often prescribed in sagebrush/grass communities of the Intermountain West to reduce sagebrush cover and release perennial bunchgrasses from competition for light and moisture. Fire improves the range for cattle grazing by increasing forage yields and enhancing cattle movement (Wright et al. 1979).

Current practice is to rest a pasture for 1 growing season before burning to allow the build-up of fine fuels, and to rest the pasture for 2 growing seasons after burning to provide perennial grasses time to recover vigor and to promote seedling establishment (Wright et al. 1979). Bunchgrasses reproduce through seed, so good seed production is essential to maintain healthy, vigorous grass stands. Forage yields are often increased (Blaisdell 1953, Harniss and Murray 1973, Uresk et al. 1976, Wright et al. 1979) but the effect of burning on seed production of bunchgrasses has not been studied.

Our purpose in this study is to examine the effect of prescribed burning on seed production of bluebunch wheatgrass, Idaho fescue, and Columbia needlegrass on basin big sagebrush *(Artemisia tridentata* spp. *tridentata)*/Idaho fescue and mountain big sagebrush *(A. tridentata* spp. *vaseyana)*/Idaho fescue habitat types (Hironaka et al. 1983).

Study Areas

Seven study sites were selected from fall prescribed burns in the Boise, Idaho; Shoshone, Idaho; and Vale, Oregon, districts of the Bureau of Land Management, USDI. The sites ranged in elevation from 1,372 to 1,743 m, aspects were generally northern, and slopes were from 1 to 34%. The average annual precipitation for the sites ranged from 30 to 41 cm. Four 1-year-old burns and one 3-year-old burn were selected for study of bluebunch wheatgrass. Two 1-year-old, one 3-year-old, and one 5-year-old burns were chosen for study of Idaho fescue. One 2-year-old burn was selected for Columbia needlegrass.

Methods

On each site, macroplots were delineated on the burn and on a comparable, nearby area that had not been burned. In most cases, the macroplots were 50 by 50 m, but in a few instances they were smaller to maintain homogeneity of site and vegetation. The control and treatment plots were paired as nearly as possible with respect to elevation, aspect, slope, soil, and understory vegetation, including density of the species under study.

Five 25-m transects were randomly located on each site and 20 points were randomly located along each transect. The bunchgrass plant nearest to each point was selected and marked. Inflorescences were collected when the seed ripened. When this method did not result in sampling at least 60 plants with inflorescences, it was felt that the sample size was inadequate. In this case, inflorescences were also collected from all plants in 1 by 25-m belt transects. The number of transects was increased until at least 400 inflorescences from at least 100 plants had been collected. Since the plants within a belt transect were not randomly selected, the average of the various characteristics of the plants within the transect had to be used as the sample unit rather than the individual plants. This resulted in a smaller sample size but less variability between samples.

In the laboratory, the inflorescences were counted, the florets removed from the inflorescences, and filled and empty florets separated and counted on a light table. The mean numbers of inflorescences per plant, seeds per plant, seeds per inflorescence, and percentage of filled florets were calculated for each plot. Data were analyzed by standard *t*-test for the means.

Results and Discussion

Bluebunch Wheatgrass

An increase in seed production by a plant may be due to a greater number of inflorescences and/or a higher number of seeds per inflorescence (i.e., more florets or a greater percentage of filled florets). Each of these factors was examined in this study.

Seed production per bluebunch wheatgrass was greater on the burn than on the control for 3 of the 5 sites examined (Table 1). There was no difference in mean seed production per plant between the burn and control for the other 2 sites. The greatest difference in seed production was between the 3-year-old burn and its control (200 vs. 20 seeds/plant). The high productivity of the plants on this burn may be due to the long recovery time since burning, the timing of the burn in relation to soil moisture availability, or greater productivity of the site. The control plot for the 3-year-old burn produced almost twice as many seeds per plant as the control for the next most productive site. In any case, there seems to be evidence that the effect of burning resulted in greater seed production.

Authors are graduate student, professor, and associate professor, Department of Range Resources, University of Idaho, Moscow 83843. The senior author's current address is Central Grasslands, Research Station, Streeter, North Dakota 58483.

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Table 1. Mean number of seeds and inflorescence/bluebunch wheatgrass plant by sample site.

Habitat type	Age of burn (years)	Treatment	Seeds/plant	Inflor./plant	Sample size[1]
basin big sagebrush/	1	burn	0.5 ± 0.5[2]	0.4 ± 0.3	100
Idaho fescue		control	0.6 ± 0.4	1.3 ± 0.6**	100
basin big sagebrush/	1	burn	30 ± 10	10 ± 2	100
Idaho fescue		control	6 ± 3***	8 ± 3	100
mountain big sagebrush/	1	burn	20 ± 10	3.2 ± 1.7	91
Idaho fescue		control	2 ± 1*	1.3 ± 0.6*	97
mountain big sagebrush/	1	burn	20 ± 10	3 ± 2	100
Idaho fescue		control	10 ± 10	3 ± 1	100
mountain big sagebrush/	3	burn	200 ± 100	45 ± 11	30
Idaho fescue		control	20 ± 20**	20 ± 10***	30

[1]n = number of plants.
[2]Means ± confidence limits ($P \leq 0.10$).
*,**,***Significant at the 0.10, 0.05, and 0.01 levels, respectively.

Table 2. Mean number of florets/inflorescence, percentage of filled florets, and seeds/inflorescence on bluebunch wheatgrass plants by sample site.

Habitat type	Age of burn (years)	Treatment	Florets/ inflorescence[1]	Filled florets (%)	Seeds/ inflorescence	Sample size[2]
basin big sagebrush/	1	burn	31	1.3 ± 0.7[3]	04. ± 0.2	9 T[4]
Idaho fescue		control	25	0.8 ± 0.5	0.2 ± 0.2	7 T
basin big sagebrush/	1	burn	22	13 ± 2	3 ± 0.6	81
Idaho fescue		control	22	4 ± 1**	0.8 ± 0.3***	53
mountain big sagebrush/	1	burn	50	10 ± 4	5 ± 2	27
Idaho fescue		control	25	5 ± 2**	1.3 ± 0.4***	25
mountain big sagebrush/	1	burn	41	16 ± 3	7 ± 2	41
Idaho fescue		control	25	13 ± 2	3.3 ± 0.8***	38
mountain big sagebrush/	3	burn	18	20 ± 5	3.7 ± 0.9	29
Idaho fescue		control	21	6 ± 3***	1.3 ± 0.7***	26

[1]Florets/inflorescence was derived by dividing seeds/inflorescence by percent filled florets.
[2]n = number of plants.
[3]Mean ± confidence limits ($P \leq 0.10$).
[4]T = number of belt transects (1 × 25 m; due to scarcity of plants, the mean of all plants in each transect was used to reduce the sample variance).
*,**,***Significant at the 0.10, 0.05, and 0.01 levels respectively.

Table 3. Mean number of seeds and inflorescences/Idaho fescue plant by sample site.

Habitat type	Age of burn (years)	Treatment	Seeds/plant	Inflor./plant	Sample size[1]
basin big sagebrush/	1	burn	1 ± 1[2]	0.3 ± 0.2	100
Idaho fescue		control	3 ± 2	1.3 ± 0.5***	100
mountain big sagebrush/	1	burn	1 ± 1	0.6 ± 0.4	100
Idaho fescue		control	1 ± 1	1.5 ± 0.4**	100
mountain big sagebrush/	3	burn	9 ± 8	8 ± 2	100
Idaho fescue		control	3 ± 1	6 ± 2	100
mountain big sagebrush/	5	burn	40 ± 10	12 ± 3	100
Idaho fescue		control	5 ± 2***	4 ± 1***	100

[1]n = number of plants
[2]Mean ± confidence limits ($P \leq 0.10$).
*,**,***Significant at the 0.10, 0.05, and 0.01 levels, respectively.

Several studies have shown an increase in the number of inflorescences per plant following burning (Blaisdell 1953, Clifton 1981[1]). In this study, the 3-year-old burn and one 1-year-old burn produced more inflorescences than their control plots ($P \leq 0.10$), but one 1-year-old burn produced fewer inflorescences per plant than its control ($P \leq 0.05$) (Table 1).

Plants on the burns produced more florets per inflorescence on only 3 of the 5 sites (Table 2). The percentage of filled florets was significantly ($P \leq 0.05$) greater for the plants on the burn on 3 of the 5 sites and not significantly ($P \leq 0.10$) different on the other 2 sites (Table 2). Through combinations of more florets per inflorescence and greater percentages of filled florets, seed production per inflorescence was significantly ($P \leq 0.01$) greater on the burns on 4 of the 5 sites (Table 2).

[1]Clifton, N.A. 1981. Responses to prescribed fire in a Wyoming big sagebrush/bluebunch wheatgrass habitat type. M.S. Thesis, Univ. of Idaho, Moscow.

Idaho Fescue

Seed production per Idaho fescue plant was greater on the 5-year-old burn than on its control (Table 3). There was no difference in seed production between the burn and its control on the

Table 4. Mean number of florets/inflorescence, percentage of filled florets, and seeds/inflorescence on Idaho fescue plants by sample site.

Habitat type	Age of burn (years)	Treatment	Florets/ inflorescence[1]	Filled florets (%)	Seeds/ inflorescence	Sample size[2]
basin big sagebrush/	1	burn	35	9 ± 6[3]	3 ± 3	12
Idaho fescue		control	30	5 ± 3	1.6 ± 0.8	32
mountain big sagebrush/	1	burn	—[4]	—[4]	4.6 ± 2.0	5 T[5]
Idaho fescue		control	44	2 ± 1	1 ± 1**	53
mountain big sagebrush/	3	burn	32	3 ± 1	1.0 ± 0.4	72
Idaho fescue		control	35	2 ± 1*	0.6 ± 0.3	78
mountain big sagebrush/	5	burn	28	12 ± 2	3.5 ± 0.7	82
Idaho fescue		control	32	5 ± 2***	1.6 ± 0.7**	64

[1]Florets/inflorescence was derived by dividing seeds/inflorescence by percent filled seeds.
[2]n = number of plants
[3]Mean ± confidence limits ($P \leq 0.10$).
[4]Not sampled.
[5]T = number of belt transects (1 × 25 m; due to scarcity of plants, the mean of all plants in each belt was used to reduce sample variance).
*,**,***Significant at the 0.10, 0.05, and 0.01 levels, respectively.

other 3 sites. There may have been an increase in seed production with time subsequent to burning, but the results are not conclusive.

The number of inflorescences per Idaho fescue plant were less on both 1-year-old burns than on their controls (Table 3). This demonstrates the sensitivity of Idaho fescue plants to burning, which has been reported by Blaisdell (1953) and Countryman and Cornelius (1957). There was no difference in the number of inflorescences per plant between the 3-year-old burn and its control, and the plants on the 5-year-old burn produced more inflorescences than the plants on the control. The Idaho fescue plants appear to have regained their vigor by the third year following burning, and improved in vigor by the fifth year.

On Idaho fescue plants, the number of florets per inflorescence was similar for burned and control plots, but the percentage of filled florets was greater for plants on the 3-year-old and 5-year-old burns (Table 4). The number of seeds per inflorescence was greater on one 1-year-old burn and the 5-year-old burn than on the control plots (Table 4).

Columbia Needlegrass

Data for Columbia needlegrass were available for only 1 site which had been burned 2 years before sampling. On this site, Columbia needlegrass seed production was greater on the burn (500 vs. 16 seeds/plant). Plants on the burn produced more inflorescences (14 vs. 2 inflorescences/plant and more seeds per inflorescence (30 vs. 10 seeds/inflorescence). Greater seed production per inflorescence was due to a greater number of florets per inflorescence (55 vs. 22 florets/inflorescence) while the percentage of filled florets (50% on the burn vs 45% on the control) did not differ significantly ($P \leq 0.10$).

The effect of burning seemed to stimulate seed production in each of these species, although for Idaho fescue this effect may not be significant until 5 years after burning. The percentage of filled florets and the number of seeds produced per inflorescence tended to be greater on the burned plots than on the controls, and this difference seemed to increase with time since burning.

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Effect of defoliation frequency and N-P-K fertilization on maidencane

R.S. KALMBACHER AND F.G. MARTIN

Abstract

Maidencane (*Panicum hemitomon* Schult.), an important grass on Florida and southeastern Gulf Coast fresh-water marsh range, was cut on 3-, 6-, 9-, 12- and 24-week intervals (T) from June to December 1982 and 1983. Half the plots were fertilized every 6 weeks with 56, 12, and 22 kg/ha N, P, and K, respectively. Dry matter yield (DM), tiller density (TD), rhizome total nonstructural carbohydrate (TNC), crude protein (CP), and in vitro organic matter digestibility (IVOMD) were determined. DM was reduced with frequent clipping, especially every 3 weeks, and 2-year average DM was described: $1981 + 660T - 22T^2$, where T is weeks between harvest. Fertilized grass yielded more DM (6,270 kg/ha) than unfertilized (4,410). TD increased as harvest interval increased. For example TD in April 1983 was $TD = 40 + 19.1T$. TNC was affected by cutting interval ($7.2 + 0.61T - 0.016T^2$) but not fertilization. CP and IVOMD declined about 0.5 and 3.0 units, respectively, for each week forage remained on range. Fertilization improved 2-year average CP (yes = 13.3%, no = 11.9%), but IVOMD was unaffected. Defoliation of maidencane every 3 to 6 weeks reduced stands and yield, and defoliation intervals longer than 3 to 6 weeks resulted in reduced protein and digestibility. Fertilizer rates and timing of application used in this study did help to maintain yield and tiller density at a higher level than unfertilized grass in the second year.

Key Words: Southeastern range, Florida range, fresh water marsh

Maidencane (*Panicum hemitomon* Schult.) is an important Florida range grass because of its high yield (Long et al. 1986a), prominence in cattle diets during summer (Kalmbacher et al. 1984), and its high forage quality (Long et al. 1986a, 1986b). Maidencane is also an important native grass in southern Louisiana (Williams 1951).

Although Florida range responds positively to fertilization (Killinger 1948, Lewis 1970), it is questionable whether the practice would be practical (Duval and Grelen 1967) when range is a scattered mixture of grasses and forbs growing on infertile, sandy spodosols frequently dominated by shrubs, especially saw palmetto (*Serenoa repens* (Bartr.) Small). Fertilization of maidencane may be justifiable because this grass usually grows in dense stands.

Since we could find no information about the response of maidencane to any management, we took advantage of a pure stand growing on a uniform site in a pasture. This was not a fresh-water marsh site, where the grass normally grows, but a uniform site that permitted us to draw inferences on dry matter (DM), crude protein (CP) content, in vitro organic matter digestibility (IVOMD), tiller density (TD), total nonstructural carbohydrate (TNC) content of rhizomes, and tissue P and K content of maidencane cut at various maturities, with and without N, P, K fertilization.

Materials and Methods

A pure stand of maidencane was selected near Bartow, Florida, on a Pomello fine sand (sandy, siliceous, hyperthermic Arenic Haplaquod) with an initial pH of 5.8 and 1.5% organic matter content. This maidencane, a very vigorous, strongly rhizomatous ecotype, became PI T29575 at the SCS plant materials center at Brooksville. The experimental area was a fenced-off portion within a Pangola digitgrass (*Digitaria decumbens* Stent.) pasture which received spring and fall applications of about 50, 10, 20 kg/ha N, P, and K, respectively. The area had been grazed November to August for the past 5 years and a single crop of hay was usually cut in October. The experimental area was not grazed during the trial.

The experimental area was cut to 7.5-cm stubble early in May 1982 and 1983, after which maidencane was cut at 3, 6, 9, 12, and 24-week intervals; each treatment with or without 56, 12, and 22 kg/ha N, P, and K (Table 1). The experiment was a 2 × 5 factorial in application of fertilizer and cutting interval. Experimental design was a randomized, complete block with 4 replications.

The first cutting was made 3 weeks after the initial staging when grass was 30 to 45 cm tall, which was about the first week in June. Forage was sampled to a 7.5-cm stubble-height with a plot harvester which cut a 0.4 × 5.20-m swath in each 2.14 × 6.11-m plot. The remainder of each plot was re-staged to 7.5 cm after samples were taken. Fertilizer was weighed and applied by hand to all appropriate plots every 6 weeks. The initial fertilization was made in early May in both years, but was discontinued when growth ceased in October. Dolomite was uniformly applied at 2,240 kg/ha on 16 December 1982 (subsequent pH measurements in 1983 indicated little pH change). The experiment was sprayed on 2 May 1983 with a 3:1 mixture of 2,4-D (2,4-Dichlorophenoxyacetic acid) and dicamba (2-Methoxy-3,6-dichloro-benzoic acid) at 2.3 liter/ha (formulation of Weedmaster(R) to control broadleaf plants such as Mexican tea (*Chenopodium ambrosioides* L.) and sedges (*Cyperus* spp.).

Plots were visually rated in May 1983 for weed contamination, particularly common bermudagrass (*Cynodon dactylon* L. Pers.), to adjust yield to that of pure maidencane. Harvested maidencane was weighed in the field and a sub-sample (0.5 kg) was weighed, dried, and re-weighed in order to calculate DM yield/ha. These samples were used for CP (Gallaher et al. 1975, Hambleton 1977), and IVOMD (Moore and Mott 1974) analyses. Tissue P (Jackson 1958) and K, Ca, and Mg were determined by atomic absorption. Soil was sampled (2 cores, 3 × 30 cm) in each plot every 3 weeks and composited over replications. Rhizomes were dug (10 × 15-cm cores) every 3 weeks for yield determination and analyzed for TNC (Smith 1969, Somogyi 1952). Rhizome samples were also composited over replications. Tiller density was determined by counting tillers in a 0.25-m^2 quadrat in each plot on 4 June 1982, 2 May and 1 Dec. 1983, and 3 Apr. 1984.

Data were analyzed by analysis of variance. Significant main effects and first order interactions were further investigated using Duncan's multiple range test or regression techniques, depending on whether the factor was qualitative or quantitative. Dates were used as replications for TNC and soil mineral analyses. Soil mineral content from fertilized plots was compared to that from unfertilized plots with a paired *t*-test. Unless otherwise stated, all statistical tests were made with $P<0.05$.

Results & Discussion

Dry Matter Yield

Yields were lower in 1983 than 1982 at more frequent cuttings because stands were weakened after 1 year of treatment (Fig. 1). Cutting every 3 weeks was especially detrimental to yield because maidencane tillers in this treatment did not grow taller than 20 to

Authors are professor/agronomist, Ona Agricultural Research Center, Ona Florida, 33865; and professor/statistician, University of Florida, Gainesville 32611.
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Table 1. Schedule of fertilization, cutting, rhizome, tiller, and soil sampling for maidencane. Bartow, Florida.

Sample taken		1982 May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	1983 May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Fertilize[1]		X	X	X	X					X	X	X		X			
Harvest	3		X X	X	X X	X	X				X	X X	X	X X			
	6		X		X	X						X	X	X			
	9			X		X						X		X			
	12				X				X				X				X
	24								X								X
Rhizomes			X X	X	X X	X	X X		X		X	X X	X	X X			X
Tiller[2]			X							X							X
Soil[3]			X X	X	X X	X	X X	X	X	X	X	X X	X	X X	X	X	X

[1]Growth terminated in October and fertilization discontinued.
[2]Tiller density also determined 3 Apr. 1984.
[3]Soil also sampled on 17 Feb., 4 Apr. 1982, 27 Jan., 8 Mar. 1983.

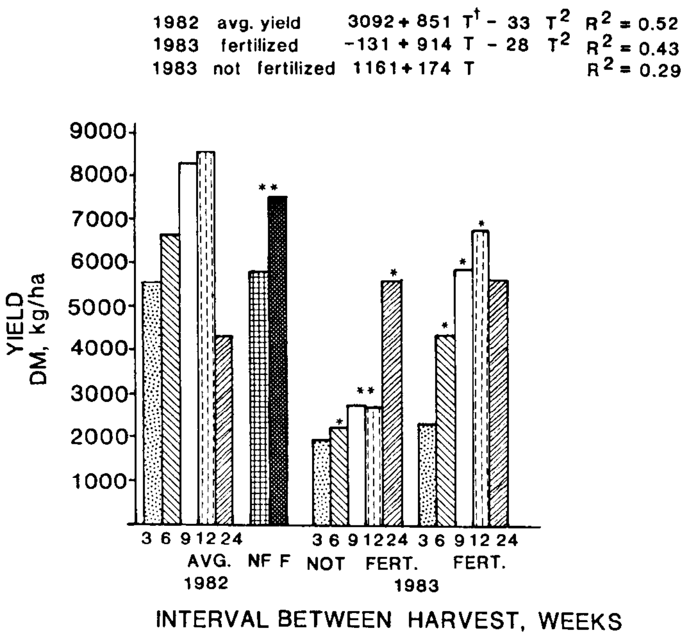

Fig. 1. *Total annual dry matter yield (observed) and prediction equations for maidencane yield as affected by interval between harvest and fertilization. Bartow, Florida. 1982 and 1983.*
† T = weeks between harvest.
***Difference between not fertilized (NF) and fertilized (F) significant (P<0.01). Fertilization was 56, 12, 22 kg/ha N, P, K every 6 weeks.*

30 cm before recutting. Such frequent defoliation is similar to that observed on maidencane ponds surrounded by poorly managed pine-palmetto range, which is a situation favoring heavy use of the ponds.

Defoliation at a 12-week interval resulted in the highest average predicted and observed 1982 DM yield of fertilized and unfertilized (no interaction with interval) maidencane (Fig. 1). Fertilized maidencane reached maximum predicted yield in 1983 with an 18-week interval, while unfertilized grass reached maximum predicted yield at a 24-week interval. Yields of unfertilized maidencane at the 24-week interval agreed with 2 reports of annual DM yields of unfertilized maidencane (4,800 and 3,470 kg/ha) from a freshwater marsh in central Florida (Kalmbacher et al. 1984).

Maidencane growth stopped after September, and many of these leaves became senescent and fell. More frequently sampled treatments, such as 3, 6, or 9 week, were not sampled after the first week in October because there was no growth (Table 1). Although 3, 6, 9, and 12-week treatments were 'scheduled' for 10, 4, 3, and 2 clippings, they were actually sampled 6, 3, 2, and 2 times, respectively. Less frequent cutting resulted in greater annual yield than repeated cutting (Fig. 1).

Maidencane herbage yield resulting from 3- to 24-week defoliation intervals from May to December was best described as quadratic because of the loss of senescent leaves in September. Yield response was linear over the 3- to 12-week intervals when the 24-week interval was deleted from the analysis. In 1982 DM yields from fertilized and unfertilized plots (3- to 12-week intervals) were described by the equation: $4560 + 357T$, where T is weeks between harvest. In 1983 there was no significant regression for unfertilized maidencane, but DM yield of fertilized maidencane was described: $1140 + 492T$.

Fertilization increased ($P<0.01$) yield of maidencane in both years. Average observed yield of nonfertilized grass was 5,780 and 3,050 kg/ha in 1982 and 1983, respectively. Fertilized grass yielded 7,550 and 4,900 kg/ha in these years, respectively. Average yield was lower in 1983 on both treatments, but addition of fertilizer resulted in less of a decline (35%) in maidencane yield than when no fertilizer was applied (47% decline).

Maidencane cut at different frequencies did not respond the same to fertilization treatments in 1983 (Fig. 1). When fertilized, maidencane cut at 6-, 9- and 12-week intervals resulted in higher yields than that interval on unfertilized maidencane. When maidencane was cut at 3- or 24-week intervals, this response was not observed. Yield response was quadratic to fertilizer application in 1983, but the response was linear without fertilizer. The curvilinear response resulted because fertilization of sparse stands (i.e., frequently cut, second year) fostered *Cynodon dactylon* and *Cyperus* spp. growth, which suppressed maidencane yield. There was no weed encroachment in the 9-, 12- or 24-week interval treatments, and good stands of maidencane responded positively to fertilizer.

Tiller Density

Defoliation frequency significantly ($P<0.01$) influenced tiller density (Fig. 2). Frequent defoliation resulted in reduced tiller density and hence lower yield (Fig. 1). Tiller density was affected by cutting and fertilization in May and December 1983. Fertilizer resulted in a quadratic response with tiller density increasing very rapidly between 3- and 9-week intervals and declining at the 24-week cutting interval. This response was similar to that of yield (Fig. 1). Without fertilizer, tiller density and yield were linear or nearly so.

Initial tiller density in June 1982 averaged 650 tillers/m². By May 1983 tiller density was less than the initial number in 3-, 6-, 9-, and 12-week cutting intervals on nonfertilized plots (Fig. 2). Tiller density in May 1983 in fertilized treatments cut at 9-, 12-, and 24-week intervals was similar to or greater than the June 1982 tiller density. When counts were made in December 1983, 18 months later after the start, maidencane in both nonfertilized and fertilized treatments had lower tiller density than June 1982 values. Tiller

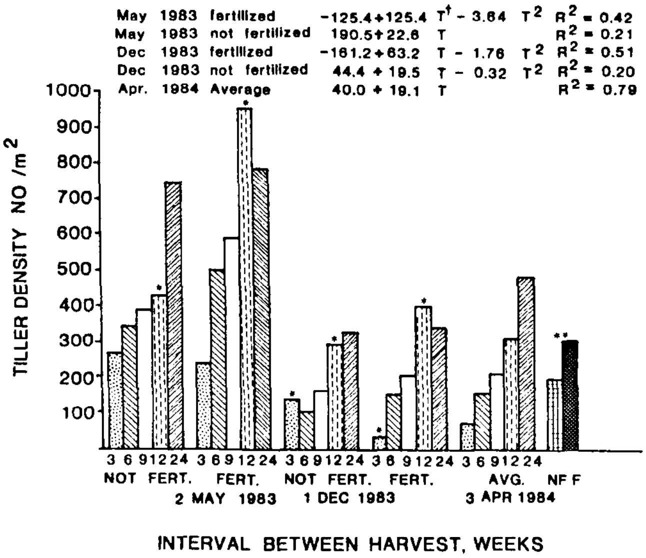

Fig. 2. *Tiller density (observed) and prediction equations for tiller density of maidencane with and without fertilization. Bartow, Florida. 1983 and 1984.*
†T = weeks between harvest.
**Difference between fertilized and not fertilized within the same cutting interval are different (P<0.01). Fertilization was 56, 12, 22 kg/ha N, P, K every 6 weeks.*
***Difference between average fertilized (F) and nonfertilized (NF) different (P<0.01).*

density of fertilized maidencane cut at 12-week intervals was greater than that of unfertilized maidencane on both 2 May and 1 Dec. 1983.

Tiller density was lower in more frequently harvested plots on 3 Apr. 1984 regardless of fertilizer treatment (Fig. 2). Fertilized plots had greater average tiller density than unfertilized plots. Comparison of tiller density at 3 Apr. 1984 or 1 Dec. 1983 with that on 2 May 1983 is difficult because counts were not made at similar times of the year. Maidencane was going into dormancy on 1 Dec. and had not completely initiated regrowth on 3 Apr.

Rhizome TNC and Yield

Rhizome TNC content and yield (Fig. 3) followed patterns similar to whole-plant yield (Fig. 1) and tiller density (Fig. 2). Predicted rhizome TNC and yield were quadratic over cutting frequencies and had low values at 3- to 9-week cutting intervals.

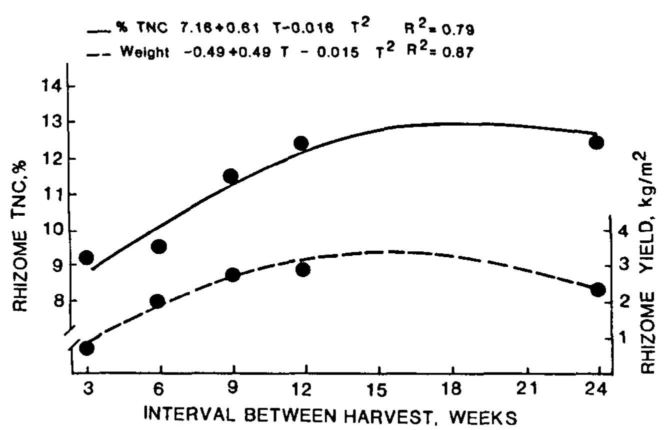

Fig. 3. *Predicted and observed maidencane rhizome total non-structural carbohydrate (TNC) content and fresh weight yield as affected by interval (T=weeks) between harvest. Bartow, Florida. 1982 and 1983.*

Maximum rhizome yield was predicted to occur at 12- to 18-week intervals, with a decline by the 24-week interval. Predicted rhizome TNC continued to rise slowly in plants cut at intervals greater than 12 weeks. There was no rhizome yield or TNC response to fertilization and no interaction. Low TNC values indicate maidencane was not maintaining enough carbohydrate to sustain vigor, especially at 3-week intervals. Even though maidencane rarely flowers (early June), it maintains the morphology of grass (culm and cauline leaves) in the jointing stage. When maidencane was cut at 7.5 cm, tillers were killed, and all new growth came from below ground.

Forage Quality

Crude protein content of maidencane in both fertilizer treatments declined as cutting interval increased in both years (Fig. 4).

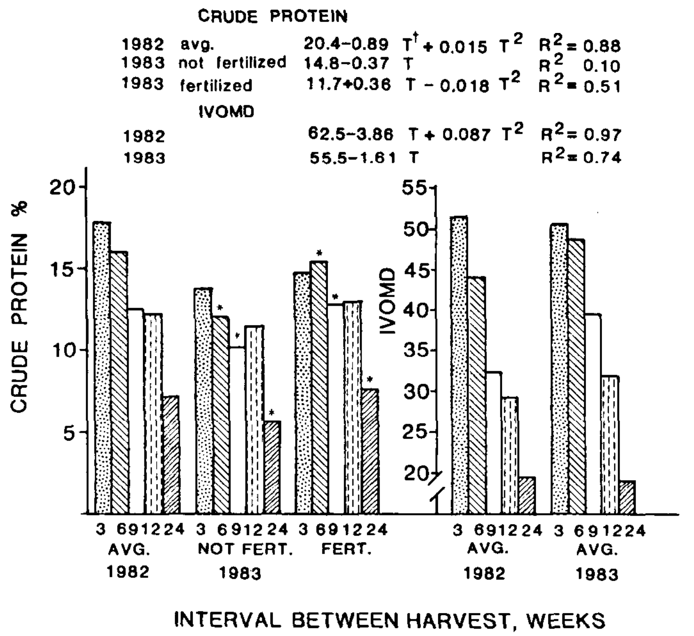

Fig. 4. *Observed crude protein and in vitro organic matter digestibility (IVOMD) and their prediction equations for maidencane with and without fertilization. Bartow, Florida. 1982 and 1983.*
†T = weeks between harvest.
**Difference between fertilized and not fertilized within the same cutting interval are different (P<0.05). Fertilization was 56, 12, 22 kg/ha N, P, K every 6 weeks.*

The decline was about 0.5% in CP for each week that maidencane remained uncut after an initial 3-week period (height of 30 to 45 cm). Fertilization did not affect CP content in 1982, but in 1983 fertilization increased CP content (independent of cutting interval) ($P<0.01$) over nonfertilized maidencane. When maidencane was fertilized in 1983, CP content was higher than unfertilized grass at 6-, 9-, and 24-week intervals. Maidencane sampled in December at the 24-week growth interval in both years had been senescent for 6 weeks prior to the first December frost.

Cutting interval affected ($P<0.01$) IVOMD, which declined as much as 3% for every week that defoliation was postponed (Fig. 4). There was a steady IVOMD decline in 1983 when IVOMD dropped 1.6% for every week between 3 and 24 weeks. Poor digestibility has been reported for hand-collected upper leaves and stems and for bolus samples from esophageally fistulated steers grazing maidencane in winter (Long et al. 1986a). The decline in both CP and IVOMD in winter emphasizes the importance of maidencane use in summer (Kalmbacher et al. 1984, Long et al. 1986a).

Fertilization improved ($P<0.01$) IVOMD in 1982, but improvement was of little practical importance (34.7% vs 36.2%). There was no fertilization effect ($P>0.05$) on IVOMD in 1983.

Two-year average CP was 12% for nonfertilized and 13.3% for fertilized maidencane and 36% IVOMD for fertilized and 37% for unfertilized maidencane. Differences due to fertilization were small by comparison to effects that cutting frequency had on both CP and IVOMD.

Mineral Content

There were no differences between fertilized and unfertilized plots ($P>0.05$) in soil P and K content, which averaged 12 and 11.7 kg/ha of P and K, respectively. Soil Ca content and pH were lower ($P<0.01$) on fertilized (495 kg/ha and 5.6) compared to unfertilized soil (547 kg/ha and 6.0). These analyses represent soil sampled over the 2-year experimental period.

There were no differences in P or K between fertilized and unfertilized maidencane during 1982. Likewise, tissue P was not different between these treatments in 1983, but K was higher in fertilized tissue (1.1%) vs unfertilized tissue (0.9%).

To determine how long fertilization effects could be detected, tissues from fertilized maidencane cut at repeated 3-week intervals were compared. Bearing in mind that fertilization was every 6 weeks, first-cut grass 3 weeks after fertilization was higher ($P<0.05$) in *P* content (0.36%) than second-cut, 3-week old grass (0.30%) in 1983 but not in 1982. Tissue K content was higher at 3 weeks (1.6%) vs 6 weeks (1.3%) in both years. Applied K usually does not accumulate on Florida's coarse textured soils, even when crop removal is small or when recycling occurs (Blue 1974).

Tissue P and K declined ($P<0.01$) in each year as maidencane culms aged (Table 2). Because maidencane was fertilized every 6 weeks, forage cut on 9- and 12-week intervals received 2 applications compared to single applications on 3- and 6-week treatments (Table 1). Still, there was a steady decline in tissue P and K. The decline was brought about by nutrient leaching from the soil, reduced uptake with plant age, and by dilution in increasing plant biomass. Grass at 12 weeks of age was especially low in P and K because of leaf senesence.

Table 2. Effect of harvest interval on P and K content in whole plant maidencane forage (on dry matter basis).

Year/mineral	Harvest interval (wks) 3	6	9	12
	%			
1982				
P[1]	0.34	0.33	0.28	0.16
K[2]	1.59	1.38	1.22	0.40
1983				
P[3]	0.30	0.34	0.27	0.12
K[4]	1.00	1.48	1.19	0.21

[1] $P = 0.3 + 2.1 \times 10^{-5}D - 9.0 \times 10^{-6}D^2$
[2] $K = 1.5 - 7.5 \times 10^{-4} - 5.0 \times 10^{-5}D^2$
[3] $P = 1.0 + 7.5 \times 10^{-4}D - 1.8 \times 10^{-5}D^2$
[4] $K = 0.4 + 0.037\ D - 7.43 \times 10^{-4}D^2 + 3.0 \times 10^{-6}D^3$
Where D is Julian date of harvest (196, 237, 279, 341 for 1982 and 209, 229, 272, 335 for 1983) minus 196, which makes the first sample date D = 0.

Management Implication

These data suggest that summer-long grazing of maidencane range at low stocking rates may not take advantage of the yield and quality potential of the grass just as deferring use through summer would not be taking advantage of the full potential of maidencane. Rotationally grazing at high grazing pressure with 5- to 7-week regrowth periods may be a compromise between yield, persistence, and quality. Fertilization with N, P, and K at the rates, frequency, and soil used in this study would not be justifiable for improvement in yield or quality. Fertilization did help to lessen decline in yield and tiller density that resulted from more frequent defoliation.

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Growth and gas exchange of *Andropogon gerardii* as influenced by burning

TONY J. SVEJCAR AND JAMES A. BROWNING

Abstract

Late spring burning response of the dominant big bluestem *(Andropogon gerardii)* was studied on a tallgrass site in central Oklahoma (USA) during a dry (1984) and a wet (1985) year. During active growth (May and June) when temperatures were not limiting, photosynthesis (PS) was higher for burned (25–27 μ moles^{-2} s^{-1}) relative to unburned plants (20–25 μmoles m^{-2} s^{-1}); but during summer drought, PS declined to <10 μ moles m^{-2} s^{-1} and treatment rank reversed. However, the 2 treatments had similar transpiration per unit leaf area, and burned plots had much higher peak big bluestem leaf area indices (6.4 in 1984 and 4.5 in 1985) than unburned plots (2.0 both years). Apparently higher transpirational demand in burned plots lowered soil moisture, thereby increasing late season moisture stress and lowering PS relative to unburned plots. Burning resulted in a doubling of big bluestem tiller numbers (997–1,034 and 498–600 tillers m^{-2} for burned and unburned plots, respectively). Peak aboveground biomass of big bluestem was about 3 times higher on burned relative to unburned prairie during both years. During both years burned vs. unburned big bluestem had higher peak values of % leaf nitrogen (N) and more total leaf N (%N* leaf mass). Thus, burning big bluestem increased leaf area during the active growth period and stimulated PS, resulting in higher carbon uptake of burned relative to unburned plants.

Key Words: prescribed burning, tallgrass prairie, water potential

The tallgrass prairie of North America has been classified as a fire-derived and fire-maintained ecosystem (Stewart 1951). Suppression of fire often reduces productivity of tallgrass species (Kucera and Ehrenheich 1962, Hadley and Hieckhefer 1963, Hulbert 1969, Rice and Parenti 1978, Knapp 1985). However, in a number of studies productivity was unaffected or reduced by burning (Kelting 1957, Owensby and Anderson 1967, Anderson et al. 1970). Several factors could explain the contradictory results obtained from burning studies: (1) in some ecosystems burning during wet years has a positive effect on primary productivity but the opposite is true for dry years (Wright 1974); (2) species response to fire varies, and thus the effect of fire may depend on the species composition of a particular tallgrass prairie site; and (3) timing of burning can affect species composition and primary production (Towne and Owensby 1984). Research from the Flint Hills of Kansas, where tallgrass prairie sites were burned annually since 1928, shows that time of burning has a major effect on community response to fire (Towne and Owensby 1984). Burning in late spring rather than at 1 of 3 earlier dates favored big bluestem (*Andropogon gerardii* Vitman) and Indiangrass (*Sorgastrum nutans* L.) Nash over other species. These 2 C_4 grasses are dominants in much of the tallgrass prairie region. Towne and Owensby (1984) further state that only 3 weeks difference in timing of a spring burn can have substantial long-term effects on the plant community.

Although there is a good deal of information concerning primary productivity and response to burning of tallgrass prairie species, few studies have concentrated on seasonal trends in physiological and morphological attributes of these species (Risser et al. 1981). During a drought year, Knapp (1985) found that big bluestem exhibited higher photosynthetic rates on burned compared to unburned prairie during the active growth period (May and June). The same author also showed that big bluestem has a high capacity for osmotic adjustment (Knapp 1984a), apparently a mechanism allowing this species to tolerate the summer drought common in the Central and Southern Great Plains.

To determine the effects of burning on big bluestem, we chose to burn a tallgrass prairie site at a time that favors productivity of this species. The objective was to monitor seasonal trends in physiological and morphological characteristics of burned and unburned big bluestem.

Materials and Methods

Study Site

Research was conducted during 1984 and 1985 at the USDA/-ARS Forage and Livestock Research Laboratory (98°0′ W, 35°*40′N; elevation* = 450 m) near El Reno, Oklahoma. Vegetation on the study site was typical of native tallgrass prairie, with big bluestem, Indiangrass, and little bluestem *(Schizachyrium scoparium* (Michx.) Nash as dominants. Soils were silt loams classified as either Udic Paleustolls or Pachic Arguistolls. These soils tend to be well drained, relatively deep (150 cm), and have high available water capacity (Fisher and Swafford 1976). The mean annual precipitation is 762 mm, of which 68% (520 mm) occurs during the April through September growing season. Precipitation was below average during 1984, when yearly and growing season total were 724 and 349 mm, respectively; the opposite was true for 1985 when yearly (969 mm) and growing season (602 mm) precipitation were both well above average. Mean annual temperature is 15.6 C. The site had not been burned for at least 15 years prior to the initiation of the study. Livestock grazed the site during the dormant period (late fall and winter) until February 1983.

Study Design

Three 30 by 60 m blocks were established in a 90 ha pasture. Half of each block was burned on 23 April 1984 and 10 April 1985, the remaining portion served as an unburned control. Data were analyzed using a randomized complete block model. Burning was conducted when leaves of big bluestem were 2 to 4 cm in length. This criterion was selected because it ensured that soil temperatures would be sufficient to support growth of native perennial grasses immediately following burning. Plots were not grazed during the study period.

Gas Exchange and Xylem Water Potential

Net photosynthesis (PS), transpiration (TR), leaf temperature, and photsynthetic photon flux density (PPFD) were measured on recently expanded leaves of big bluestem from burned and unburned treatments with an LI-6000 portable photsynthesis meter (Li-Cor, Inc., Lincoln, NE) equipped with a 0.25 l leaf chamber. Measurements were taken between 1300 and 1500 hrs on clear days. Leaves were monitered for CO_2 uptake and water vapor losses over a 30-s period. About 20 minutes after being removed from the leaf chamber the leaf was wrapped with a moist paper towel, excised, and xylem water potential (ψ) measured with a pressure chamber (3000 Series, Soil-moisture Equip. Corp., Santa

Authors are range scientist, USDA-ARS, 920 Valley Road, Reno, Nevada 89512 and graduate research assistant, Dept. of Wildland Recreation Management, University of Idaho, Moscow 83843. At the time of the study, authors were research agronomist and biological technician, USDA-ARS, P.O. Box 1199, El Reno, Oklahoma 73036.
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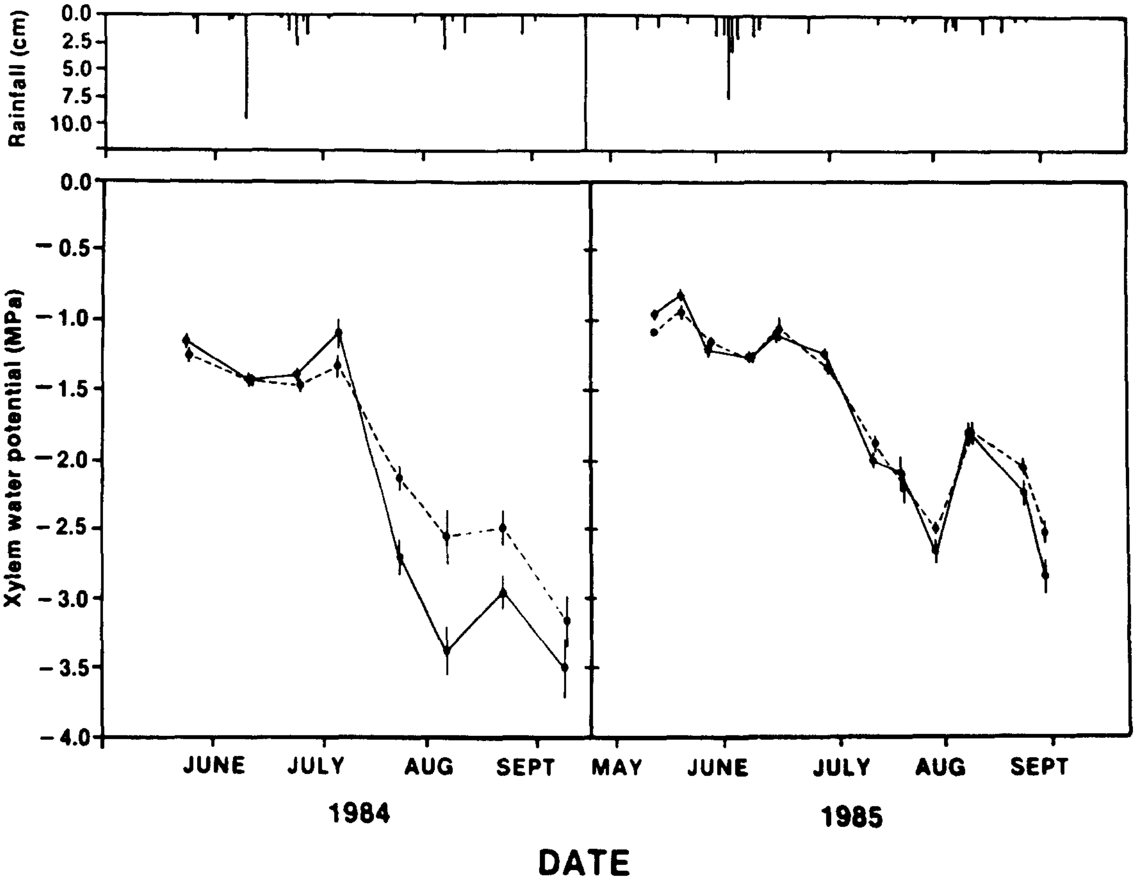

Fig. 1. *Seasonal trends in precipitation, and big bluestem xylem water potential (measured 1300 to 1500 h, CDT) from burned (solid lines) and unburned (dashed lines) tallgrass prairie during 1984 and 1985 growing seasons. Vertical lines are ± one standard error of the mean (n = 12). Treatment differences were significant (P≤.05) during the last half of 1984 and for the first two sampling dates of 1985.*

Barbara, Calif.) Leaves were stored between layers of moist towels and upon return to the laboratory measured for area with an LI-3000 area meter with conveyer belt assembly (Li-Cor, Inc., Lincoln, Nebr.). These values were used to calculate PS and TR on a leaf area basis. Measurements were taken on 8 occasions during May to September, 1984, and on 13 occasions during the same period in 1985.

Phytomass, Tillers, Leaf Area and Nitrogen

To assess the effect of burning on phytomass and morphological attributes of big bluestem, 15 × 25-cm quadrats were sampled on 3 dates in 1984 (4 quadrats per treatment/block combination on each date) and 8 dates in 1985 (6 quadrats per treatment/block combination on each date). Number of big bluestem tillers per quadrat were counted, then clipped to ground level. A portion of the tillers were selected at random and leaves removed and placed in glass jars over moist toweling. The remaining tillers were placed in paper bags. Phytomass of other species were also sampled. Leaves collected in glass jars were scanned on an LI-3000 area meter, dried at 50° C for 48 h, and weighed, and specific leaf weights (dry mass per leaf area) calculated. The remaining portion of the big bluestem sample was separated into leaf and stem (stem plus sheath) components. Oven-dry weights were deteremined for leaf and stem of big bluestem and total phytomass of other species. Leaf area index (LAI) of big bluestem was calculated from leaf mass and specific leaf weight. Leaf nitrogen (N) was determined by micro-Kjeldahl analysis (A.O.A.C. 1970) and total leaf N calculated from % N and leaf mass.

Data were analyzed using the Statistical Analysis System (SAS) analysis of variance procedures. Years were analyzed separately, and because treatments and time generally interact, we also analyzed the data by sampling date within each year.

Results

Xylem Water Potential, Gas Exchange, and Nitrogen

The 2 years differed in rainfall distribution with a more severe late summer stress period in 1984 than in 1985 (Fig. 1). Minimum ψ for burned big bluestem prior to senescence was -3.50 MPa in 1984 and -2.70 MPa in 1985. During both years ψ was declining at the end of the measurement period. Measurements were continued until we could no longer find leaves which appeared alive and exhibited a positive carbon balance. From long-term weather records, it appeared that the pattern in 1984 was relatively typical, i.e., May and June were moist, followed by summer drought in July and early August, with sporadic thunderstorms in late August. However, 1985 was the fourth wettest in the past 30 years. There were more cloudy days and thus evaporation potential was assumed to be lower in 1985 than in 1984. Burned big bluestem was generally under slightly less water stress early in the season, and more stress later in the season than unburned plants. Late season differences between treatments were particularly evident in 1984 (e.g., in early August the difference between treatments was 0.75 MPa).

Photosynthetic rate exhibited a treatment crossover during the season; burned plants had PS rates 11% higher than unburned plants during the moist portion of the season, but rates were 36% lower during the dry portion (Fig. 2). The actual difference between treatments was 2.5 μmoles $m^{-2} s^{-1}$ and 2.87 μmoles $m^{-2} s^{-1}$ during the wet and dry parts of the growing season. Early in the growing season ψ was fairly high for both treatments, and during this period TR appeared to be more affected by evaporative demand than by internal plant water relations (Figs. 1 and 2).

However, during the latter portion of the growing season as soil moisture declined and temperatures increased it appeared that internal plant water relations rather than evaporative demand controlled TR.

Seasonal trends in 1985 were not as clearly defined as in 1984 (Fig. 2). Certainly the mid- to late-summer drought was less well defined in 1985 relative to 1984, and in addition, May and June temperatures on the second and fifth sampling dates of 1985 appeared to have a definite impact on both TR and PS. Minimum temperatures the 2 days preceding the second measurement date averaged 8.5° C, whereas, those preceding the first and third sampling dates were 14.5 and 13.5° C, respectively. Minimum

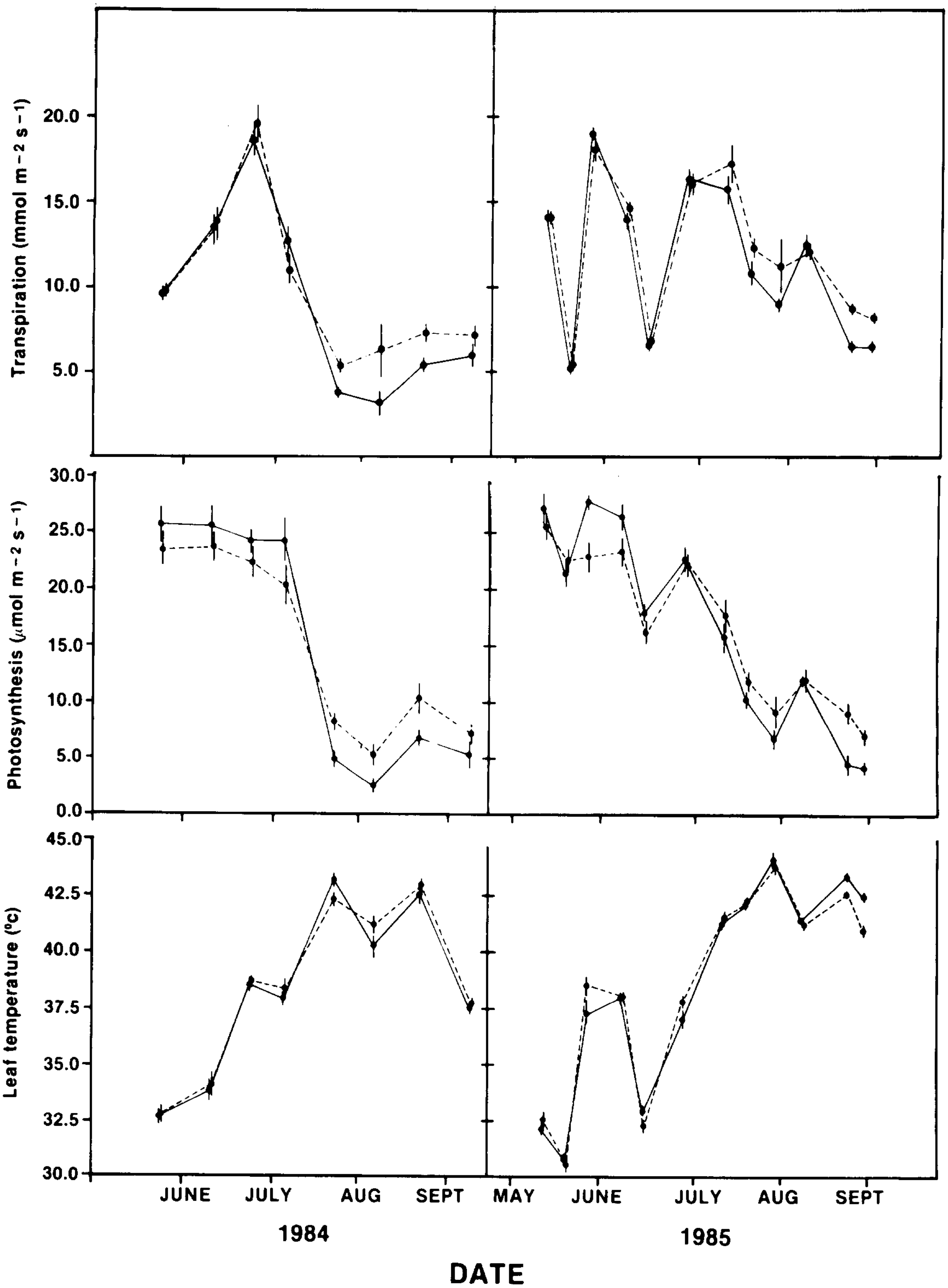

Fig. 2. *Transpiration, photosynthesis, and leaf temperature of big bluestem (measured 1300 to 1500 h, CDT) from burned (solid lines) and unburned (dash lines) tallgrass prairie during 1984 and 1985 growing season. Vertical lines are ± one standard error of the mean (n = 12). Treatment differences were significant (P≤.05) for photosynthesis during the moist portion (first 4 sampling dates) of 1984, and the third sampling of 1985 and for both photosynthesis and transpiration during the last 2 sampling dates of 1985.*

temperatures for the 2 days prior to the fourth, fifth, and sixth sampling dates in 1985 were 19, 11, 19.5° C, respectively. During 1984 there were no unusually cool nights prior to a sampling date.

Although moisture stress was not as severe in 1985 as it was in 1984, PS of both burned and unburned plants declined during July. There was an increase in PS in early August, which presumably was associated with reduced water stress (Fig. 1 and 2) resulting from a late summer thunderstorm. However, the increase in PS was brief, and by late August 1985 PS reached values similar to

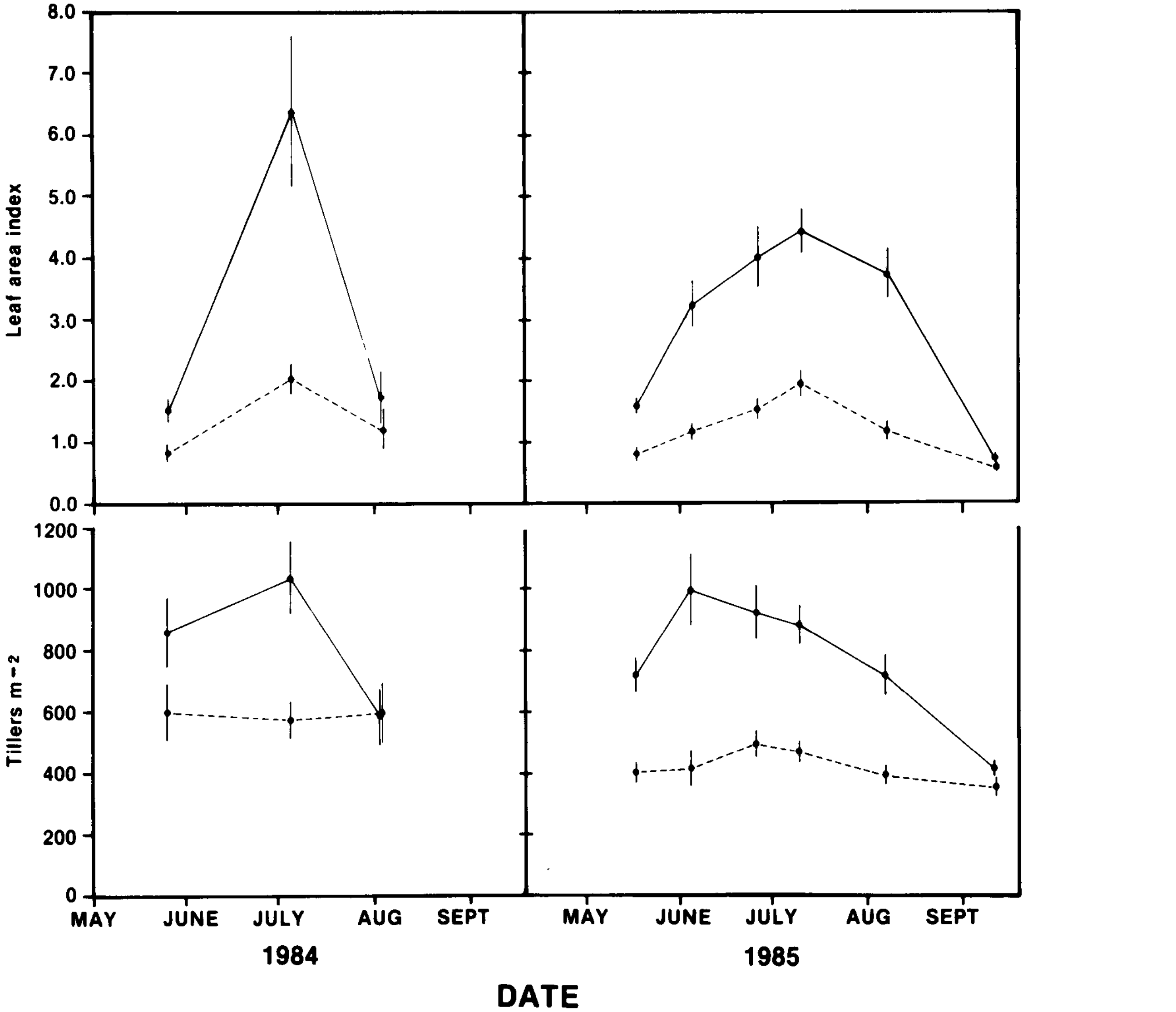

Fig. 3. *Leaf area index and tillers m*$^{-2}$ *of big bluestem from burned (solid lines) and unburned (dashed lines) tallgrass prairie during 1984 and 1985 growing seasons. Vertical lines are ± one standard error of the mean* (n = *12 for 1984,* n = 18 for 1985). Treatment differences were statistically significant (P≤*.01) for leaf area index on the first 2 sampling dates of 1984, and all but the last sampling date in 1985. Treatments were different for tillers m*$^{-2}$ *on the second sampling date of 1984 (*P≤*.05) and on the first, second, fourth, and fifth sampling dates of 1985 (*P≤*.01).*

Table 1. Season trends in nitrogen and phytomass components of big bluestem from burned (B) and unburned (U) tallgrass prairie; LN = % leaf nitrogen, TLN = total leaf nitrogen (% leaf nitrogen * leaf weight), LWT = leaf weight, SWT = stem and sheath weight, TWT = total weight. Phytomass of species other than *A. gerardii* (WT OTHER SPECIES) appears at the bottom of the table.[1]

	1984						1985													
	May 25		July 5		Aug 3		May 17		June 5		June 26		July 10		Aug 7		Sept 11			
Variable	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U		
LN (%)	2.3**	2.0	1.2	1.3	0.9	0.9	1.7*	1.5	1.4	1.3	1.1	1.2	0.8	1.0	0.7*	0.8	0.6**	0.7		
TLN (g m^{-2})	1.9**	0.9	5.2*	1.8	1.9	1.3	1.5**	0.8	2.7**	1.0	3.0**	1.3	3.0**	1.5	1.8**	1.0	0.6	0.6		
LWT (g m^{-2})	83.8*	47.8	425.3*	139.6	213.1	141.8	92.1**	53.4	201.9**	79.0	280.4**	108.4	365.8**	155.4	261.1**	127.4	94.5	75.6		
SWT (g m^{-2})	21.8	17.6	177.0**	42.2	232.8*	64.9	24.8**	12.8	73.7**	24.0	125.8**	40.1	235.8**	49.7	328.4**	40.0	238.4**	47.8		
TWT (g m^{-2})	105.7	65.4	602.5**	181.8	445.9*	206.7	117.0**	65.4	275.4**	102.6	406.1**	148.3	602.1**	205.2	535.2**	167.3	332.9**	123.3		
WT OTHER SPECIES (g m^{-2})	34.3	55.6	202.6	178.7	246.2	93.3	33.9**	94.3	89.2	124.9	134.8	110.7	106.6	157.4	87.7	110.3	82.7	87.5		

[1]Asterisks indicate significant differences (* = *P*<.05, ** = *P*<.01) between burned and unburned treatments on a particular sampling date (*n* = 12 and 18 for 1984 and 1985, respectively).

those measured during the dry portion of 1984. Transpiration rates remained relatively high (>10.0 mmole m^{-2} s^{-1}) until the end of August; this contrasted with the late season response in 1984, especially for plants from the burned prairie.

Concentration of N in leaves of big bluestem from burned plots was generally higher than in unburned leaves during late May and early June. After mid June % N was similar between treatments or slightly lower in leaves from burned prairie (Table 1). The total amount of N (g m^{-2}) contained in big bluestem leaves was generally 2 to 3 times higher in burned relative to unburned prairie. The greatest total amount of N in leaf material was 5.2 g N per m^{-2} ground area on burned prairie in early July, 1984.

Leaf Area Index, Tiller Numbers, and Phytomass

During both years LAI increased rapidly during late May and June, peaked in early July, declined in late summer (Fig. 3). However, peak LAI was 2 to 3 times greater for burned relative to unburned big bluestem and the stimulation of LAI from burning was greater in 1984 than 1985. During both years, LAI of unburned big bluestem peaked at 2.0, whereas peak values for burned plants were 6.4 and 4.5 in 1984 and 1985, respectively. Leaf folding occurred during August 1984, and leaf area values presented in Figure 3 are folded leaf area. We physically unfolded the leaves to determine what total leaf area would have been had the leaves not been folded. Folding resulted in a 26 and 29% reduction in leaf area for unburned and burned big bluestem, respectively.

Number of big bluestem tillers m^{-2} were relatively static throughout the growing season on unburned plots, ranging from 577 to 600 in 1984, and 355 to 498 in 1985 (Fig. 3). There would probably have been more of a decline in tillers m^{-2} in 1984 had we continued to sample past early August. There was, however, a great deal of seasonal variation in tillers m^{-2} of big bluestem from burned prairie, with numbers ranging from 600 to 1,037 in 1984 and 416 to 997 in 1985.

Burning greatly stimulated production of big bluestem leaves and stems. The increase in stem production following burning was relatively greater than the increase in leaf production, thus the leaf to stem ratio was less for burned than unburned plants (Table 1). However, the proportion of leaf and stem contributing to peak standing crop was different between years, with more leaf in 1984 than in 1985. Burned plots had significantly ($P \leq .05$) more big bluestem phytomass than unburned plots on all sampling dates except 25 May 1984. In early July of both years, burned plots yielded about 3 times more big bluestem phytomass than unburned plots.

Discussion

Burning has been shown to affect plant growth in the tallgrass prairie, but only recently have the mechanisms responsible been examined. We found that burning elevated PS rate during the active growth period (late spring and early summer), which generally agrees with the findings of Knapp (1985). The mechanism responsible for the increase in early season PS with burning is not completely clear. The removal of standing dead and litter by burning improves the light environment of emerging shoots (Knapp 1984b). All leaves we measured received full sunlight during the sampling period; however, Knapp and Seastadt (1986) suggest that differences in morphology between burned and unburned big bluestem leaves as a result of initial light environment helps explain the lower PS rates of unburned prairie. Another potential explanation for the higher PS rates is that the release of dormant buds created a higher demand for photosynthate, thus increasing PS rates. Burning doubled the number of big bluestem tillers produced during the active growth phase (Fig. 3). Two previous studies also measured a doubling of big bluestem tiller numbers as a result of spring burning (Hulbert 1969, Knapp 1984b).

The increase in peak tiller number resulting from burning has been attributed to both light levels and soil temperature. Knapp (1984b) found that burning increased PPFD reaching emerging shoots by almost 60% during the initial 30 days of growing season. Deregibus et al. (1985) have shown that increased red light at crown level increased the tillering rate of 2 humid grassland species. Increased tillering as a result of burning has also been attributed to higher soil temperature (Rice and Parenti 1978). Nitrogen nutrition may also be important in explaining tillering response. Burned plants had higher leaf %N than unburned plants (Table 1). Langer (1963) suggests that one of the main effects of N nutrition is on duration of tillering, and plants with an inadequate N supply stop producing new tillers at an early date. If Langer's conclusion applies to our conditions, lower N levels in unburned plants would explain the relatively stable tiller numbers on unburned prairie and the increase into late spring and burned prairie. The trend in leaf N among burned and unburned treatments is consistent with results from other locations in the tallgrass prairie (Old 1969, Owensby et al. 1970, Hayes 1985, Knapp 1985). Burned plots appear to initially have more available N, but the flush of growth uses N and as plant maturity occurs, there is a "dilution" of N as structural material accrues (Hayes 1985). Total leaf N was higher for burned relative to unburned big bluestem on a number of dates when burned plants had lower % leaf N, as a result of the increased leaf mass with burning.

The model used by Risser and Parton (1982) predicted that root uptake of N was higher on burned compared to unburned tallgrass prairie the first 2 years of burning, but that N uptake would be depressed by continuous annual burning. In the present study total leaf N of big bluestem declined about 40% from the first to second year of burning, whereas peak values were similar for the 2 years on unburned treatment. The results presented by Towne and Owensby (1984) showed that 56 years of continuous late-spring burning was not detrimental to tallgrass prairie in Kansas, which suggests any decline in N must have leveled off before detrimental effects on the plant community were manifested. A good deal of uncertainty exists in our understanding of the tallgrass prairie N-cycle (Risser and Parton 1982) and a better understanding of uptake, soil transformations, and internal conservation (see Hays 1985) of N will be necessary before accurate predictions of N-cycling can be made.

Leaf area is a functionally important factor that is not routinely measured on rangeland. The relationship between gas exchange and leaf area determines total carbon uptake and transpirational water loss. For example, the high LAI values for burned compared to unburned prairie, yet comparable TR rates among treatments, indicates soil moisture would probably be depleted more quickly on burned prairie. Trends in ψ (Fig. 1) and soil moisture measurements (unpublished data) support this conclusion. In the same vein, burned prairie should have a good deal more carbon available for growth given slightly higher early season PS rates and much higher LAI compared to the unburned treatment. Most aboveground growth occurred during May and June based on standing crop data (Table 1). We think our data support Knight's (1973) contention that leaf area development is most important during the early part of the growing season when LAI is relatively low and soil moisture is available.

In general, mass of tallgrass prairie vegetation increases with burning (Hadley and Kieckhefer 1963, Peet et al. 1975, Knapp 1984, Towne and Owensby 1984), although the magnitude of the increase is affected by timing of burn, climatic conditions, prior site, history, community composition, etc. Our results show peak mass of big bluestem is increased almost 3-fold by burning (Table 1). There is a trend over the 2-year period for lower production of species other than big bluestem on burned plots, but the difference between treatments is not statistically significant. The increase in production of big bluestem more than compensates for the decline in productivity of other species with burning, and thus total aboveground primary production was greatly stimulated by late-spring burning.

Measurement of whole canopy physiological function is difficult in complex native communities, and does not allow evaluation of response of individual species. We suggest that response to environment can best be explained when both physiological and morphological attributes of a species are considered. In this study, burning influenced leaf area PS rate of big bluestem, but there was a much greater effect on tiller numbers and LAI. It would have been difficult to account for the 3-fold increase in big bluestem production resulting from burning based on a slight stimulation in PS rate. The stimulation of leaf N with burning may also help explain big bluestem response to fire; however, the mechanisms responsible for higher leaf N are not completely understood. We feel that the relationship between physiological and morphological attributes, which has been studied quite extensively in crop species, deserves more attention in the ecological literature.

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Mechanical shrub control on flatwoods range in south Florida

GEORGE W. TANNER, JOHN M. WOOD, ROBERT S. KALMBACHER, AND FRANK G. MARTIN

Abstract

Relative plant abundance, canopy cover, and aerial biomass of shrubs on a poor condition, flatwoods range in south Florida were measured before, 1, and 3 yr after a single pass of a roller chopper or web plow when soils were dry (May 1981) and when soils were saturated (September 1981). Aerial biomass of herbaceous species was measured at the post-treatment sample dates. Abundance of saw-palmetto (*Serenoa repens* (Bartr.) Small) plants, the dominant shrub, was reduced 70% by web plowing compared to 25% by roller chopping. Reductions of saw-palmetto canopy cover and aerial biomass also were greater on web-plowed than on roller-chopped plots. Runner oak (*Quercus minima* (Sarg.) Small) was the only other shrub which had more than 5% canopy cover before treatment. Both types of mechanical treatments controlled runner oak by approximately 50%. However, responses of runner oak abundance, canopy cover, and aerial biomass were not significantly different between roller chop and web plow treatments.

Key Words: roller chopping, web plowing, saw-palmetto, runner oak

Flatwoods range provides much of the forage for cow-calf enterprises in south Florida (Kirk et al. 1974). Frequent winter burning (2- to 3-yr interval) traditionally is used to remove accumulations of senescent forages and to stimulate nutritious regrowth. Winter fires, however, only temporarily reduce shrub competition. Saw-palmetto (*Serenoa repens* Bartr.) Small) can regain 80% of pre-burn canopy cover in 1 growing season (Hilmon 1968).

Past range improvement practices attempted to control saw-palmetto and increase production of bluestems (*Andropogon* spp.) and other grasses (Yarlett 1965). Roller drum choppers, usually pulled in tandem at off-set angles, have been the most commonly used mechanical method for saw-palmetto control. The web plow was originally developed in south Florida for conversion of rangeland to cropland and has been used for saw-palmetto control. The web plow has a flat, V-shaped sharpened, steel blade that is mounted on a road grader. The blade plows at a depth of 10 to 15 cm and causes very little surface soil disturbance.

Saw-palmetto control with double passes of a roller chopper varied from 45% reduction in canopy cover at 3 yr post-treatment (Kalmbacher and Martin 1984) to 94% 2 yr post-treatment (Moore 1974). Lewis (1972) reported 42% reduction in saw-palmetto canopy cover 6 months after web plowing. However, saw-palmetto control on web-plowed rangeland appears to be much greater than Lewis' estimate.

The objective of this study was to compare shrub control and forage responses following web plowing and roller chopping. The treatments were installed at the extremes of soil moisture, i.e., during a drought and during saturated (flooded) conditions.

Study Area

This study was conducted on the Desoto County Land and Cattle Company, 30 km southeast of Arcadia, Desoto County, Florida. Climate within this area is characterized by hot, humid summers and mild winters. Freezing temperatures are sporadic and associated with rapidly passing cold fronts. Annual rainfall (30-yr average) recorded in Arcadia is 141 cm, most of which is received between June and September.

Soils of the Myakka series (sandy, siliceous, hyperthermic Aeric Haplaquod) dominated the south Florida flatwoods study site. These sandy soils developed from strongly acid marine sediments and are poorly drained due to the development of spodic horizons at depths of 30 to 50 cm. Sheet flow over the nearly flat terrain occurs during rainy seasons, while in dry seasons the water table may recede to depths of more than 1 m.

The study site was treeless, but scattered slash pines (*Pinus elliottii* Engelm.) were in the vicinity. Saw-palmetto was the dominant shrub. Pineland threeawn (*Aristida stricta* Michx.) was the dominant grass. Although several bluestem species were present, the site was in poor condition.

The study area had been burned on an approximate 2-yr cycle and grazed continuously for many years. A deferred-rotation grazing system providing 4 to 6 months of rest each year was begun in 1980.

Methods

Twenty 1.8-ha plots were established on the study site in March 1981. Four plots were roller chopped and 4 were web plowed during a dry spring (1 May 1981) and each treatment was applied to 4 plots during the following wet summer (3 September 1981). Four untreated plots served as checks. Treatments were assigned in a completely random design. Chopping was a 1-way treatment with tandem-drum, Marden[R] M-10 chopper filled with water and pulled at 8.0 to 10.0 km/hr with a 104.4 kilowatt rubber-tired tractor. Each of the tandem drums was a 3.05 m in length and weighed approximately 5.7 mT.

Pretreatment estimates of shrub biomass, canopy cover, and relative abundance (number of plants/linear distance) were made 20 to 27 March 1981 and 31 August to 2 September 1981. Four randomly located, 40-m line transects were permanently marked in each plot. Canopy cover and number of intercepted plants of each shrub species were recorded for each line transect. Total aerial biomass of each shrub species was estimated by harvesting from 10, 0.25-m^2 quadrats along each transect. Green weights were recorded in the field. A subset of shrub biomass samples was oven-dried at 60° C for 48 hr, for converting field weights to dry weights. Post-treatment estimates were taken in the same manner 13 and 14 December 1982 and 9 and 10 October and 19 November 1984.

The entire study site was burned in February 1984 to remove any accumulation of standing dead vegetation in all treated and untreated plots and to promote regrowth. This would highlight the potential difference between mechanically treated and untreated plots. The burn was not intended to affect shrubs. Hilmon (1968), Moore et al. (1974), and Abrahamson (1984) documented that the major shrub species characteristic of Florida's flatwoods range replace their pre-burn canopy cover within the growing season following a winter fire.

The experimental design consisted of a completely random allocation of chop and web machine treatments when the soil condition was very dry (May 1981) and again randomly allocated when the soil condition was saturated (September 1981). Data from wet and dry experiments were pooled and analyzed as a series of

Authors are associate professor and biologist, Department of Wildlife and Range Sciences; professor, Department of Agronomy; and professor, Department of Statistics, University of Florida, Gainesville 32611. Fla. Agric. Exp. Sta. Journal Series No. 6693.

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experiments following the Cochran and Cox (1957) methodology for analyzing data from experiments repeated in time or space. Analyses of covariance were used to estimate shrub abundance, canopy cover, and aerial standing crop. Pretreatment estimates were used as the covariates. Pair-wise *t*-tests, using least square means, were made between the untreated plots and the 4 machine type-soil condition treatment combinations.

Results

Soils at the study site were extremely dry at time of treatment in May 1981. Only 1.8 cm of rain was recorded in Arcadia, Florida (ca 48 km to the NW), during March and April. Almost 35 cm of rain were received in late August, resulting in approximately 5 to 10 cm of standing water on the site at the time of treatment in September 1981.

Although 14 shrub species were encountered in the study plots, only saw-palmetto and runner oak (*Quercus minima* Sarg.) Small) had pretreatment canopy cover estimates greater than 5%. The other 12 shrub species were combined into an "other shrub" category which consisted of ground huckleberry (*Gaylussacia dumosa* (Andr.) Torr & Gray), dwarf wax myrtle (*Myrica cerifera* L. var *pumila* Michx.), Chapman's oak (*Quercus chapmanii* Sarg.), American beautyberry (*Calicarpa americana* L.), queen's delight (*Stillingia sylvatica* L.), gallberry (*Ilex glabra* (L.) Gray), fetterbush (*Lyonia lucida* (Lam.) D. Don), staggerbush (*L. ferruginea* (Walter) Nutt.), St. John's-wort (*Hypericum brachyphylum* (Spach) Steud.), St. Peter's-wort (*Ascyrum stans* Michx.), ground blueberry (*Vaccinium myrsinites* Lam.), and paw-paw (*Asimina* spp.).

Saw-palmetto Responses

Estimated saw-palmetto plant abundance was lower in both roller chopped and web plowed plots at 1 and 3 yr following treatment (Table 1). Also, web plowed plots had lower saw-palmetto plant abundance (ca 50% lower) than roller chopped plots at both sampling dates. These results represent an overall reduction of saw-palmetto plant numbers by about 25% and 68% 3 yr following chopping and webbing, respectively, compared to pretreatment conditions. Abundance of saw-palmetto in the chop-dry treatment combination was not significantly different from the untreated plots, at 1 and 3 yr after treatment, whereas, abundance estimates in the other 3 treatment combinations were different from the untreated plots.

Canopy cover estimates of saw-palmetto in chopped and webbed plots were significantly lower compared to the untreated plots in both 1 and 3 yr after treatment (Table 1). Also, average saw-palmetto canopy cover estimates in the webbed treatment were significantly lower (by about one half) than in chopped plots in both years. In comparison to pretreatment conditions, chopping and webbing reduced saw-palmetto by about 50% and 72%, respectively, at 3 yr post-treatment. Saw-palmetto canopy cover in the chop-dry treatment combination was not significantly different from canopy cover in the untreated plots at both post-treatment sampling dates.

Estimated aerial biomass of saw-palmetto following both mechanical treatments was significantly lower than the untreated plots 1 and 3 yr after treatment (Table 1). Saw-palmetto biomass in chopped and webbed plots was similar. Saw-palmetto biomass in the chop-dry treatment combination was not significantly different from estimates in the untreated plots 1 and 3 yr after treatment.

Runner Oak Responses

Runner oak was the second most abundant shrub on the study site, averaging about 35 plants/40 m in 1981 (Table 2). Both mechanical treatments resulted in lower abundance estimates than in untreated plots 1 and 3 yr following treatment. However, runner oak abundance was similar in roller-chopped and web-plowed areas. Runner oak abundance in all 4 machine-soil condition treatment combinations was significantly lower than in untreated plots.

Runner oak canopy cover estimates were significantly lower following both mechanical treatments than in untreated plots 1 and 3 yr after treatment (Table 2). Chopping and webbing caused similar reductions in canopy cover of runner oak. Canopy cover of runner oak in chop-wet and web-dry treatment combinations was significantly lower than in the untreated plots in 1982 and 1984.

Runner oak biomass in the untreated plots also were significantly greater than in both mechanical treatment plots 1 and 3 yr post-treatment (Table 2). As with saw-palmetto biomass, runner oak biomass was similar in chopped and webbed plots. Runner oak biomass was significantly lower following the chop-wet treatment combination than in the untreated plots in 1982 and again in 1984 along with the web-dry treatment response.

"Other Shrub" Responses

Abundance of the "other shrub" category was significantly lower on untreated plots than in both mechanical treatments 1 yr after treatment (Table 3). St. Peter's-wort was stimulated by machine treatment and accounted for the increased abundance in the "other shrub" category. However, the prescribed fire in February 1984 reduced St. Peter's wort abundance below pretreatment conditions on all study plots when measured 3 yr after mechanical treatment. Plots chopped and webbed under wet soil conditions had signifi-

Table 1. Average shrub abundance, canopy cover and aerial biomass of saw-palmetto before mechanical treatment (1981) and 1 and 3 yr after roller chopping and web plowing in a dry April and a wet September, Desoto, Co., Florida.

		Machine type[1]			Machine-soil condition combination[2]			
	Year	Untreated	Chop	Web	Chop-Dry	Chop-Wet	Web-Dry	Web-Wet
				(no plants/40m)				
Relative (abundance)	'81	51.4a	50.7a	52.8a	41.6	59.7	65.2	45.4
	'82	62.8a	37.6b	15.9c	49.9	25.3*	17.0*	15.3*
	'84	59.8a	39.4b	18.1c	49.6	29.9*	20.1*	16.6*
				(%)				
Canopy cover	'81	34.7a	30.6a	30.6a	20.2	40.9	26.4	33.0
	'82	44.4a	16.4b	7.4c	23.6	9.3*	9.1*	6.3*
	'84	36.4a	15.3b	8.6c	20.0	10.6*	10.6*	7.4*
				(%)				
Aerial biomass	'81	1785.6a	1856.1a	1887.1a	1846.0	1866.3	2192.6	1703.7
	'82	1592.0a	552.0b	187.6b	890.9	213.1*	106.7*	176.1*
	'84	1177.5a	387.4b	215.7b	597.8	176.9*	268.7*	183.8*

[1]Mean values among machine treatments within each species-year combination followed by the same letter are not significantly different at the 0.05 level according to analysis of variance F-tests.
[2]An asterisk (*) denotes significant differences ($P<0.05$) from the check value in each species-year combination excluding 1981 according to pair-wise *t*-tests.

Table 2. Average shrub abundance, canopy cover and aerial biomass of runner oak before mechanical treatment (1981) and 1 and 3 yr after roller chopping and web plowing in a dry April and a wet September, Desoto Co., Florida.

		Machine type[1]			Machine-soil condition combination[2]			
	Year	Untreated	Chop	Web	Chop-Dry	Chop-Wet	Web-Dry	Web-Wet
		(no plants/40m)						
Relative (abundance)	'81	30.6a	41.2a	33.7a	7.0	6.2	11.1	2.0
	'82	26.9a	12.3b	15.3b	0.8*	1.1*	0.9*	2.1*
	'84	37.9a	18.9b	21.1b	0.9*	3.1*	2.1*	1.4*
		(%)						
Canopy cover	'81	6.4a	7.5a	6.5a	4.5	10.6	3.5	8.3
	'82	9.4a	3.2b	3.8b	4.3	2.2*	2.1*	4.9
	'84	11.8a	4.9b	5.4b	5.4	4.4*	2.3*	7.2
		(kg/ha)						
Aerial biomass	'81	239.5a	428.7a	381.3a	256.1	601.4	181.7	501.1
	'82	312.1a	110.6b	159.0b	151.9	69.3*	122.9	180.6
	'84	458.2a	189.6b	188.4b	231.1	148.0*	69.4*	259.6

[1]Mean values among machine treatments within each species—year combination followed by the same letter are not significantly different at the 0.05 level according to analysis of variance F-tests.
[2]An asterisk (*) denotes significant differences ($P<0.05$) from the check value in each species—year combination excluding 1981 according to pair-wise t-tests.

Table 3. Average shrub abundance, canopy cover and aerial biomass of "other shrubs" before mechanical treatment (1981) and 1 and 3 yr after roller chopping and web plowing in a dry April and a wet September, Desoto, Co., Florida.

		Machine type[1]			Machine-soil condition combination[2]			
	Year	Untreated	Chop	Web	Chop-Dry	Chop-Wet	Web-Dry	Web-Wet
		(no plants/40m)						
Relative (abundance)	'81	12.2a	13.8a	15.3a	1.3	1.5	1.9	1.3
	'82	12.1a	24.7b	20.1b	10.9	38.5*	11.3	25.4*
	'84	10.3a	8.2a	4.7b	7.0	9.3	4.1*	5.1*
		(%)						
Canopy cover	'81	2.8a	2.5a	2.5a	1.8	3.2	2.5	2.5
	'82	3.0a	4.6a	3.8a	1.9	7.3*	1.6	5.1
	'84	2.3a	1.5a	1.1a	1.4	1.6	0.8*	1.2
		(kg/ha)						
Aerial biomass	'81	141.8a	108.5a	140.6a	97.2	119.7	148.5	135.9
	'82	240.8a	130.1a	130.3a	98.9	161.3	61.5	171.5
	'84	121.7a	74.2a	63.3a	88.9	59.5	42.4	75.8

[1]Mean values among machine treatments within each species—year combination followed by the same letter are not significantly different at the 0.05 level according to analysis of variance F-tests.
[2]An asterisk (*) denotes significant differences ($P<0.05$) from the check value in each species—year combination excluding 1981 according to pair-wise t-tests.

cantly higher "other shrub" abundance than untreated plots in 1982. However, in 1984, "other shrub" abundance in webbed plots under both dry and wet soil conditions was significantly lower than in untreated plots.

Canopy cover estimates of the "other shrubs" category following both mechanical treatments were not significantly different from those in untreated plots 1 and 3 yr after treatment (Table 3). An approximate 30-fold increase in St. Peter's-wort canopy cover (from 0.1 to 3.2%) during the year immediately following mechanical treatment masked reductions in canopy cover that occurred for all other combined species but ground blueberry. Canopy cover of the "other shrubs" category was significantly higher following the chop-wet treatment than in untreated plots in 1982, but was significantly lower following the web-dry treatment in 1984. The prescribed fire in February 1984 reduced the influence of St. Peter's-wort.

Aerial biomass of the "other shrubs" category was not significantly reduced by either mechanical treatment (Table 3). Biomass of St. Peter's-wort increased sharply in the year following treatment (3 to 5 fold) then declined by 1984 in a similar manner to abundance and canopy cover of this species due to the fire.

Discussion

Both roller chopping and web plowing can reduce relative abundance, canopy cover, and aerial biomass of saw-palmetto for at least 3 yr. Also, the data indicate that web plowing was more effective in controlling saw-palmetto than roller chopping. Chopping provided less control than webbing due to the apparent ineffectiveness of the single pass roller chopper treatment when soils were dry.

Visual observations of the roller chopping process indicated that blade penetration into the soil was not as great at the dry May treatment date as at the wet September date. The apparent inability of roller chopping to control saw-palmetto during drought conditions with a single pass can not be ascertained from this study but warrants further research. Past studies using double chopping treatments (2 passes over same area) indicated best saw-palmetto kill during dry soil conditions (Hilmon et al. 1963, Lewis 1970, Moore 1974). The first pass of the roller chopper crushes the plant, and the second pass usually severs above-ground prostrate stems and lifts the plants out of the ground. Results of this study suggest that a single pass of a roller chopper during saturated soil conditions may give adequate control of saw-palmetto. Further study is needed to test this possibility since a single chop treatment would be much less costly than the traditional double chop treatment.

Web plowing apparently was effective in controlling saw-palmetto in both dry and wet soil moisture conditions. The web plow is mechanically inserted below ground; therefore, dry sandy soil conditions do not impede the root-cutting ability of the machine. Web plowing, however, requires more specialized machinery (road grader) than roller chopping.

Many of the other woody plant species (e.g., gallberry, fetterbush, staggerbush, and runner oak) characteristic of flatwoods range sprout readily from roots and are not effectively controlled by these mechanical treatments. Runner oak, the woody species second in dominance on this study site, is a low-growing (<0.5 m in height) shrub that is an important mast-producing wildlife food source (Harlow and Jones 1965, Moore 1974). Although initially reduced in plant abundance, canopy cover, and aerial biomass the first year following treatment, this species appeared to be making a recovery by the third year post-treatment. Likewise, ground blueberry, an important deer browse species (Harlow et al. 1975) included in the "other shrubs" group, recovered by 3 yr post-treatment.

Overall responses of the "other shrubs" category were dominated by the St. Peter's-wort individual response. Plant abundance, canopy cover, and aerial biomass of St. Peter's-wort increased sharply following mechanical treatment but decreased to below treatment levels by the third year. This single-stemmed, non-rooting-sprouting species was susceptible to the prescribed fire.

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Titles are now being solicited for papers to be presented at the 42nd Annual Meeting of the Society for Range Management, February 19-23, 1989, in Billings, Montana. Complete the following form and submit to Dr. J.E. Taylor, SRM Program Chairman, Department of Animal and Range Sciences, Montana State University, Bozeman, MT 59717, Phone (406)994-5575. Deadline for abstracts is August 1, 1988. See the inside front cover of April *Rangelands* for additional information.

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Breed comparisons and characteristics of use of livestock guarding dogs

JEFFREY S. GREEN AND ROGER A. WOODRUFF

Abstract

Research has shown that dogs can protect livestock from coyotes *(Canis latrans)*, but information is lacking on comparative effectiveness of dog breeds and on how successfully dogs are being used by livestock producers. We mailed questionnaires to 948 livestock producers in the U.S. and Canada who were likely to be users of livestock guarding dogs. Three hundred ninety-nine written responses were received reporting data on 763 dogs, almost all recognized guarding breeds. Respondents were livestock producers from 47 states and 7 provinces. Producers rated their dogs as very effective (71%), somewhat effective (21%), or not effective (8%) in deterring predation; the majority (82%) said dogs were an economic asset. No particular breed was rated more highly, and the rate of success between males and females was not different. Fifty nonrespondents were telephoned, and although fewer of them had dogs than respondents, their rating of the dogs they used was not significantly different from that of respondents. The data indicate that, when used by producers, livestock guarding dogs are an effective method to manage predation.

Key Words: ***Canis latrans*****, coyotes, predation, predator control, sheep**

Historically, in some parts of the world it was common to use dogs to protect livestock from predators, but it is a relatively novel approach for most livestock producers in the United States. During the late 1970's research was initiated in the United States by several organizations to evaluate using guarding dogs to protect livestock from coyotes *(Canis latrans)* and dogs. In general, dogs were capable of reducing predation on sheep in a variety of management systems (Linhart et al. 1979; McGrew and Blakesley 1982; Coppinger et al. 1983; Green and Woodruff 1983a, 1983b; Black and Green 1985).

Several breeds of dog can be used to protect livestock, but comparative information on their effectiveness is rare. In addition, use of guarding dogs by livestock producers remains poorly described. Although we conducted 2 surveys of producers who used livestock guarding dogs (Green and Woodruff 1980, Green et al. 1984), they were made early in the period that guarding dogs were being researched, and a relatively small number of producers responded (72 and 67, respectively). Information on breed effectiveness and how dogs are currently being used by livestock producers is of value for planning effective programs of predator management. In this paper we report the results of an extensive survey of livestock guarding dog users in North America as they relate to breed effectiveness and current use of guarding dogs.

Methods

A questionnaire was developed and sent to livestock producers whom we believed used guarding dogs. Questionnaires were also sent to each state extension service with a request that they be forwarded to producers using guarding dogs. The questionnaire asked for information on the type of livestock operation (pasture or rangeland) and the number of livestock involved, the type of training the dog(s) received (5 predefined types of training were given as choices), and whether the producer recommended the use of guard dogs.

The following was requested for each guard dog: breed, sex, and age; age when acquired; age when placed with livestock; spayed, neutered, or unaltered; not effective, somewhat effective, or very effective as a predator deterrent; economic asset, break-even, or liability; whether the dog injured sheep or bit people; whether the dog stayed with sheep rarely, usually, or most of the time; and whether the dog was aggressive toward predators and other dogs.

Questionnaires were mailed to 948 people during January to August 1986. They were sent to 47 states and 7 Canadian provinces; about 20–30 were returned as undeliverable. We telephoned 50 randomly selected nonrespondents to determine if they had guard dogs and if the evaluations of dogs were comparable to respondents.

We were interested in answering several questions. Was any breed or sex of guarding dog rated more highly? How did livestock producers rate the effectiveness of guarding dogs? Did producers consider dogs an economic asset? Under what type of grazing conditions were most dogs used? Chi-square procedures were used to analyze the data.

Results and Discussion

Respondents

We received 399 written responses reporting on 763 dogs. The nonrespondents we telephoned reported on 45 dogs. Ratings of dogs by questionnaire respondents and nonrespondents did not differ ($P>0.05$) although fewer nonrespondents had used livestock guarding dogs. This information alleviated our concern that producers failed to respond primarily as a result of a negative experience with a guarding dog. All data reported hereafter refer to questionnaire respondents.

Three hundred thirty-three (90%) producers grazed their livestock primarily on pastures, and 39 (10%) on rangeland. (Because some respondents did not answer all questions, totals may not equal 399.) Small pasture operations (<50 head of livestock, n = 109) had from 4–50 head (median = 25). Seventy-eight had sheep exclusively, 26 had only goats, and 5 had sheep and goats. Large pasture operations (n = 208) had from 56–8,000 head (median = 200). One hundred seventy-five had sheep exclusively, 22 had only goats, and 11 had sheep and goats.

Three hundred eighteen of 322 (99%) pasture operators recommended use of guard dogs, and 4 (1%) did not. These producers each used from 1–20 dogs (2 ± 2) ($x \pm SD$) and rated them as follows: 475 very effective (71%), 144 somewhat effective (21%), and 52 not effective (9%).

Range operators who provided data on numbers of livestock (n = 37) had from 12–16,000 head (median = 1,000). Thirty-three had sheep exclusively, and 4 had only goats. Thirty-eight of 39 operators recommended the use of livestock guarding dogs, and 1 producer made no recommendation. Range producers each used from 1–12 dogs (3 ± 2) and rated them as follows: 60 very effective (66%), 17 somewhat effective (19%), and 14 not effective (15%). Ratings of dogs from small pasture operations were better than for dogs on large pasture operations or rangeland ($P<0.05$).

Producers characterized the type of training their dog(s) received

Authors are research wildlife biologist, USDA-Agricultural Research Service and scientific aid II, University of Idaho, both at the U.S. Sheep Experiment Station, Dubois, Idaho 83423.

G. Richardson helped with the design of the study and statistics.
The authors thank each livestock producer who participated in the survey.
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Table 1. Summary of data characterizing the livestock guarding dogs reported in the survey. (With the exception of n, all numbers are percentages).

	n	Effectiveness			Economics			Aggressive	
		Very	Somewhat	Not	Asset	Breakeven	Liability	To predators	To dogs
Pyrenees	437	71	22	7	83	11	6	95	67
Komondor	138	69	1	12	82	8	10	94	77
Akbash	62	69	22	9	71	12	12	100	92
Anatolian	56	77	13	10	82	8	10	96	86
Maremma	20	70	20	10	84	5	11	94	94
Shar	11	40	30	30	50	0	50	88	89
Kuvasz	7	57	29	14	80	0	20	100	67
Hybrid*	23	87	4	9	84	5	11	95	85
Other	9	43	29	28	20	20	60	83	100
Total	763	71	21	8	82	9	9	95	74

*Hybrids were crosses of 2 or more guarding breeds.

Table 1. cont.

Breed	Problems			Stays with Sheep			Dog injured sheep	Dog bit people
	Major	Minor	None	Mostly	Usually	Rarely		
Pyrenees	11	47	42	53	24	23	7	4
Komondor	14	48	38	50	23	27	24	17
Akbash	15	49	36	71	12	17	20	6
Anatolian	10	48	42	69	16	15	14	9
Maremma	18	24	58	79	16	5	20	5
Shar	20	40	40	30	20	50	33	25
Kuvasz	14	86	0	33	33	34	40	0
Hybrid*	19	38	43	70	13	17	18	0
Other	33	50	17	33	17	50	43	29
Total	13	46	41	55	22	22	14	7

*Hybrids were crosses of 2 or more guarding breeds.

as follows: (1) dog raised exclusively with sheep or goats, human contact minimized, 57%; (2) dog raised in a loose association with sheep or goats, 30%; (3) dog received obedience training, 2%; (4) no specific rearing or training program, 6%; and (5) other, 5%. Many producers (n = 70), especially those who raised more than 1 dog, selected more than 1 type of training.

Dogs

Over 95% of the dogs were recognized guarding breeds with Great Pyrenees and Komondor most common (Table 1). Despite the indication that mixed-breed dogs of nontypical guarding stock may be effective guardians (Black and Green 1985), few were identified in this survey.

The rate of success among Pyrenees, Komondor, Akbash, Anatolians, Maremma, and hybrids was not different (sample size was insufficient to allow comparison with the other breeds) nor was there a difference between the success of males and females or intact and neutered dogs ($P>0.05$). Forty-six percent of the dogs were males, and 29% of the dogs were neutered. Most of the dogs were aggressive to predators and other dogs. More Komondors bit people than did Pyrenees, Akbash, or Anatolians, and fewer Pyrenees injured livestock than did Komondors, Akbash, or Anatolians ($P<0.01$).

Most dogs (64%) were used on large (>50 head of livestock) or small pasture (23%) operations rather than range operations (13%). The majority of dogs stayed with sheep "most of the time" and were considered an economic asset (Table 1).

Fifty percent of the dogs were acquired by 3 months-of-age, and 82% were acquired by 1 year-of-age. The remaining dogs (n = 117) were acquired between 13 and 84 months-of-age. There was no difference in success between dogs acquired at ≤2 months and those acquired at >2 months-of-age ($P>0.05$). However, dogs that were reared with livestock from the time they were ≤2 months old (n = 280) had a higher rate of success than those that were older than 2 months-of-age (n = 227) when placed with livestock ($P<0.01$). Dogs ranged in age from 4–168 months with 64% of the dogs 3 years old or less.

Conclusions

Based on the results of this and our previous surveys (Green and Woodruff 1980, Green et al. 1984), the use of livestock guarding dogs is increasing, and most producers who use dogs consider them effective. No particular breed or sex was rated more highly, but breeds differed in frequency of biting people and injuring livestock. Success was higher when dogs were reared with livestock from the time they were ≤2 months old. It appears that livestock producers who face unresolved predation problems may do well to consider the use of guarding dogs.

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Electric fences for reducing sheep losses to predators

ROGER D. NASS AND JOHN THEADE

Abstract

The use of anti-predator electric fences for reducing predation on sheep was investigated by interviewing 101 sheep producers in the Pacific Northwest. Significant reductions in sheep losses to predators were reported after installation of electric fences compared to pre-fence losses. Low sheep losses to predation were also reported by those producers that acquired sheep after installation of electric fences. The expenses of construction and maintenance were important considerations in management plans; however, most producers were satisfied with electric fences for sheep containment and predator exclusion.

Key Words: sheep, predation, fencing

Anti-predator electric fences may provide some producers with a reliable self-help method for reducing losses of sheep to coyotes and dogs. Details of construction, maintenance, costs, and some evaluation of this non-lethal control method have been reported (deCalesta and Cropsey 1978, deCalesta 1983, Gates et al. 1978, Henderson 1978, Linhart et al. 1982, Shelton 1984, Thompson 1979). Previously, most electric fences for excluding predators had not been in use long enough to provide an adequate data base for pre- and post-fence predation loss evaluations or assessments of long-term problems or benefits.

Recent animal husbandry surveys indicated that many farm flock sheep producers installed electric fences during the past 2 to 4 years. This survey was designed to collect data on efficacy of electric fences for reducing predation. This information may stimulate interest by other sheep producers in this method.

Methods

Electric fence users in California, Oregon, and Washington were interviewed during 1984–85 about their operational successes or failures for reduction of predation on sheep. Data were obtained for fence construction dates, area enclosed, area grazed, flock sizes, numbers of predator-killed sheep during pre- and post-electric fence periods, months of fence use per year, management considerations, lethal control implications, and problems associated with electric fence use. Fences or portions of fence were checked for general condition and maintenance excluding those in areas remote from the interview site.

Mean numbers of predator-killed sheep per year were compared between pre- and post-electric fence production years for each producer. Comparisons were made for long-term (2–7 years) and for all producers with pre- and post-electric fence experience (1–7 years). Pre- and post-electric fence predator losses were evaluated by testing the null hypothesis of no differences at $P = 0.05$. Data were also obtained on predator-killed sheep for producers who had always used electric fences.

Results

Interviews were conducted with 101 livestock producers (Oregon 79, Washington 18, California 4) that were using electric fences. Of these, 51 had sheep before and after installing fences, 43 acquired sheep after erecting fences, and 7 used charged fences for livestock containment, but not predator exclusion.

Producers with pre- and post-electric fence experience enclosed a mean of 301 acres (SE = 87, Range = 1-3840) with electric fencing out of a mean 387 acres (SE = 99, Range = 3-3840) available for grazing. Fifty-three percent (27 of 51) enclosed their entire grazing areas and 47% (24 of 51) had additional grazing acreage outside charged fences. Mean flock size 1,036 head (SE = 398, Range = 20–20,000) and 22 of the 51 (43%) had 300 or fewer sheep. Electric fences were used for protection from predation a mean of 10.6 months (SE = 0.4, Range = 2–12) per year, and 46 of 51 (90%) fences were judged to be in good repair. Five producers (10%) lost no sheep to predators before using electric fences; however, significantly more, 28 (55%), reported no losses to predators after installation of charged fences ($t_s = 5.21$, $P = <0.01$). Reported sheep losses to predators were significantly reduced after installation of electric fences for 46 producers with 2 or more years (long-term) of electric fence experience (Table 1). The null hypothesis of no difference between pre- and post-electric fence sheep losses to predators was rejected ($t = 3.76$, df = 45, $P = <0.01$), and the alternate hypothesis of a reduction in post-fence sheep losses was accepted. The percentage of predator-killed sheep declined from 3.9 (pre-fence) to 0.3 (post-fence).

Similar results were obtained for pre- and post-electric fence sheep losses to predators when including the 5 producers with 1

Authors are research biologist , Predator Research Station, P.O. Box 593, Twin Falls, Idaho 83303-0593; and biological technician, Predator Studies Branch, Denver Wildlife Research Center, Animal and Plant Health Inspection Service, U.S. Department of Agriculture. This study was conducted under the guidance and support of the U.S. Fish and Wildlife Service, Department of the Interior. The Center transferred to the Animal and Plant Health Inspection Service (APHIS) on 3 March 1986.

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Table 1. Predator-killed sheep numbers and years of data for pre- and post-electric fence use by 46 sheep producers with 2 or more seasons' experience with anti-predator type electric fences.

Statistic	Pre-electric fence		Post-electric fence		Difference between pre- and post-electric fence sheep loss to predation
	Sheep lost to predators/year	Years of loss data	Sheep lost to predators/year	Years of loss data	
X	41	3.3	3.5	4.1	37.2
SE	10.7	0.2	1.4	0.2	9.9
Range	0–454	1–7	0–35	2.7	0–424

year (short-term) of experience with electric fences ($t = 4.46$, $df = 50$, $P = <0.01$). The mean decrease in sheep losses to predators between the last year with conventional fences and the first year with electric fences was 36.2 ± 15.9 (95% confidence limits) per producer. The percentage of predator-killed sheep declined from 4.3 before electric fence use to 0.7 after electric fences were used.

A reduction in the need for lethal control after installation of electric fences was reported by 38 of 51 (75%) producers. Livestock management workloads decreased after fence installation for 32 of 51 (67%) producers.

Producers with only post-electric fence experience enclosed a mean of 84 acres (SE = 16, Range = 3-500) out of a mean of 159 acres (SE = 32, Range = 3-880) available for grazing. Forty-two percent (18 of 43) enclosed their entire grazing areas. Mean flock size was 392 head (SE = 58, Range = 19-1200) and 25 (58%) had 300 or fewer sheep. Electric fences were used for protection a mean of 9.7 months (SE = 0.4, Range = 5-12) per year and 35 (81%) kept fences in good condition. These producers used electric fences for a mean of 4 years (SE = 0.3, Range = 1-10). The mean annual loss to predators was 1 (SE = 0.3, Range = 0-12). Twenty-six (60%) had not lost any sheep to predators. Eighteen (42%) producers indicated that lethal control was necessary to complement their use of electric fences to reduce predation.

Four producers reported no problems with their electric fences; however, about 95% said electrical malfunction, (shorting out) was a chronic maintenance problem. Vegetation, limbs, bears, and deer frequently caused problems and coyotes or dogs sometimes entered pastures through washouts and gates. Most producers were satisfied with their fences even though expenses of construction and maintenance were cited as important liabilities.

Discussion

Data from sheep producers interviewed during this study indicated that electric fences were effective in minimizing predation on sheep. Reported reduction of losses between pre- and post-electric fence use and minimal losses of those with only post-electric fence experience indicate that electric fences can deter predation on sheep. Even the 6 producers with extreme losses ($X = 62$) the first year after using electric fences showed a 51% reduction in predation over the previous year when conventional fencing was used.

Four producers with severe predation problems had large flocks on large grazing areas. Potential for electrical malfunctions, physical damage, additional gates, more washouts, and predator ingress increase as fenced areas increase in size. Continuous maintenance and vegetative control were cited for proper fence operation and to insure that the sheep stay confined and that predators stay excluded.

Most producers agreed that electric fencing decreased the need for intense lethal control; however, they indicated that lethal control was still needed to prevent predators from entering fenced areas and to protect sheep that were grazing outside of protected pastures.

Costs of new electric fences are greater than for electrical modifications of existing conventional net wire fences. New, anti-predator, electric fences are cheaper than net wire anti-predator fences (deCalesta and Cropsey 1978, Shelton 1984). DeCalesta (1983) calculated that 4 miles of fence, labor, maintenance, and interest cost $2,218 per year over an estimated 20-year life expectancy. If sheep were worth $60, a producer must save 37 per year to justify fencing 640 acres. Most of the producers in this study had much smaller grazing areas and the average lamb price during July, 1987, was $78.30/cwt (Idaho Agricultural Statistical Service 1987); therefore protection costs would be cheaper than shown above.

Anti-predator electric fences can reduce predation on sheep. An investment in this management tool should be explored by those farm flock producers with persistent predation problems.

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A seed midge pest of big bluestem

M.R. CARTER, G.R MANGLITZ, M.D. RETHWISCH, AND K.P. VOGEL

Abstract

A Cecidomyiid midge reared from the panicles of big bluestem (*Andropogon gerardii* Vitman (var. *gerardii)* at Mead, Neb., was identified as *Contarinia wattsi Gagné*. This midge was previously known only from panicles of little bluestem (*Schizachyrium scoparium* (Michx.) Nash) in New Mexico. In Nebraska, *C. wattsi* appears to have a minimum of 3 generations per season. Larvae of the earlier generations leave the florets after completing development, making it difficult to associate floret damage with the midge. Larvae of the last generation of a season remain in diapause, in the floret, throughout the winter. Evidence obtained in this study in 1985 indicates that, at harvest time, 7 and 15% of the florets in the 2 fields studied contained diapausing midges. However, when an estimate of seed loss by the earlier generations (as indicated by empty florets and small seed) was considered, the total loss was probably closer to 40%. An unidentified species of thrips (Thysanoptera: Thripidae) also was found in big bluestem florets during this study. However, evidence suggests that thrips do not damage big bluestem seed as seriously as the midge.

Key Words: seed production, *Contarinia wattsi*

Commercial seed production of big bluestem *(Andropogon gerardii* Vitman var. *gerardii)* in cultivated seed production fields began in the 1930's in eastern Kansas (Cornelius 1950). In the early years of commercial seed production, seed yields averaged from 80 to 170 kg/ha pure live seed (PLS) although seed yields as high as 334 kg/ha were reported (Cornelius 1950, Schumacher 1962). In recent years seed growers have regularly produced seed yields as high as 560 kg/ha by using improved production practices (Vogel and Gabrielsen 1986, Nebraska Crop Improvement Association 1986, personal communication), but occasionally seed yields have plummeted to levels less than the early seed yields for no apparent reason (personal communications from Nebraska seed growers). Cornelius (1950) reported from Kansas that orange colored larvae of an insect were found occupying the caryopsis space in 13% of the florets of big bluestem examined in 1945. He was unable to identify the insect. Vogel and Gabrielsen (1986) suggested that insects may be an undocumented problem in seed production fields of native prairie grasses.

The level of fertility and abortion of big bluestem florets in the absence of insects is unknown. However, in fields and nurseries in Kansas comparable to those in this study, Law and Anderson (1940) reported average seed set percentages of 18 to 46% and Cornelius (1950) found an average seed set of 41%. In these studies, seed set was the number of florets containing a caryopsis divided by the total number of florets examined. On individual plants, Law and Anderson (1940) reported seed set percentages ranging from 0 to 84%. These reports did not indicate if pedicellate spikelets were included in the counts.

Very few midges (Diptera: Cecidomyiidae) have been recognized as pests of grass seed production. One reported midge is *Contarinia* (=Stenodiplosis) bromicola (Marikovsky and Agafonova) which was reported to reduce seed production of smooth bromegrass (Agafonova 1962, Neiman and Manglitz 1972). This bromegrass seed midge apparently was distributed widely in both the USSR and US before it was discovered and its damage realized. Another midge, Contarinia wattsi Gagné, was described by Gagné (1966) from specimens collected from little bluestem (*Schizachyrium scoparium* (Michx.) Nash) in New Mexico. *C. wattsi* destroyed 20% of the little bluestem seed (Watts and Bellotti 1967). The objectives of this study were to determine if insects were damaging florets or developing seeds of big bluestem and if so, to determine the effect of this damage on seed yield.

Materials and Methods

Insect populations were sampled during 1983 and 1985 in a foundation seed field of 'Pawnee' big bluestem (Field 1) at the University of Nebraska's Agricultural Research and Development Center at Mead, Neb. Sampling in 1983 began in late-July and continued on a weekly basis until 21 September. In 1985, the same field was sampled twice weekly from mid-July through 21 September. A polycross nursery of clones selected from 'Kaw' big bluestem (Field 2) was also sampled on 21 September 1985. The 2 fields were about 2 km apart. The midge population was sampled by randomly collecting 25 to 35 panicle-bearing culms from the fields. The culms were taken to the laboratory and placed in water-filled flasks, which were placed in dark insect-rearing cages. Insects emerging from florets were collected in glass vials inserted in the side of the cages. Culms and racemes remained in the rearing cages for 4 weeks, then they were transferred to paper bags and held at 2° C for later dissection.

In 1985 numbers of insects and seed development stage were determined by dissecting approximately 25% of the florets collected on each date. Big bluestem has both sessile and pedicellate spikelets. According to Hitchcock (1951) the floret of the sessile spikelet is fertile but the pedicellate spikelet is sterile. However, in breeding nurseries and in seed production fields, the pedicellate spikelete can be fertile (Boe et al. 1983). Boe et al. (1983) reported that in eastern South Dakota nurseries as many as 86% of the big bluestem plants had fertile pedicellate spikelets. In this study both sessile and pedicellate spikelets were dissected since the plants were grown in nursery and field conditions conducive to seed set in the pedicellate spikelets. Dissected florets were visually classified according to size, stage of development, and the presence or absence of insects using the following categories.

1. Normal seed—fully developed, large and medium sized seed.
2. Small seed—developed but very small.
3. No seed—floret ovaries were destroyed by the midge or failed to develop for other reasons.
4. Midge—orange diapausing pupae (or puparium) was found in the floret.

Results and Discussion

The insect which emerged most frequently from panicles of big bluestem in 1983 was *Contarinia wattsi Gagné*. Its association with big bluestem and its occurrence in Nebraska are both new records;- thus, determining the seasonal occurrence of and damage potential for *C. wattsi* became the primary focus for the remainder of the observations.

Authors are former graduate research assistant, Dept. of Entomology, Univ. of Nebraska; research entomologist, USDA-ARS; former graduate research assistant, Dept. of Entomology, Univ. of Nebraska; and supervisory research geneticist, USDA-ARS; Univ. of Nebraska, Lincoln 68583.

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The numbers of *C. wattsi* that emerged from the panicles in the rearing cages at weekly intervals indicate that at least 3 generations per year occurred in Nebraska in 1985. Generations were indicated by emergence peaks that occurred about every 13 to 16 days (Fig. 1). In 1983, collection of panicles was initiated too late in August to record the first generation. However, what appeared to be second and third generations were observed. Emerging midges left no evidence of their former presence in the floret. This lack of evidence makes damage assessment very difficult.

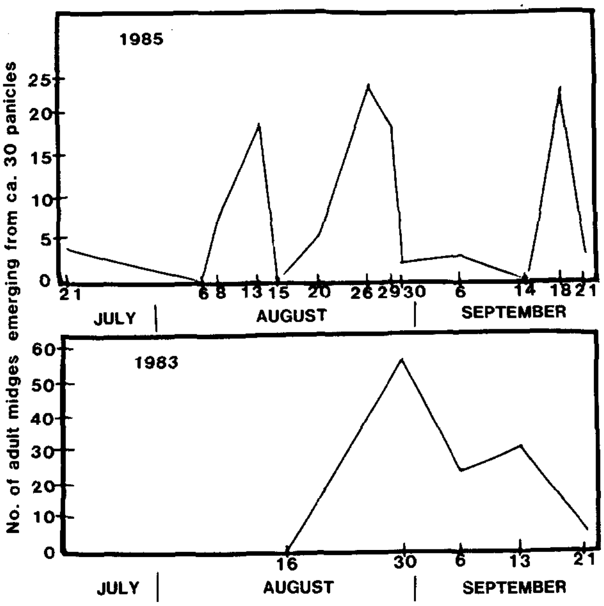

Fig. 1. *The emergence of adult midges from field collected panicles of big bluestem during the summers of 1983 and 1985 at Mead, Neb.*

Dissection of florets collected early in the season revealed the presence of immature larvae, which would be expected to complete development and emerge as adults later in the season. As the season progressed, the percentage of the dissected florets that contained diapausing midge larvae increased (Table 1). Midge larvae were found in 18 and 7%, respectively, in the Pawnee and Kaw florets sampled on 21 September (Table 2). In addition, an unidentified species of thrips (Thysanoptera: Thripidae) was found in the Pawnee florets; but the number of florets containing thrips was relatively low (1.8 on 29 August) until September (17.8 on 21 September), when the caryopses were nearly mature. Therefore, the influence of these thrips on seed production is probably not significant. More observations are needed to fully assess the damage potential of the thrips to big bluestem seed. On the 21 September sampling date 77% of the Pawnee florets and 59% of the Kaw florets had either midges, no seed, or small seed (Table 2). The florets with no seed or small seed may have been damaged by earlier generations of midges. Assuming that in the absence of these insects and under optimal conditions all sessile and pedicellate spikelets set seed, then 15% of the Pawnee florets contained midges rather than caryopses. Many of the florets which were empty (47%) or contained small seeds (12%) probably were damaged by earlier generations of midges (Table 2). Since many of the pedicellate spikelets do not set seed under field conditions, we conservatively estimate that 40% of the potential seed crop in the Pawnee field was destroyed by midges. The damage was less in the Kaw field but it was still substantial since only 41% of the florets had "normal" seed.

Table 1. Seasonal progression of diapausing midges in 'Pawnee' big bluestem field during mid- to late-summer, Mead, Nebraska, 1985.

	Diapausing midges	
Collection date	Mean infested florets (%)	95% confidence interval (range)
August 7	0	——
13	1.4	0.35 - 2.75
21	0.7	0.08 - 2.66
29	1.8	0.39 - 3.69
September 6	4.9	1.83 - 7.38
21	14.9	6.48 - 27.27

$X^2 = 213.352$ ($X^2_{0.05}$ 5 d.f. = 11.070)[1]

[1]Rejects hypothesis that % midges in florets does not change as season progresses. Analysis used is according to Zar (1984).

Table 2. Seed development and presence of insects in 2 seed fields of big bluestem in eastern Nebraska. Samples taken 21 September 1985.

Floret categories	Field 1, 'Pawnee' No.	Field 1, 'Pawnee' %	Field 2, 'Kaw' No.	Field 2, 'Kaw' %
Normal seed	110	23	377	41
Small seed	56	12	318	34
No seed	226	47	169	18
Midges	87	18	63	7
Total	479	100	927	100

In summary, this study represents the first report of the seed midge, *Contarinia wattsi*, on big bluestem and only the second time it has been reported in North America. Judging from the few but widespread locations where it has been found, including South Dakota (Arvid Boe, 1986, personal communication), the midge probably is widely distributed and may be found in many areas where native stands of big bluestem remain. Additional research will be needed to further quantify the damage of this bluestem seed midge and the unidentified thrips on seed yields of big bluestem and to develop control practices.

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Estimating digestibility of oak browse diets for goats by in vitro techniques

ANASTASIOS S. NASTIS AND JOHN C. MALECHEK

Abstract

Predicting digestibility of shrubs is important to evaluating many of the world's rangelands. We examined laboratory procedures for predicting in vivo digestion of browse-alfalfa *(Medicago sativa)* mixed diets and how drying temperature and inoculum source affect digestibility. In addition, we considered the effect of oak tannin on pepsin activity and dry matter digestion. The commonly used Tilley and Terry (1963) two-stage in vitro digestion technique was a precise (r^2=0.97) but inaccurate predictor of in vivo apparent digestibility of mixed oak *(Quercus gambelii)* and alfalfa diets for goats. The Van Soest et al. (1966) neutral detergent method for predicting true digestibility was less precise (r^2=0.76). Estimates from the Goering and Van Soest (1970) summative equation were not correlated ($P \leq 0.05$) with in vivo digestion. Separate regression equations are necessary if in vitro methods are to predict accurately in vivo digestibility of browse diets. In vitro digestibility was inversely related to percentage of oak in the diets and the amount of oak in the inoculum donors' diets. High drying temperatures depressed digestibility of oak browse and this effect was greater for immature than for mature forage.

Key Words: in vitro digestibility, *Capra hircus, Quercus gambelii*, tannins

Digestion trials are important in determining the nutritional value of a forage. However, the time and expense involved in collecting sufficient forage to feed animals required for in vivo trials limits their application. Laboratory procedures requiring only small samples have frequently been used as alternatives (Pearson 1970). These include in vitro methods of estimating apparent (Tilley and Terry 1963, Barnes 1967) or true (Van Soest et al. 1966) digestibility. The summative equation of Goering and Van Soest (1970), which is based on chemically partitioned forage fractions, is another potential technique for indirectly estimating digestibility.

These techniques, when applied to conventional forages and within relatively narrow and well-defined boundaries of variation, have proven to be accurate and inexpensive. However, use of indirect methods to estimate in vivo digestibility of mature shrub species has been problematic (Short et al. 1974, Urness et al. 1977, Mould and Robbins 1981).

Secondary chemical compounds such as tannins may also complicate prediction of in vivo digestion (Burns et al. 1972, McLeod 1974). They can affect apparent digestibility of protein (Robbins et al. 1987) as well as microbial and enzyme activity (Tagari et al. 1965). The source of inoculum used in in vitro fermentations can potentially introduce yet another factor of variation (Knipfel and Troelsen 1966, Calder 1970, Milchunas and Baker 1982).

It is important that microdigestions be compared to standard in vivo digestion trials using the same or similar forage before results can be generally useful. We compare in vivo digestibility of oak-containing diets by goats *(Capra hircus)* with estimates derived from 3 microdigestion techniques. Effects of drying temperatures and composition of inoculum donors' diets on in vitro fermentation and the effect of oak tannin on pepsin activity and digestion are also reported.

Authors are with the Dept. of Range Wildlife Sci. 236, Univ. of Thessaloniki, Greece, and Dept. of Range Sci., Utah State University.
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Materials and Methods

Oak *(Quercus gambelii)* was collected in June, during the season of rapid growth, and in August, after twig elongation had ceased and stems had hardened. Oak browse included only terminal portions (up to 15 cm in length) of the current year's growth and was hand-plucked from various positions in the tree canopies. From the June collection a diet was formulated containing 80% oak and 20% alfalfa *(Medicago sativa)*. From the later collection 4 diets were formulated containing 20, 40, 60, and 80% oak with alfalfa making up the complement. A pure alfalfa diet was used as the experimental control.

In vitro dry matter digestibility of these 6 diets was measured using techniques described by Tilley and Terry (1963) (hereafter called IVAP), Van Soest et al. (1966) (hereafter called IVND), and Goering and Van Soest (1970) (hereafter called (SUEQ). The Tilley and Terry technique was modified by terminating fermentation with HCl instead of HgCl.

Inoculum for in vitro digestion trials was obtained by vacuum aspiration of rumen fluid from 2 ruminally fistulated goats (donor animals) fed the test diets. The donor animals were fed the 6 diets in sequence beginning with pure alfalfa (control) and proceeding in order of increasing oak content. The 80% oak diet made from browse collected in June was fed last. Donor animals were allowed at least 5 days to adjust to each new diet before rumen fluid was collected for in vitro trials. Rumen inoculum corresponding to a specific test diet was termed a *source* of inoculum. For each source, all 6 diets were fermented in duplicate for each of the 2 in vitro techniques. The rumen fluid obtained from the 2 donors at any particular collection was aggregated and handled according to the procedures outlined by Tilley and Terry (1963).

We determined the effect of drying temperature upon in vitro digestion in a completely random experiment. Samples of oak browse were hand harvested at monthly intervals throughout the growing season and subsamples of these materials were freeze-dried at –2° C, air-dried at 0° C and 25° C, and oven-dried at 55° C, 65° C, and 100° C. Subsamples of the material were then subjected to in vitro digestion using the IVAP procedure.

In addition, tannin content of the diets (expressed as tannic acid equivalent) was determined by the spectrophotometric method of Burns (1963); Folin Denis reagent was used. To determine whether tannins contained in oak had any effect on activity of pepsin used in the second stage of the IVAP procedure, an enzyme activity test was conducted according to the methods of Tang (1970). Each of the 6 diets was prepared for the test by refluxing a 0.5-g sample in 100 ml of distilled hot water for 6 hrs. After cooling, the mixture was centrifuged for 10 min at 500 G to remove suspended solids. Then, 50 ml of the supernatant was transferred to a 250 ml Erlenmeyer flask and 2 ml of pepsin solution (concentrations 5%, W/V) was added. From this point, the steps outlined by Tang (1970) were followed. Results are reported as the quantity (micromols) of diliodotyrosine liberated per minute (Ryle 1970) from N-Acetylephenylalanyl-l-diliodotyrosine (APD) by pepsin under the conditions of the assay.

Results from experiments on the 3 microdigestion techniques were analyzed by regression procedures. In vitro values were regressed on corresponding in vivo digestibility values determined in a related digestion balance experiment (Nastis and Malechek 1981). Regression procedures were also used to relate oak content of diets to their in vitro and in vivo digestibilities. Results of the enzyme test, the inoculum source effect, and the drying-temperature tests were evaluated statistically by analysis of variance procedures. Where significant effects were found by analysis of variance, an LSD test (Steel and Torrie 1980) was applied to isolate specific differences between means at the 0.05 probability level.

Results and Discussion

Diet Composition and Digestibility

Digestibility of diets that contain mature browse is typically low (Short et al. 1972, Urness et al. 1975). Nastis and Malechek (1981) reported 46.7% apparent digestibility for the mature browse used in this study. When such material is added to an alfalfa diet in a progressive fashion as in this study, the orderly decline of digestibility that we observed (Fig. 1) might be expected. However, the

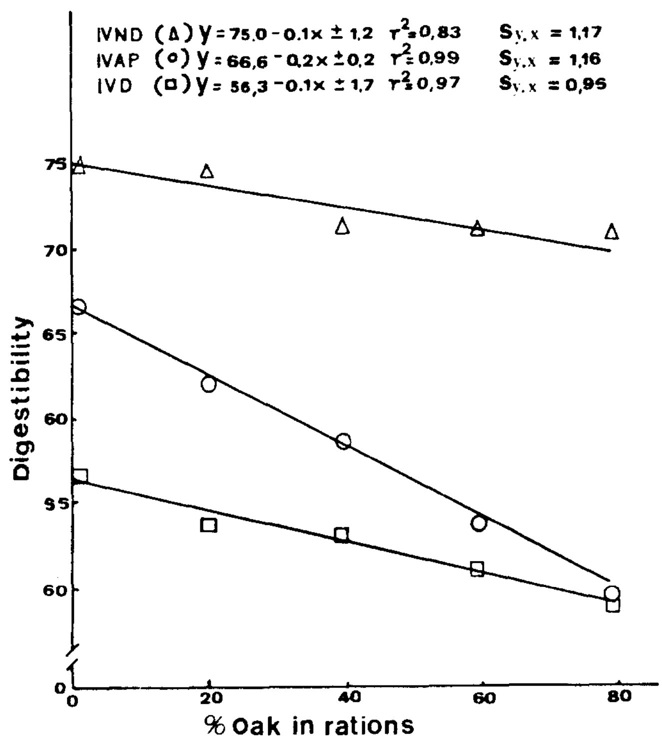

Fig. 1. *Relations of IVAP digestibility (Y), IVND digestibility (Y) and in vivo digestibility (Y) by goats (IVD) to oak foliage content of experimental diets (X).*

explanation for the decline, especially in an in vitro system and when oak is the browse component, is not obvious. Some of the decline is undoubtedly due to the effect of poorly digestible components (Nastis and Malechek 1981). Another factor is the influence of tannins. Tannins have the property of precipiting proteins from aqueous media (Swain 1979, Robbins et al. 1987). They form complexes with both plant and animal proteins which are insoluble or variably soluble (McLeod 1974, Rosenthal and Janzen 1979, Robbins et al. 1987). Tannin precipitated proteins, though, are digested in vivo up to 88% as reported by Robbins et al. (1987). This shows that the over-all digestion is only slightly affected by the reduced protein digestion.

Oak tannin reduced pepsin activity (Table 1) as oak content of the diet increased. However, reduction in enzyme activity was no different in the two 80% oak diets, although the diets differed in tannin content. This may indicate that tannins from mature oak foliage are more effective in reducing enzyme activity than tannins from immature oak. In the present experiment, mature oak browse

Table 1. Pepsin activity as influenced by oak tannin content of diets. Enzyme concentrations and amounts of forage were similar to those in the Tilley and Terry (1963) in vitro procedure.

Diets		Tannin	Quantity of substrate
Oak	Alfalfa	content%	liberated (μmol/min)
00	100	1.0	13.0 ± 0.2a [1]
20	80	2.4	12.9 ± 1.0ab
40	60	3.2	10.4 ± 1.5bc
60	40	4.8	7.9 ± 0.9cd
80	20	6.9	5.6 ± 1.8d
80[2]	20	8.9	8.8 ± 1.4d

[1]Quantity of diiodotyrosine liberated from the substrate (±95% confidence intervals) followed by common letters are not significant by $P \leq 0.05$ different.
[2]Oak collected in June during the season of rapid growth. Oak of the other diets was collected in August after elongation had ceased and stems had hardened.

contained less fiber than did alfalfa (31.7% vs. 39.6% ADF) but considerably more tannin (8.7% vs. 1.0%) (Table 1) and its digestibility was significantly lower (Fig. 2). Similarly, Burns et al. (1972) reported results for Serica lespedeza *(Lespedeza cuneata),* which is

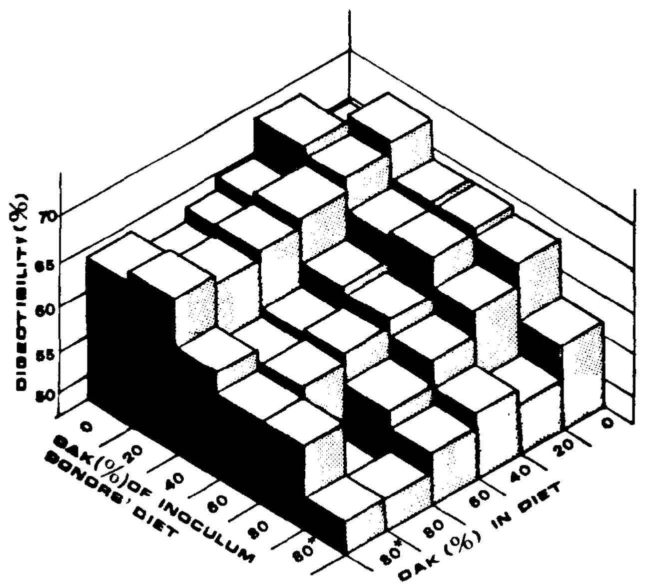

Fig. 2. *In vitro digestibility (%) of an alfalfa diet and 5 oak-containing diets in relation to composition of the inoculum donors' diets. Values are means of estimates from the Tilley and Terry (1963) method and the Van Soest et al. (1966) method. (*) Oak collected in June during the season of rapid growth. Oak in the other diets was collected in August after elongation had ceased and stems had hardened.*

similar to alfalfa in fiber content but contains almost 3 times as much tannin and was 14.2 digestibility units less digestible. The tannins' inhibitory properties might be involved in our estimates of digestibility. Tagari et al. (1965) also reported that tannins act as inhibitors affecting microbial fermentation and/or enzymatic proteolysis.

In vitro techniques generally either underestimate in vivo digestibility of browse forage (Urness et al. 1977, Sidahmed et al. 1981) or provide close estimates (Newman and McLeod 1973). But when browse high in tannins and related phenolic compounds is tested, in vivo digestion is likely to be overestimated by in vitro methods (Fig. 3) because of increased fecal excretion of protein. In a related study (Nastis and Malechek 1981), we observed that increasing levels of oak in goats' diets led to elevated levels of fecal nitrogen excretion and progressively lower levels of apparent digestion of cellular constituents. The overestimation of in in vivo digestibility

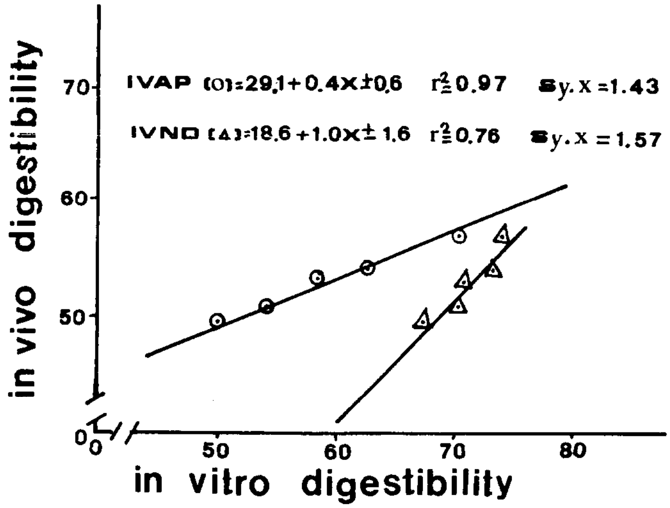

Fig. 3. *Relation of digestibility determined by the in vitro acid pepsin method (IVAP) and the in vitro neutral detergent method (IVND) to in vivo digestibility.*

can be attributed mainly to the low in vivo digestion of cell contents. Maximum in vivo digestibility of oak browse cell contents (Nastis 1977) was 74.8±2.0% as compared to 98±2.5% assumed for conventional forages by Van Soest (1967).

Comparison of In vitro Techniques

Regression analysis relating the 2 in vitro techniques to in vivo digestion (Fig. 3) indicated that the IVAP method was more precise, (r^2=0.97, Sy.x=1.43) than the IVND procedure (r^2=0.76, Sy.x=1.57). Results using the SUEQ were not significantly correlated with in vivo digestion ($P\leq0.05$). Averaged over all inoculum sources and diets, the mean estimate provided by IVND was 71.0% and 56.5% for IVAP, compared to a mean of 52.9% for in vivo trials.

The discrepancy between the 2 in vitro techniques can be explained partly in terms of differences in their principles. The IVAP approach provides estimates of apparent digestibility (Tilley and Terry 1963) whereas the IVND procedure estimates true digestibility (Van Soest et al. 1966).

Our estimates of digestibility derived from the summative equation (Goering and Van Soest 1970) were not significantly ($P\leq0.05$) correlated with in vivo digestion.

Two points should be kept in mind when rationalizing the utility of in vitro techniques for estimating in vivo digestibility of oak-containing diets and possibly other diets high in tannin-containing browse. First, the Tilley and Terry (1963) procedure seems to provide precise estimates of digestibility which may not be accurate unless corrected (e.g., Fig. 3). This, of course, means that a limited number of in vivo digestion trials must be conducted.

Secondly, estimates of true digestibility (Van Soest et al. 1966) are valuable in certain contexts, but in the case of diets such as those used in this study, the factors contributing to high excretion of metabolic fecal components and affecting the extent of cell constituents digestion cannot be overlooked. Until these relationships are better understood, in vitro procedures that estimate apparent digestibility would seem to have the greatest utility in determinations of dietary quality.

Inoculum Donors' Diet

Inoculum source had a significant effect on in vivo digestibility with a tendency towards lower values as the composition of donors' diets increased in oak content (Fig. 2). When donors were fed a diet composed of oak collected in June, even lower in vitro digestibility resulted. Moreover, composition of donors' diets and composition of test diets interacted significantly ($P\leq0.05$). Test diets containing high percentages of oak had lower in vitro digestibility estimates when the inoculum donor's diet contained higher levels of oak than when it contained only alfalfa or small amounts of oak. Figure 2 indicates that digestibility of diets containing less than 60% oak was slightly affected by the donors' diet, while digestibility of diets containing 80% oak was influenced by the inoculum donors' diet.

The interaction of in vitro methods with inoculum sources was also significant. Digestion by IVAP was more affected by inoculum source than was IVND digestion (Table 2). The IVAP seems to be sensitive to factors affecting the microbial population, such as tannins which most probably covary with nitrogen and fiber content of forage. Results of the enzyme activity test suggested some reduction in pepsin activity owing to compounds extracted from oak-containing diets (Table 1). The IVND, which differs in the second stage from IVAP by including digestion with neutral detergent, seems to dissolve fractions undigested by the IVAP procedure, thus yielding higher digestibility values.

Table 2. In vitro digestibility (%) of dry matter, with inoculum from donors consuming oak-alfalfa diets in varying proportions, by Tilley and Terry (1963) and Van Soest et al. (1966) methods averaged over all diets.

Inoculum donors' diet		Tilley and Terry	Van Soest
% Oak	% Alfalfa	apparent	true
00	100	58.8 ± 3.0a[1]	72.1 ± 4.2ab
20	80	57.5 ± 3.0b	73.3 ± 1.6a
40	60	57.8 ± 3.0b	71.8 ± 3.6b
60	40	57.3 ± 2.6b	71.8 ± 1.3b
80	20	55.8 ± 3.1c	70.9 ± 0.9c
80[2]	20	51.6 ± 3.3d	67.0 ± 1.5d
Average		56.5 ± 0.3	71.1 ± 0.3

[1]Digestibility averages (±95% confidence intervals) in a particular column followed by common letters are not significantly different ($P\leq0.05$).
[2]Oak collected in June during the season of rapid growth. Oak in the other diets was collected in August after elongation had ceased and stems had hardened.

Phenological Stage and Drying Temperature

In vitro digestibility of oak foliage was significantly affected by drying temperatures (Fig. 4). Lower digestibilities were associated with higher drying temperatures. Van Soest (1965) demonstrated that heating in the presence of moisture alters carbohydrate structure and diminishes nitrogen solubility by forming insoluble polymers that are measured in the lignin fraction.

Phenological stage of plant material also caused significant variation in in vitro digestibility. Averages of in vitro digestion across all drying temperatures decreased through the growing season (Fig. 4). Oak collected in June had a higher digestibility ($P\leq0.05$) than oak collected in July and they were both higher than from oak collected in August and September. However, there were no significant differences between the last 2 sampling periods. Chemical composition of oak through the growing season showed a gradual decrease in crude protein from 20% to 13%, an increase in acid detergent fiber from 29% to 36%, and a slight increase in lignin content from 10% to 11%. These chemical changes probably contributed to the decrease in digestibility of oak over the range of phenological stages.

Interactions between phenological stage and drying temperature (Fig. 4) were also significant ($P\leq0.05$). High temperature depressed IVAP digestibility to a greater extent in early-harvested material than in late-harvested material. This is probably related to the higher concentrations of moisture, soluble carbohydrates, and nitrogen-containing compounds in young foliage, which upon heating, provide substrates for formation of the insoluble, dark-colored polymers discussed by Van Soest (1965) and Raguse and Smith (1965). Findings from this experiment suggest that results of in vitro digestibility assays on oak browse diets may be comprom-

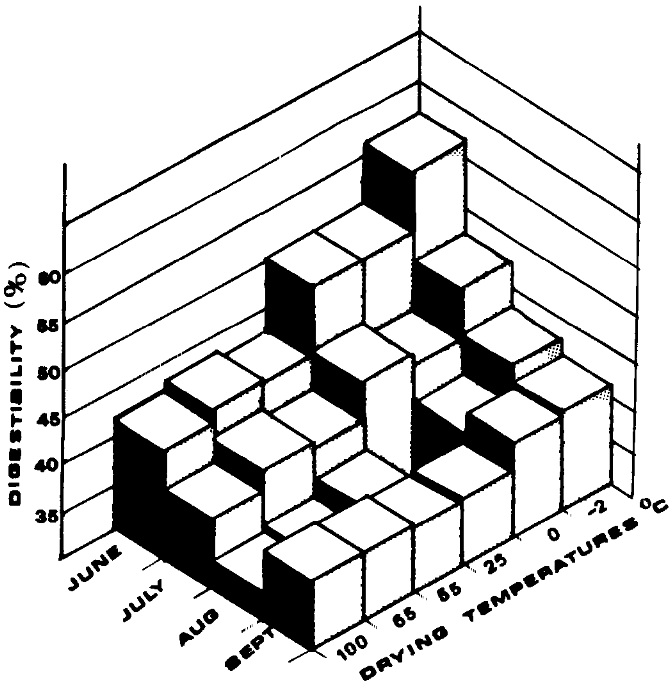

Fig. 4. *Effects of drying temperature and stage of maturity on oak foliage digestion determined by the Tilley and Terry (1963) in vitro method.*

ised by any drying procedure other than freeze-drying.

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Heifer nutrition and growth on short duration grazed crested wheatgrass

KENNETH C. OLSON AND JOHN C. MALECHEK

Abstract

Animal performance and nutrition under short duration grazing (SDG) and season-long grazing (SLG) were compared on spring-grazed crested wheatgrass [*Agropyron desertorum* (Fisch.)Schult. and *A. cristatum* (L.)Gaertn.] range to determine if SDG has the potential to improve livestock production on such rangelands. Livestock performance was evaluated by measuring weight gains twice per grazing season. Diet quality was assessed by determining crude protein concentration and in vitro organic matter digestibility of extrusa samples collected from esophageally fistulated heifers. Three variables of ingestive behavior were measured: ingestion rate, biting rate, and grazing time. Daily forage intake was calculated as the product of ingestion rate and grazing time. Animals in the SLG treatment gained significantly more than those under SDG in 1983 (1.07 vs. 0.81 kg/hd/d), but no statistical differences were detected in 1984 (1.13 vs. 1.07 kg/hd/d for SDG and SLG, respectively). In 1985, animals under SDG gained the most (1.03 vs. 0.87 kg/hd/d for SDG vs. SLG, respectively). No differences were detected in diet quality between SDG and SLG throughout the study. No treatment differences were detected in ingestive behavior during 1984, but ingestion rate was greater and grazing time less under SDG than SLG during 1985. Results indicate that forage intake was greater, while energy expenditures were lower under SDG than SLG in 1985. The hypothesis that SDG extends the season of nutritious forage was not supported.

Key Words: *Agropyron desertorum, A. cristatum,* diet quality, ingestive behavior, feed intake, livestock production, grazing management

Short duration grazing (SDG) is gaining popularity as a type of grazing management that purportedly enhances both livestock production and range condition. Livestock production is reported to be improved by increases in both carrying capacity and animal performance (Savory 1978). A salient feature of SDG is the purported effect of rapid rotation on forage maturity and diet quality. It is proposed that this allows animals to maximize selection for the most nutritious, youngest plant parts, and then they are moved to new, ungrazed vegetation. During the rest period, the plants recover from grazing and regrow. The forage on offer during the next grazing period is thus young and highly nutritious. This hypothesized maintenance of the sward in a phenologically immature state thereby may extend the season of nutritious forage. Thus, animal performance under SDG is expected to be better than under traditional grazing schemes.

Most literature concerning SDG reports weight gain as a measure of livestock response. Results have been variable; higher average daily gain (ADG) has been reported under SDG than under season-long grazing (SLG) in some cases when stocking rates were equal (Daugherty et al. 1982, Sharrow 1983), while other studies reported equivelant ADG between SDG and SLG, both when stocking rates were equal (Jung et al. 1985) and when the stocking rate was substantially increased under SDG (Heitschmidt et al. 1982, Jung et al. 1985). These results indicate that carrying capacity or gain per animal may be seasonally enhanced by using SDG, thus allowing an increase in gain per area. However, a more detailed approach focusing on potential mechanisms of animal interaction with the sward would be more likely to define causes of the weight responses and allow determination of how changes in management (length of graze and rest periods, and stocking density) might affect weight gains and carrying capacity. Such an approach should involve analysis of nutritional and behavioral factors as an interface between livestock response and vegetation characteristics that result from grazing management.

Winter-spring range, typically foothill range seeded to crested wheatgrass [*Agropyron desertorum* (Fisch.)Schult. and *A. cristatum* L.Gaertn.], is the major forage supply constraint on livestock production in the Intermountain West. This constraint is caused by two factors: (1) there is a limited amount of this seeded foothill range (Banner 1981), and (2) crested wheatgrass matures rapidly, with a concomitant decline in nutritive quality (Cook and Harris 1968). This growth characteristic limits the time span that crested wheatgrass can effectively meet the nutrient requirements of beef cattle. Because of these limitations, SDG might improve livestock nutrition and production on spring range in the Intermountain West by increasing carrying capacity or extending the season of nutritious forage.

The objective of this study was to determine if SDG alters livestock performance, diet quality, ingestive behavior, and forage intake relative to SLG.

Materials and Methods

A multi-disciplinary project to evaluate SDG on crested wheatgrass was initiated in 1983 involving several investigators studying aspects of SDG germane to their area of expertise; including vegetal, hydrologic, livestock, and economic responses to SDG.

Study Site

The study was conducted on the Tintic Experimental Pastures in Juab County, west-central Utah. The SDG cell consisted of ten 8.4-ha (21 acre) paddocks arranged radially around a central watering and handling facility. The SLG treatment was a 28-ha (70 acre) pasture located about 0.5 km from the SDG cell.

The study area was typical of most crested wheatgrass seedings throughout the Intermountain West. The site was renovated in 1951 by removing unpalatable woody species, including big sagebrush (*Artemisia tridentata* Nutt.), rabbitbrush [*Chrysothamnus nauseosus* (Pallas)Britt.], and juniper trees (*Juniperus* spp. L.), and seeding to introduced wheatgrasses (Cook 1966). The SLG treatment and most of the SDG cell was seeded to crested wheatgrass. A portion of the SDG cell was seeded to intermediate wheatgrass [*A. intermedium* (Host)Beauv.], but this area was avoided as much as possible for sampling. The vegetation in both treatments was dominated by crested wheatgrass with localized patches of western wheatgrass (*A. smithii* Rydb.). Big sagebrush and rabbitbrush were encroaching throughout both treatments. Localized stands of juniper occurred in the grazing cell.

Authors are range research scientist, Fort Hays Branch, Kansas Agr. Exp. Sta., Hays 67601; and professor, Range Sci. Dep., Utah State Univ., Logan 84322. At the time of the research, the senior author was research assistant, Range Sci. Dep., Utah State Univ.

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Grazing Management

The SDG cell was stocked with 90 black Angus replacement heifers and 3 to 5 bulls, resulting in a stocking rate of 0.7 ha (1.7 acres) per AUM[1]. The heifers weighed 230 to 270 kg (500 to 600 lb) at the beginning of each grazing season. The SLG pasture was stocked with 30 heifers and 1 or 2 bulls to achieve the same stocking rate as the SDG cell. However, the stocking density in the SDG cell was 0.14 ha (0.35 acres) per AU[1], while the SLG stocking density was 1.4 ha (3.5 acres) per AU.

Animals in the SDG cell were moved approximately every 3 days in 1983 and 1984. Two complete cycles were made through the grazing cell. In 1985, the animals were moved approximately every 2 days during the first 2 cycles, and every day during a third cycle. Length of grazing period in specific paddocks was adjusted based on forage availability (±1 day). Animals were moved at midday to avoid interference with normal morning and evening grazing activity.

Field Methodology

Livestock Performance

All animals were weighed in the morning after an overnight fast period at the beginning, middle, and end of the grazing season.

Diet Quality

Heifers having esophageal fistulae were used to collect samples of grazed forage for nutritional analysis. In 1983, 3 fistulated animals were used in each treatment. In 1984 and 1985, this number was increased to 5 animals in each treatment. These animals were cohorts of the herds that grazed the experimental pastures.

Samples were collected in the early morning or at the time of entry to a particular paddock. Animals were fasted for 5- to 10-hours before sample collection to insure grazing. Chacon and Stobbs (1977) found that bite size and diet quality were influenced more by stage of defoliation and individual animal variability than by fasting or diurnal variations in time of sampling, as long as fasting was less than 12 hours. Fistula extrusa samples were frozen in the field immediately following collection by immersion in a dry ice-alcohol bath. Samples were then stored in a freezer until laboratory analysis.

Esophageal extrusa was collected whenever animals were in 3 pre-selected paddocks. These paddocks were spaced evenly around the grazing cell. In 1983, extrusa was collected on the days of entrance to and exit from paddocks 3, 6, and 9. Extrusa was collected in the SLG treatment during intervening periods. In 1984 and 1985, extrusa was collected on each consecutive morning that the heifers occupied paddocks 1, 4, and 7. In 1985, extrusa was also collected immediately after movement into the paddocks (i.e., at midday), to gain information on response to ungrazed swards. In 1984 and 1985, the SLG treatment was sampled on 3 occasions evenly spaced through the grazing season.

Ingestive Behavior and Forage Intake

An understanding of behavioral responses to the physical characteristics of vegetation can be used to estimate forage intake (Stobbs 1973, 1974) and has been implicated with livestock performance (Ebersohn and Moir 1984). Stobbs (1974), working on tropical pastures in Australia, estimated daily forage intake from the product of 3 variables of ingestive behavior: bite size (g/bite), biting rate (bites/min), and grazing time (mins/day). This approach provides the opportunity to evaluate forage intake response to the effects of grazing management on the sward, as mediated by ingestive behavior.

Three variables of ingestive behavior were measured in this study during 1984 and 1985: ingestion rate, biting rate, and grazing time.

Ingestion rate, or intake per unit time, was measured in conjunction with collection of esophageal extrusa samples. Extrusa harvested during timed periods of sampling was weighed in the field immediately following collection. Ingestion rate per sample period was calculated for each heifer by dividing the weight by the grazing time during the sample period. Several precautions were taken to improve the probability that all forage ingested during an extrusa collection went into the bag. In 1983, foam rubber plugs were placed in the esophagus posterior to the fistula during sample periods as recommended by Stobbs (1973). However, animals were often observed to be irritated by the presence of the foam rubber plug, and thus did not graze normally. In 1984 and 1985, a cannula insert was used in lieu of the foam plugs to facilitate total sample collection (Olson and Malechek 1987).

Biting rate was measured by ocular counts during the period of intense grazing in early morning. These counts were made immediately before esophageal extrusa collections. Animals to be observed were selected in a stratified manner to maximize independence of samples. Consecutively observed individuals were separated by a distance that was subjectively deemed adequate to minimize possible effects of social facilitation on behavior. For a particular animal, time elapsed to prehend and ingest 100 to 200 bites were recorded with a stop watch while counts were made. Timing was interrupted during nongrazing intervals, such as when animals raised their heads to brush hornflies away or to walk.

Grazing time was recorded by fitting 4 animals in each treatment with vibracorders. These instruments remained on the animals throughout the grazing season. Charts were changed weekly, so grazing time was continuously recorded.

Laboratory Methodology

A subsample of each extrusa sample was used to determine dry matter (DM) and organic matter (OM) content (Harris 1970) to adjust ingestion rates to an OM basis. Another subsample of each frozen extrusa sample was freeze-dried and ground through a 1-mm screen in preparation for diet quality analysis. Extrusa samples were not composited across animals, days, or paddocks because all of these sources of variation were of interest for this or other studies. Ground samples were analyzed for Kjeldahl nitrogen (Harris 1970) and in vitro organic matter digestibility (IVOMD) by use of a cellulase technique (McLeod and Minson 1978). Crude protein (CP) was calculated as Kjeldahl nitrogen times 6.25. All results are reported on an OM basis to alleviate potential problems caused by variable salivary mineral contamination.

Data Analysis

Estimated daily forage intake was the product of ingestion rate and grazing time (Freer 1981).

Statistical differences in livestock performance between SDG and SLG were determined using Student's *t*-tests (Steel and Torrie 1960). Differences in diet quality and ingestive behavior were analyzed by least squares analysis of variance (ANOVA) using the Rummage statistical program (Bryce 1980). Main effects were treatment (SDG versus SLG), date, and their interaction. Date compares different periods in the grazing season. These dates are delineated by each sample collection period in the SLG treatment. There were 5 sample periods under SLG in 1983 and 3 each in 1984 and 1985. Data from SDG during equivalent portions of the grazing season were used for comparison. Separate analyses were run for each year with no comparisons made among years because of differences between years in sampling schedules and grazing management. Mean separations were determined by LSD for significant ANOVA main effects. Statistical significance was inferred at $P \leq 0.05$. We recognize that the lack of replication of true experimental units (pastures or grazing cells) limits the application of results to locations other than the study site.

Results and Discussion

Livestock Weight Gain

Average daily gains in both treatments appeared to be greater in

[1]AUM (animal unit month) and AU (animal unit) follow the standard definition wherein 1 animal unit equals a 454 kg cow with calf or the equivalent, and an animal unit month is the forage demand of 1 animal unit for 1 month.

Table 1. Average daily gain (ADG) of heifers (kg/hd/d) and total livestock production (kg/ha) on crested wheatgrass under short duration grazing (SDG) and season long grazing (SLG) during the springs of 1983, 1984, and 1985.

	SDG	SLG
1983		
period 1 ADG	1.09[a1]	1.21[a]
period 2 ADG	0.54[a]	0.94[b]
mean ADG	0.81[a]	1.07[a]
kg/ha	50.5	65.7
1984		
period 1 ADG	1.54[a]	1.62[a]
period 2 ADG	0.72[a]	0.52[a]
mean ADG	1.13[a]	1.07[a]
kg/ha	72.0	67.5
1985		
period 1 ADG	1.12[a]	0.96[b]
period 2 ADG	0.88[a]	0.73[b]
mean ADG	1.03[a]	0.87[b]
kg/ha	58.4	49.5

[1]Means within rows differ ($P \leq 0.05$) when followed by different letters.

Table 2. Mean annual crude protein concentration (CP) and in vitro organic matter digestibility (IVOMD) of esophageal extrusa, ingestion rate, biting rate, and grazing time by heifers grazing crested wheatgrass under short duration grazing (SDG) and season long grazing (SLG), 1983-1985.

		1983	1984	1985
CP	SDG	13.40[a1]	14.07[a]	13.66[a]
(%)	SLG	11.32[a]	14.27[a]	14.49[a]
IVOMD	SDG	65.94[a]	64.95[a]	67.93[a]
(%)	SLG	64.87[a]	64.51[a]	66.75[a]
ingestion rate	SDG	[2]	9.20[a]	10.31[a]
(g OM/min)	SLG		12.20[a]	5.42[b]
biting rate	SDG		56.13[a]	50.65[a]
(bites/min)	SLG		60.19[a]	55.10[a]
grazing time	SDG		10.67[a]	9.65[a]
(hrs/day)	SLG		9.84[a]	10.90[b]
forage intake	SDG		5.89	5.97
(kg OM/day)	SLG		7.20	3.54

[1]Means within years and dependent variables differ ($P \leq 0.05$) when followed by different letters.
[2]Ingestive behavior variables and forage intake were not measured in 1983.

1984 than in either 1983 or 1985 (Table 1). This may have been a reflection of compensatory gain resulting from a particularly hard winter and short feed supplies immediately before the 1984 grazing season. When comparing relative differences between treatments, a trend appears through the 3 years. While SLG provided greater ADG than SDG in late 1983, no differences were detected in 1984, and SDG was superior throughout 1985. There are 2 possible explanations for these responses. First, the effects of SDG on the vegetation may be cumulative over successive grazing seasons. Three years could possibly have been required for SDG to overcome its initial lower level of animal performance in 1983, and finally gain superiority by 1985. In this case, SDG would be the superior grazing method in terms of livestock production. Conclusions concerning such vegetation responses are yet to be determined from other components of the overall study of SDG. Second, grazing management in the SDG treatment was changed during 1985, from 3- to 2-day grazing periods in paddocks. Therefore, weight gains may have been higher in the SDG cell only in 1985 because animals were not forced to utilize poorer quality forage as defoliation progressed through the third day.

Gains per ha, calculated from seasonal mean weight gains, were initially greater under SLG, but subsequently greater under SDG in 1984 and 1985 (Table 1). Because there were no differences in stocking rates, individual weight gains are directly reflected in these production figures. However, increased growth does not automatically confer improved reproduction on young animals. In fact, pregnancy rates of heifers subjected to SDG were lower than for the heifers used in the SLG treatment during this study (3.6, 6.5, and 8.2 percentage units in 1983–1985, respectively) (Chuck Warner, pers. comm.). Reductions in conception rates or lifetime productivity of replacement heifers resulting from SDG would negate any benefit of increased growth. Although causes of these differences in reproductive performance have not yet been determined, the nutritional factors examined in this study were found to be adequate, and thus not the cause.

Diet Quality

Annual means for CP and IVOMD of diets between SDG and SLG were not significantly different in any of the 3 years (Table 2). Taylor et al. (1980) compared CP and IVOMD of livestock diets under SDG to that under high intensity-low frequency (HILF) and Merrill deferred-rotation grazing systems on west Texas native range. Both dietary CP and IVOMD were the same for SDG and Merrill grazing, but significantly less for HILF. Their results for SDG and their most extensive grazing system (Merrill deferred-rotation), which uses season-long grazing periods, are in agreement with our results.

Crude protein and IVOMD annual means were relatively uniform among years, and sufficiently high to provide adequate nutrition for heifer growth (i.e., the NRC (1976) CP requirement for 250 kg growing heifers to gain 1.1 kg/day is 11.4%). Apparently, animals were able to maintain adequate overall diet quality in both grazing teatments, although SDG may have altered the seasonal pattern of forage quality.

Significance of the method by date interaction term would suggest that the seasonality of diet quality was altered by SDG. Although the annual means were not different in 1984, method by date was significant for both CP and IVOMD (Table 3). Method by date was not significant for either variable in 1983 or 1985. In 1984, CP was the same under both SDG and SLG in period 1 and declined as the season progressed, as would be expected (Cook and Harris 1968). However, CP declined more rapidly in SLG than SDG, possibly indicating an extension of the season of nutritious

Table 3. Grazing method by period means for variables within years when the method by date interaction was significant ($P \leq 0.05$).

		period 1	period 2	period 3
		1984		
CP	SDG	17.93[a1]	13.55[b]	10.72[c]
(%)	SLG	19.84[a]	11.62[c]	11.34[c]
IVOMD	SDG	71.02[a]	67.25[b]	56.59[c]
(%)	SLG	77.96[d]	62.39[e]	53.17[f]
biting rate	SDG	64.01[a]	52.68[b]	51.69[b]
(bites/min)	SLG	59.73[a]	59.82[a]	60.73[a]
grazing time	SDG	10.18[a]	11.02[b]	10.81[ab]
(hrs/day)	SLG	8.69[c]	10.38[a]	10.45[a]
		1985		
grazing time	SDG	9.79[a]	9.50[a]	9.67[a]
(hrs/day)	SLG	10.69[b]	11.04[b]	10.98[b]

[1]Means within years and dependent variables differ ($P \leq 0.05$) when followed by different letters.

forage under SDG. This difference was short-lived, however, because it was eliminated by the end of the grazing season, as indicated by the lack of significant difference in period 3. IVOMD was higher under SLG than SDG in period 1, but it declined more rapidly by period 2, and was significantly less under SLG throughout periods 2 and 3. Again, this suggests an extension of the season of nutritious forage. Because years when growth of heifers differed among grazing methods (i.e. 1983 and 1985) did not correspond with years when the method by date interaction was significant (i.e. 1984), the differential gains are not explained by diet quality responses.

Ingestive Behavior and Daily Forage Intake

Annual mean ingestion rates were the same in both treatments in 1984, although they approached being significantly ($P<0.10$) greater under SLG than SDG (Table 2). Ingestion rates were significantly less under SLG in 1985 (Table 2). Ingestion rate can be considered a measure of foraging efficiency because it approximates intake of nutrients or energy per expenditure of time, with grazing time serving as an estimator of energy expenditure (Osuji 1974). Thus, animals foraged more efficiently under SDG during 1985. Method by date interactions were nonsignificant for ingestion rate during both years.

Annual mean biting rates did not differ among grazing methods in either year (Table 2). Method by date interaction was significant for biting rate in 1984 (Table 3), but not in 1985. While biting rates remained constant through the grazing season under SLG in 1984, they declined from period 1 to period 2 under SDG, and remained lower than SLG throughout periods 2 and 3. Biting rate is a component of ingestion rate, along with bite size (Freer 1981). Because of the lack of seasonal treatment differences in ingestion rate, this seasonal response of biting rate is of minor importance. It appears that animals in different treatments made adjustments in bite size to maintain equal ingestion rates as the season progressed.

Annual mean grazing time did not differ begween SDG and SLG in 1984, but was significantly greater under SLG in 1985 (Table 2). Method by date interaction was significant for grazing time in 1985 (Table 3), and approached significance in 1984 ($P=0.06$). In 1984, grazing time was significantly less under SLG at the beginning of the grazing season. As the grazing season progressed, grazing time increased under both grazing methods, but did so to a greater degree under SLG. By the third period, no difference was detected in grazing time. In 1985, the method by date interaction occurred because grazing time tended to decrease as the season progressed under SDG, while it tended to increase under SLG. However, grazing time was significantly less under SDG throughout all 3 periods of the grazing season.

Because of the selective nature of livestock grazing, variations in canopy structure, determined by plant species, stage of maturity, and prior grazing affect ingestive behavior (Chacon and Stobbs 1976). The main behavioral response of cattle to the changes in canopy structure caused by defoliation was a decrease in bite size (Chacon et al. 1976, Chacon Stobbs 1976). Biting rate and grazing time increased to compensate for this decline in bite size (Chacon and Stobbs 1976). Apparently, increased ingestion rate, as found under SDG in 1985, allows a concomitant decrease in grazing time, which agrees with Chacon and Stobbs (1976). Because biting rate annual means did not differ in this study, changes in ingestion rate directly reflect bite size. The result was that time, and thus energy, expended to graze was reduced by SDG in 1985. Walker et al. (1986) found that mean grazing time was an hour longer under continuous grazing than under SDG (10.9 vs. 9.8 hrs.). Their values are remarkably similar to our 1985 results.

Mean daily forage intake was a mathematical product of ingestion rate and grazing time (Table 2). Because ingestion rate and grazing time were determined on 2 different sets of animals, the mean for each variable was used. The product was 1 date point for each sample date, with no valid measure of variability around that data point. Therefore, statistical analyses on these data would be inappropriate. These calculated intake values range from 1.3 tc 2.6% OM of body weight. NRC (1976) recommendations for min imum DM intake, when converted to a percent of body weigh basis, range from 2.3 to 2.9% DM to obtain weight gains compara ble to those observed in this study. If calculated intake values ar converted to a DM basis, assuming an average OM content of 90% they range from 1.4 to 2.9% DM. Under these conditions, all value except intake under SLG in 1985 fall between 2.4 and 2.9% DM These values, that are very similar to expectations based on NRC (1976) requirements, lend credibility to these calculated values a estimates of daily forage intake.

It appears that forage intake was largely a function of ingestio rate, with the compensatory response of increasing grazing tim under SLG during 1985 having little effect on the decline in forag intake as ingestion rate declined. This agrees with conclusions o Stobbs and Hutton (1974) and Chacon and Stobbs (1976) that bit size is a better indicator of sward effects on intake than is grazin time.

The ingestive behavior and resultant forage intake response may explain the differences in animal performance (Tables 1 an 2). This is in contrast to the lack of differences in diet quality (Tabl 2). In 1985, animals under SDG appeared to forage more effi ciently, as evinced by a greater intake per unit time and less tim (energy) expended grazing to gain a higher total daily forag intake. Apparently, sward characteristics that determine ingestiv behavior can directly affect animal performance. Identifying thes sward attributes might make it possible to design grazing manage ment methods (SDG or others) to further improve animal perfor mance. These relationships have been explored, and the results ar presented in Olson et al. (1986).

Conclusions

In terms of animal performance, ADG was significantly greate under SLG during the latter half of 1983, no differences wer detected during 1984, and the SDG animals gained significantl more weight throughout 1985. However, it is not possible to con clude that a trend in favor of SDG was developing over the 3-yea period because there were several confounding factors, includin cumulative grazing management effects and changes in grazin management.

Diet quality was the same under both treatments throughout th study. However, ingestion rate was significantly greater and graz ing time was significantly lower under SDG in 1985, providin possible reasons for the differences in animal performance Because of the inconsistent method by period interaction results there is little indication that SDG alters the seasonal dynamics o diet quality and ingestive behavior responses. Therefore, th hypothesis that SDG extends the season of nutritious forage wa not supported.

Although SDG provided significant improvement in livestoc weight gain by the end of the study that may translate into eco nomic gain, caution should be exercised before SDG is widel recommended for crested wheatgrass ranges. Despite the apparen adequate plane of nutrition for animal growth found in this study pregnancy rates of heifers under SDG were 3.6 to 8.3 percentag units lower than heifers under SLG. Until causes for this differenc are understood and can be overcome, use of SDG with reproduc tive livestock cannot be recommended. If it is assumed that th difference in animal growth can be maintained over time, the SDG may be a promising method for use with stocker cattle.

Livestock response appears to be very sensitive to the rapi changes in sward conditions as SDG paddocks are defoliated, a indicated by the increased performance in 1985 when the grazin period was a day shorter. This indicates that proper rate of rotatio through paddocks is critical to successful maintenance or improve ment of livestock performance. A subsequent paper will discus daily changes in animal nutrition as paddocks were defoliated i this study. Further research to enlighten the mechanisms of plant animal interaction will be fruitful in improving SDG management, as well as grazing management in general.

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Herbage dynamics of tallgrass prairie under short duration grazing

J.E. BRUMMER, R.L. GILLEN, AND F.T. MCCOLLUM

Abstract

Simulated 8-pasture short duration grazing systems were studied in 1985–86 to determine the effect of timing and intensity of grazing on seasonal herbage dynamics. Treatments consisted of 3 grazing schedules (2, 3, or 4 rotation cycles per 152 day grazing season) and 2 stocking rates (1.3X and 1.8X the recommended normal). Average seasonal standing crop increased from 4-cycle to 2-cycle grazing at the light stocking rate but did not respond to grazing schedule at the heavy stocking rate. Within the grazing season, herbage standing crop was affected by grazing schedule in late summer in 1985 but not in 1986. Favorable growing conditions resulted in light forage utilization which averaged 30% over all treatments. Net herbage accumulation rates were not affected by any experimental factor and averaged 34 kg ha^{-1} d^{-1} over all treatments. Time trends for net herbage accumulation rate from May to September were also similar across treatments. Total herbage disappearance and herbage disappearance per animal-unit-day (AUD) were significantly higher under 4-cycle grazing at the heavier stocking rate than under all other treatments.

Key Words: herbage accumulation, herbage disappearance, rotation grazing, stocking rate

Short duration grazing (SDG) is a multi-pasture, one-herd grazing system that involves rapid rotation of livestock. Proper implementation of SDG on rangeland has been reported to allow large increases in stocking rates (Savory 1978).

Stocking rates may be increased if SDG brings about an increase in herbage production (Heitschmidt et al. 1982b). Short duration grazing has been observed to increase herbage production relative to ungrazed areas (Heitschmidt et al. 1982a) and continuous grazing (Jung et al. 1985). Tainton et al. (1977) observed a trend of increased herbage production as the grazing period decreased and the rest period increased. However, Ralphs et al. (1984) found that herbage production was not affected under 4 stocking rates on a SDG system. Because of these inconsistent results, more work is needed on the factors that affect herbage production under SDG before increased stocking rates are advocated based on increased herbage production alone.

Stocking rates can also be increased if SDG increases harvest efficiency by the grazing animal (Heitschmidt et al. 1982b). Harvest efficiency has been shown to increase under SDG as stocking rates increased (Ralphs et al. 1984). Harvest efficiency is directly related to grazing pressure in that as grazing pressure increases, harvest efficiency increases (Stuth et al. 1981, Allison et al. 1982). However, grazing pressure is continuously changing during the growing season and adjustments must be made in stocking rate, stocking density, and/or the length of the grazing period to maintain optimum herbage allowances for increased harvest efficiency (Stuth et al. 1981). Because stocking rates, stocking density, and the length of the graze/rest periods can be adjusted, the grazing pressure in a SDG system can be more precisely controlled than in any other grazing system (Heitschmidt 1984). Thus, increased harvest efficiency is probably the principal factor by which stocking rates can be increased under SDG (Heitschmidt et al. 1982b, Walker 1984).

Authors are former graduate research assistant and assistant professor, Agronomy Department, and assistant professor, Animal Science Department, Oklahoma State University, Stillwater 74078. Brummer is currently range research coordinator, West Central Research and Extension Center, Route 4, Box 46A, North Platte, Neb. 69101.

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The objective of this study was to determine short-term vegetation responses of tallgrass prairie to short duration grazing. The test hypothesis was that herbage standing crop, net herbage accumulation rate, and herbage disappearance would not be affected by speed of rotation or stocking rate.

Study Area

The study area was located on the Oklahoma State University Range Research Area approximately 21 km southwest of Stillwater, Oklahoma. The climate is continental with an average frost-free growing period of 204 days extending from April to October. Average precipitation at Stillwater is 831 mm with 65% falling as rain from May to October. Mean temperature is 15° C with average minimum and maximum temperatures ranging from –4.3° C in January to 34° C in August (Myers 1982).

The soils found on the area are primarily the Grainola and Coyle series, comprising approximately 60 and 35% of the area, respectively. The Grainola series has a loam surface and silty clay loam subsoil and is a member of the fine, mixed, thermic family of Vertic Haplustalfs. The Coyle series has a fine sandy loam surface and sandy clay loam subsoil and is a member of the fine-loamy, siliceous, thermic family of Udic Argiustolls. Range site classification of the Grainola soil is shallow prairie while the Coyle soil is loamy prairie.

The study area was established in 1984 on native tallgrass prairie. The area was dominated by big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), and switchgrass (*Panicum virgatum* L.), each comprising approximately 18% of the vegetation by weight in August 1984. Other important species included indiangrass (*Sorghastrum nutans* (L.) Nash), tall dropseed (*Sporobolus asper* (Michx.) Kunth), and western ragweed (*Ambrosia psilostachya* DC.).

Methods

Three grazing schedule (GRSC) treatments under 2 stocking rates (STRT) were investigated. Grazing schedule treatments were based on the number of complete grazing cycles (2, 3, or 4) in an 8 pasture rotation that could be completed during a 152-day spring-summer grazing season. Within treatments, shorter graze/rest periods were used at the beginning of the grazing season when the vegetation was in a rapid growth stage and were gradually lengthened during the season as the vegetation matured (Table 1). Each

Table 1. Days of grazing and rest per cycle for the 3 grazing schedule treatments.

Grazing schedule	Cycle 1		Cycle 2		Cycle 3		Cycle 4		Mean	
	DG[1]	DR[2]	DG	DR	DG	DR	DG	DR	DG	DR
2-cycle	6	42	13	91	–	–	–	–	10	67
3-cycle	4	28	6	42	9	63	–	–	6	44
4-cycle	3	21	4	28	5	35	7	49	5	33

[1]DG = Days of grazing per cycle.
[2]DG = Days of rest per cycle.

treatment pasture received 19 total days of grazing. Grazing began on 1 May and 19 April in 1985 and 1986, respectively. All pastures were burned approximately 2 weeks before the starting dates in both years.

Stocking rate treatments were set at 1.3 (light) and 1.8 (heavy) times the Soil Conservation Service recommended rate for the range sites under study. Three animals were grazed on 0.40-ha pastures to obtain the light stocking rate while 5 animals were grazed on 0.48-ha pastures to obtain the heavy stocking rate. Stocker steers and heifers with a starting weight of approximately 275 kg were used. Stocking rates averaged 110 AUD ha^{-1} for the light rate and 154 AUD ha^{-1} for the heavy rate.

Treatments were applied using a simulated 8-pasture SDG system. Pasture number 4 in the rotation was used to determine the mean system effect. Grazing treatments were arranged factorially in a randomized complete block design with 3 replications. Each block also contained an ungrazed control pasture 0.20 ha in size.

Total herbage standing crop measurements were taken before and after each grazing period in a given pasture. The before and after sampling dates, however, did not fall on the same dates for all grazing schedule treatments because of differences in the length of the graze/rest periods. To allow direct comparison between treatments, all pastures were sampled on 5 additional dates. These dates were on 1 May, 9 June, 16 July, 22 August, and 28 September in 1985; and 19 April, 29 May, 3 July, 13 August, and 17 September in 1986.

Current year's standing crop, both live and dead, was sampled by clipping 0.1-m^2 plots to ground level. Fifteen random samples were taken per pasture on each sampling date. In addition, 10 cages were placed in each pasture just prior to a grazing period. At the end of each grazing period, standing crop was sampled under the cages using 0.1 m^2 plots. Herbage samples were bagged and dried in a forced-air oven to a constant weight.

Net herbage accumulation rate was calculated for each rest period by subtracting the standing crop at the beginning of the rest period from the standing crop at the end of the rest period and then dividing by the number of days in the period. Net accumulation rates were then weighted by the number of days in the rest period and averaged to arrive at an average net herbage accumulation rate for each treatment.

Herbage disappearance was calculated for each grazing period by subtracting the uncaged standing crop from the caged standing crop at the end of the grazing period. Total herbage disappearance was then calculated for each treatment by summing the disappearance for each grazing period within that treatment. Herbage disappearance was also expressed on an animal-unit-day (AUD) basis by dividing total herbage disappearance by the total number of AUD ha^{-1} for each treatment.

All data were analyzed using analysis of variance techniques for a randomized complete block design with repeated measures. Grazing schedule and stocking rate were whole plot factors while year and sample date were repeated factors. Least significant differences (LSD) for interaction means were calculated with $\alpha = .05$. Statistical procedures followed the methods of Milliken and Johnson (1984).

Results and Discussion

Precipitation for the period of November 1984 to October 1985 was 51% above normal. However, July and August rainfall amounts were about average, so that, as normal for this region, a period of unfavorable growth conditions occurred from August to mid-September. November 1985 through September 1986 precipitation was 24% above average. Precipitation through July was about average but August–September precipitation was over twice normal resulting in excellent late-summer growing conditions.

Herbage Standing Crop

Grazing schedule and stocking rate interacted to affect average herbage standing crop (Table 2). Standing crop increased as rest periods lengthened at the light stocking rate. Standing crop did not respond to grazing schedule at the heavy stocking rate.

Table 2. Herbage standing crop (kg ha^{-1}, averaged over year and sample date) and net herbage accumulation rate (kg ha^{-1} d^{-1}, averaged over year) as affected by the interaction of grazing schedule and stocking rate.

Grazing schedule	Herbage standing crop: Stocking rate — Light	Heavy	Accumulation rate: Stocking rate — Light	Heavy
2-cycle	3490	2820	35	33
3-cycle	3230	3180	37	35
4-cycle	2980	2980	31	35
$LSD_{.05}$	390		NS	

Herbage standing crop was affected by the interaction of grazing schedule and sample date in 1985 (Fig. 1). There were no significant differences in standing crop between grazing schedules on any date

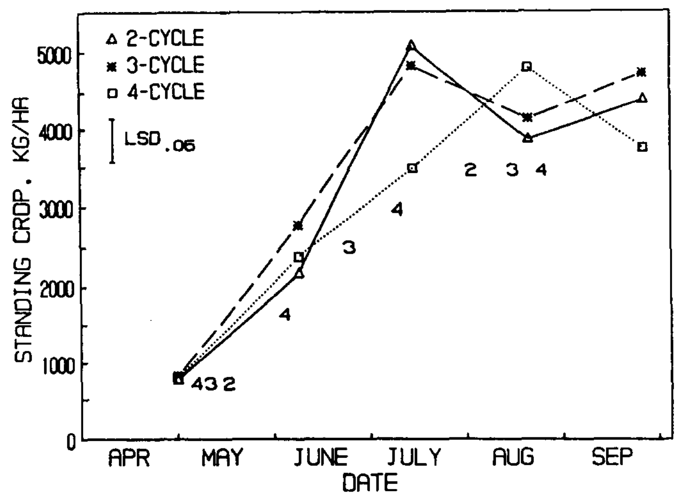

Fig. 1. *Herbage standing crop for 3 grazing schedules in 1985. The LSD refers to grazing schedule comparisons within sample dates. Numbers below graphs indicate the occurrence of grazing periods for the 2, 3, or 4-cycle grazing schedules.*

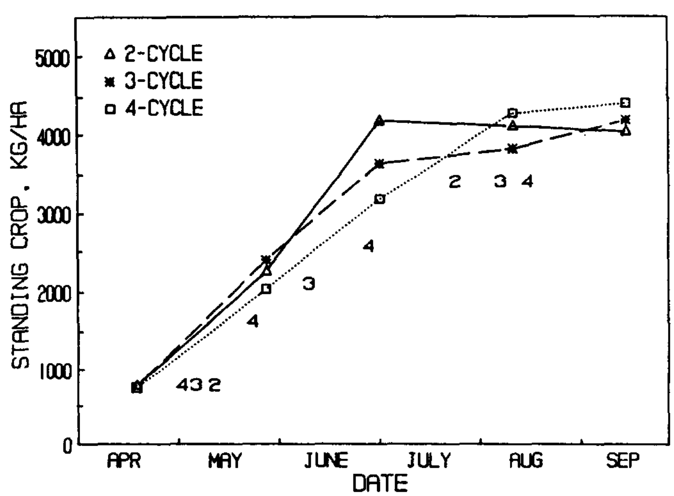

Fig. 2. *Herbage standing crop for 3 grazing schedules in 1986. There were no significant differences (P=.05) between grazing schedules. Numbers below graphs indicate the occurrence of grazing periods for the 2, 3, or 4 cycle grazing schedules.*

in 1986 (Fig. 2). Possible reasons for the different response patterns between years in late summer are not clear but may be related to unfavorable growing conditions during this period in 1985 compared to favorable growing conditions in 1986. The occurrence of peak standing crop was delayed in the 4-cycle treatment both years, probably as a result of the more frequent early grazings under this treatment. By the third sample date, the 4-cycle treatment had been grazed 3 times for a total of 12 grazing days. The 2-cycle and 3-cycle treatments had been grazed once for 6 total days and twice for 10 total days, respectively, by the same date. This pattern is not an inherent characteristic of the grazing schedules but is a result of sampling the fourth pasture in an 8 pasture rotation. Grazing schedule will not affect the balance of grazing days between early and late summer when the entire rotation system is considered.

Utilizaton, based on final standing crops in grazed treatments and ungrazed control pastures, was generally low because of above average overall growing conditions in both years. Utilization averaged 30% over all grazing schedules and 26% vs. 34% under light and heavy stocking rates.

Net Herbage Accumulation Rate

Net herbage accumulation rates (NHAR) were not significantly affected by any experimental factor (Table 2). NHAR averaged 34 kg ha^{-1} d^{-1} over all grazed treatments and 35 kg ha^{-1} d^{-1} in ungrazed controls. Trends in NHAR over time were similar among treatments and years. NHAR averaged 60 kg ha^{-1} d^{-1} in early May and declined linearly to 5 kg ha^{-1} d^{-1} in late August-early September.

Herbage Disappearance

Total herbage disappearance was significantly affected by the interaction of grazing schedule and year (Table 3). Differences were only significant in the 4-cycle treatment in 1986. We believe these interactions are a product of the 4-cycle, light stocking rate treatment. Total disappearance in this treatment went from 1,070 kg ha^{-1} in 1985 to 3,090 kg ha^{-1} in 1986, a 190% increase. All other treatments increased an average of 23% from 1985 to 1986. Evaluation of raw data indicated abnormally low disappearance values for 2 grazing periods in the 4-cycle, light treatment for 1985 which can not be easily explained. Thus, there is an indication of increased herbage disappearance under the 4-cycle grazing schedule. Total herbage disappearance was increased under the heavy stocking rate compared to the light stocking rate (2,950 vs. 2,000 kg ha^{-1}, respectively; $P = .03$).

Table 3. Total herbage disappearance (kg ha^{-1}) and herbage disappearance per animal-unit-day (kg AUD^{-1}) as affected by the interaction of grazing schedule and year.

Grazing schedule	Total disappearance Year 1985	Total disappearance Year 1986	Disappearance per AUD Year 1985	Disappearance per AUD Year 1986
2-cycle	1900	2370	15	18
3-cycle	2170	2310	17	17
4-cycle	2190	3890	16	29
$LSD_{.05}$	1490		NS	

Results for herbage disappearance per AUD were similar to those for total disappearance (Table 3). The indication of increased herbage disappearance under the 4-cycle grazing schedule is still present. Expressing disappearance on an AUD basis removed the main effect of stocking rate.

Ralphs et al. (1984) reported that total herbage disappearance was similar between stocking rate treatments under simulated SDG. Therefore, as stocking rate increased, disappearance per AUD decreased and harvest efficiency apparently increased (Ralphs et al. 1984). Allison et al. (1982) found that as grazing pressure went from 50 to 10 kg of herbage AUD^{-1} herbage disappearance decreased from 16.3 to 8.5 kg AUD^{-1} and harvest efficiency increased from 53 to 99%, respectively. Grazing pressure on this study ranged from 135 kg AUD^{-1} on the 4-cycle light treatment to 30 kg of herbage AUD^{-1} on the 2-cycle heavy treatment with an average across all treatments of 70 kg of herbage AUD^{-1}. Grazing pressures may have been too low for increased stocking rate to affect herbage disappearance AUD^{-1} in this study.

Summary

Grazing schedule had limited and inconsistent effects on short-term herbage dynamics of tallgrass prairie. This response pattern may be partly attributed to above-average growing conditions which resulted in relatively low utilization levels. Under seasonal grazing, the observed utilization rates would certainly fall below recommended allowable levels. Under yearlong grazing where herbage must be conserved for dormant-season use, the observed growing-season utilization rates would be closer to recommended levels for moderate grazing. Under the conditions studied, grazing schedule caused differences in herbage standing crop on some sampling dates but average seasonal standing crop only responded to grazing schedule at the lighter stocking rate. Grazing schedule or stocking rate did not affect net herbage accumulation rate. There was some indication that shorter grazing cycles increased herbage disappearance per AUD. However, it is not known if this increased disappearance was a result of greater herbage intake or greater nonconsumptive herbage losses. While higher stocking rates caused greater total herbage disappearance, herbage disappearance per AUD was not generally affected by stocking rate.

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Technical Notes

A mapping table for obtaining plant population data

JEANNE C. CHAMBERS AND RAY W. BROWN

Abstract

The construction and use of an acrylic mapping table for obtaining basic demographic information from plant populations is described. The table permits accurate and precise location of mapping quadrats and study plants from acetate "maps."

Key Words: plant demography, recruitment, survival, mortality, mapping quadrat

Researchers and managers alike are placing greater emphasis on understanding the life history characteristics of plants. Basic demographic data, including patterns of recruitment, reproduction, and survival, are central to understanding plant population dynamics. Such information, in combination with the proper correlative data, allows prediction of changes in plant populations in response to environment, competition, herbivory, or other factors (Schall 1984). Applied uses of these data are many and varied. For example, acquiring detailed life history information on rare and endangered plants can help managers devise strategies for insuring their preservation.

Mapping tables are routinely used for collecting plant demographic data (Moore and Chapman 1986, Mack and Pyke 1983, Mack and Harper 1977), but seldom is detailed methodology presented. We describe the construction and use of an acrylic mapping table designed for obtaining basic demographic information from plant populations. Our primary objective was to design and construct a table that would allow accurate and precise relocation of mapping quadrats and plants using acetate sheets as "maps." The table differs slightly from others that have been described: (1) It was designed so that permanent mapping quadrats were relocated from the positions of permanent corner stakes marked on acetate sheets, rather than from fitting table legs over permanently set stakes. This eliminates the necessity of precise stake locations which is often impossible in rocky soils. (2) The table was built with easy-to-adjust legs so that its surface could be quickly leveled on uneven ground. This is a mapping table requirement, as the angle of viewing influences the ability to exactly relocate objects on the ground. (3) The table was constructed from light-weight, but extremely durable materials. A mapping table should be portable but sturdy enough to support a mapper leaning upon it and stable enough not to move during mapping. (4) The spotting device included 2 sets of "cross-hairs" to facilitate accurate location of permanent stakes and plants.

Authors are range scientist and research forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, 860 N. 1200 E., Logan, Utah 84322-8000.

The use of trade or firm names in this paper is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

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Mapping Table Construction

Our mapping table consisted of a sheet of 60 × 60-cm Plexiglas acrylic, 1-cm thick, mounted on 2 pieces of solid aluminum bar (2.5 × 1 cm × 60 cm) with attached leg supports (Fig. 1). The dimensions of the mapping table can be adjusted to accommodate the desired mapping quadrat size, but the acrylic thickness should be at least 1 cm to provide the desired rigidity. The aluminum bars were attached to opposing sides of the acrylic with counter-sunk bolts to provide a smooth table surface. To facilitate placement of the bolts, holes were drilled into the acrylic, and matching holes were threaded into the aluminum bars. Leg supports, consisting of 7.5-cm lengths of square aluminum tubing (2.5 × 2.5 cm with a 2.0-cm bore), were welded vertically onto each end of the aluminum bars. A small triangular brace made from a piece of aluminum bar was then welded between the tubing and the aluminum bars supporting the table to provide added strength. Wing-nut bolts mounted on the leg supports were used to position the legs at the desired height. Small pieces of aluminum bar, 2.5 cm^2, were affixed to the leg supports as reinforcement for the wing-nut bolts. Holes for the bolts were then threaded through both the wing-nut base and the tubing of the leg support. The legs were 75-cm lengths of solid aluminum rod, 2 cm in diameter. To provide increased stability for the table, circular aluminum plates 8 cm in diameter were cut from 3-mm sheet aluminum and welded onto the legs.

A small carpenter's level with 2 bubbles at right angles to each other was mounted on the lower right-hand corner of the table surface for leveling. A mapping quadrat (20 × 50 cm) was then

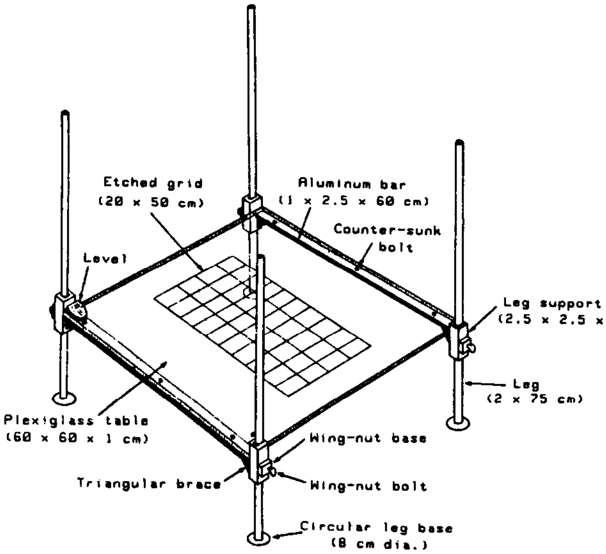

Fig. 1. *Detail of mapping table.*

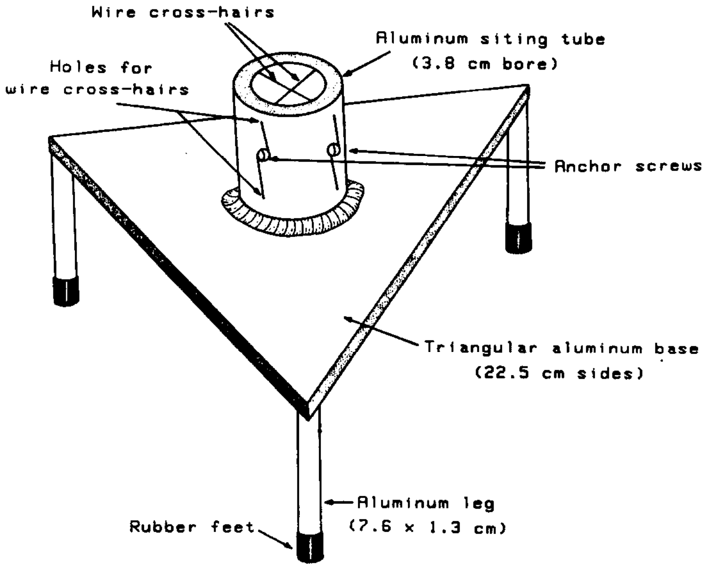

Fig. 2. *Spotting device for alignment of stakes and plants.*

Fig. 3. *Researcher use of the mapping table in the field.*

etched onto the bottom surface of the acrylic with a diamond stylus. The mapping quadrat was gridded using a 5-cm spacing to facilitate searching for plants.

A spotting device was constructed to enable precise relocation of stakes marking the mapping area and plants (Fig. 2). The eye piece was a section of 5.4-cm diameter aluminum pipe (3.8-cm bore), 5.5-cm long, welded to a triangular base. Two sets of wire "cross-hairs" were mounted in the eye piece, each 4-cm apart vertically. Each set consisted of 4 holes (0.51 mm) drilled into the pipe at right angles from one another. Wire (chrome, 0.40 mm) was threaded through the holes and fastened in place with anchor screws. The base was constructed from a 0.5-cm aluminum sheet that measured 22.5 cm on each side, and that had a 3.8-cm hole drilled in the center for alignment with the pipe. The 3 legs were 1.3-cm aluminum pipe, 7.6-cm long, welded to the 3 corners of the triangular base. Rubber feet were fitted over the bottoms of the legs to prevent scratching of the table surface or acetate maps.

Mapping Table Use

Repeated mapping of individual plants requires placing the table over permanent mapping area locations (Fig. 3). Mapping area locations were marked on the ground with three metal stakes, 1 cm in diameter and 45 cm long, placed at 3 corners of the mapping area. Stakes were placed 5 cm outside of the mapping quadrat boundaries to minimize interference with the plant population. A template was used to insure accurate locations of stakes. Stakes were driven into the ground so that about 5 cm extended above the soil surface. We used metal "rebar" (concrete reinforcing rod) as it resists movement due to frost action when driven 35 to 40 cm into the soil, can be driven into rocky soils, and provides inexpensive, permanent stakes. However, aluminum welding rod (3-mm dia.) will also resist frost heave, will not corrode and release undesirable metal compounds into the soil, and is probably a better choice. Metal stakes can be relocated with a metal detector in dense vegetation.

Acetate sheets taped to the mapping table surface were used to relocate mapping areas and to census populations within the mapping quadrats. The acetate sheets were cut large enough to include both the area of the mapping quadrat and the permanent stakes. The 4 corners of the mapping quadrat (not the stakes) were marked on the acetate sheets, and the acetate sheets were taped over the mapping quadrat that was etched on the table.

Relocation of the mapping quadrat was solely dependent upon accurate positioning of the mapping table over the 3 permanent stakes delineating the mapping area. To insure exact positioning, the corners of the mapping table were adjusted using the carpenter's level so that the table surface was horizontally level. The exact positions of the stakes delineating the mapping area were then located by aligning the 2 sets of "cross-hair" wires of the spotting device on the stakes. For the first mapping, the positions of the stakes were marked on the acetate sheets with permanent-ink marker pens. While looking through the spotting device and aligning both "cross-hair" wires on the stakes, the mapper reached under the spotting device and outlined the top of the stakes with the marking pen. During subsequent mappings, previously mapped acetate sheets were repositioned on the table, and the table was then moved until stake positions marked on the acetate sheets were exactly aligned with stakes in the ground and with the 2 sets of "cross-hair" wires on the spotting device.

Once the mapping table was accurately located over the mapping quadrat, plant populations were censused. This involved first locating an individual and then aligning its base exactly with the 2 sets of "cross-hair" wires on the spotting device. While looking through the spotting device, a plant's location and status (i.e., new introduction, dead, reproducing, etc.) were recorded on the acetate sheets by reaching under the spotting device with a marking pen and drawing the appropriate symbol. Different colors of marking pens and different symbols were used to record population data, and to differentiate sample dates and species.

Two different mappers used tables of this design to monitor 115 permanent quadrats 8 to 16 times during 2 growing seasons. Once a mapper became proficient with the use of the mapping table and spotting device, set-up time was minimal. The first time a quadrat was mapped, it required about 8 to 10 min to locate and drive the permanent stakes and to set up the mapping table. Subsequent mappings required 3 to 5-min set-up time. Acetate maps of the various quadrats were assessed interchangeably by the 2 mappers over the 2 years. Plants were almost always accurately marked and, therefore, easily relocated by either mapper. Errors arose only if (1) the table shifted or became unlevel during mapping, or (2) the mapper had not exactly aligned the plant with the 2 sets of "cross-hairs" during the first mapping. These errors were negligible as the mappers became more experienced.

The mapping table is limited to fairly low-growing vegetation or during the early phases of seedling establishment on disturbed or open areas. We used the mapping table in an alpine ecosystem to record seedling survival under a variety of treatments. Seedling establishment within dense vegetation and beneath mulch was determined by reaching under the table and gently spreading the vegetation or lifting the mulch with a metal chaining stake. The mapping table could be used for recording other vegetation characteristics, including aerial or basal cover, vegetative establishment via rhizomes or stolons, and phenology. In addition, the table could be used for detailed mapping of soil surface characteristics such as cryptogamic crusts.

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An inexpensive alternative esophageal cannula for growing steers and wethers

M.L. NELSON

Abstract

A method for manufacturing esophageal cannulas from plastic tee couplers of suitable size for growing steers and wethers is described.

Key Words: cannula, measurements

The plethora of recent papers that described esophageal cannulas is indicative of the difficulty in preparing and maintaining fistulated cattle and sheep. Many authors have discussed esophageal irritation, 'pouching', 'esophageal depression', 'pocketing', pressure necrosis, and the accumulation of granulated tissue due to heavy or permanent esophageal cannulas (Van Dyne and Torell 1964, Osbourn and Bredon 1971, Denney 1981, Forwood et al. 1985, Walker et al. 1985, Grunwaldt and Sosa 1986). Furthermore, some manufactured cannulas are too large to fit the esophageal lumen of growing steers and wethers. If cannula are too large, esophageal occlusion or expansion of the esophagus around the fistula is likely. This paper describes the manufacture of lightweight flexible split-tee cannulas of suitable dimensions for growing steers and wethers.

Material and Methods

Flexible, plastic, split tee cannulas were manufactured from

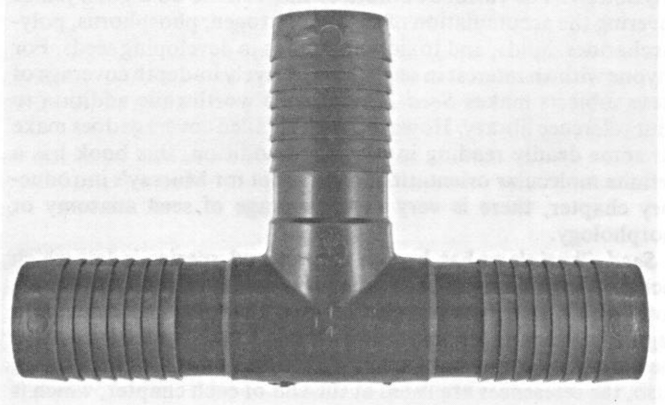

Fig. 1. *3.2-cm plastic tee coupler used to manufacture esophageal cannulas for steers.*

plastic tee couplers (Fig. 1). Tee-couplers were cut (Fig. 2) similar to Walker et al. (1985) and filed or sanded smooth to form esophageal cannulas (Fig. 3). Stoppers were made from wooden dowels and covered with nontoxic enamel paint or lacquer. A completed cannula could be made in about 1 h.

Results and Discussion

Three sizes of plastic split-tee cannulas were manufactured. For 250-kg steers, 3.2 cm plastic tee coupler was used to manufacture

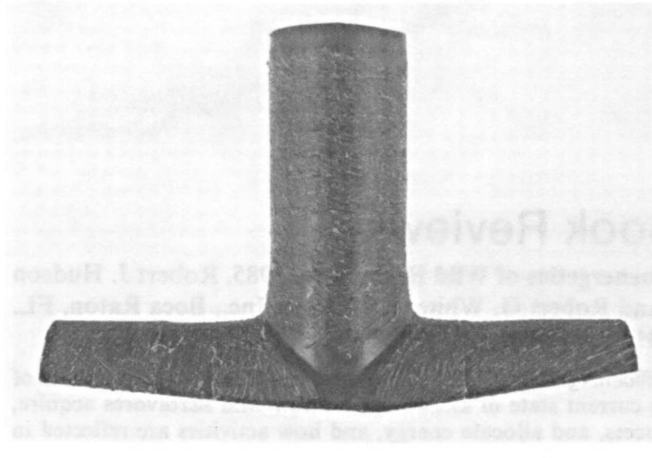

Fig. 2. *3.2 cm plastic tee coupler partially shaped into an esophageal cannula.*

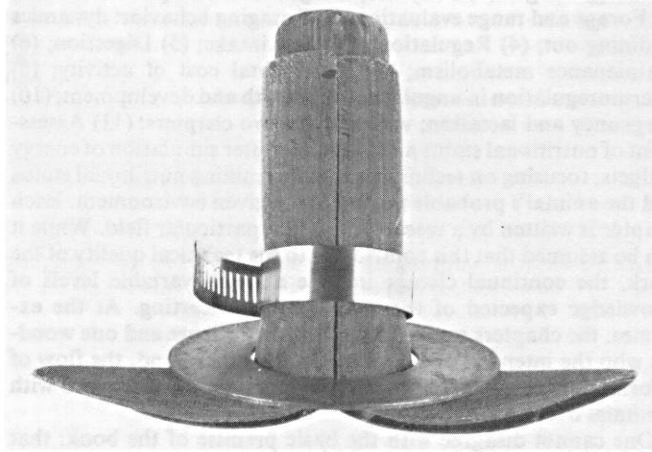

Fig. 3. *Plastic split-tee esophageal cannula for steers manufactured from 3.2 cm plastic tee coupler.*

cannulas with 3.5 × 14-cm blades with 3.3-cm plug diameters. These cannulas weighed 50% less than polyvinyl chloride cannulas (Walker et al. 1985) and only 11% greater than the stainless steel[1] sleeve type cannulas for cattle (Osbourn and Bredon 1971). For 25-kg wethers, 1.9-cm tee couplers were used to make cannulas with 1.5 × 8.5-cm blades with 1.5-cm plug diameters. For 50-kg wethers, 2.5-cm tee couplers were used to make cannulas with 2.5 × 9.0-cm blades with 2.5-cm plug diameters. The cannulas for wethers weighed 65% less and only 6% greater than stainless steel sleeve type cannulas for 1.5-cm and 0.25-cm diameter cannulas, respectively.

Van Dyne and Torell (1964) reported greater survival rate of fistulated animals due to more efficient cannulas. Further, Forwood et al. (1985) indicated that heavy metal cannulas caused esophageal depression and irritation. Therefore, cannulas should be low maintenance, light weight, easily manufactured from readily available materials, of proper size for the animal, and of a design

Author is assistant professor, Department of Animal Sciences, Washington State University, Pullman 99164. Scientific paper No. 7685, College of Agriculture and Home Economics Research Center, Project No. 0713.
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[1]Precision Machine Co., Inc., 2933 N 36th, Lincoln, NE 68504.

to minimize esophageal blockage, depression and cannula loss. The plastic, split-tee cannulas described herein meet these requirements.

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Book Reviews

Bioenergetics of Wild Herbivores. 1985. Robert J. Hudson and Robert G. White. CRC Press Inc., Boca Raton, FL. 314 p. $169.00 US/194.00 Outside US.

Bioenergetics of Wild Herbivores is a comprehensive review of the current state of knowledge on how wild herbivores acquire, process, and allocate energy, and how activities are reflected in their morphology, habitat selection, and behavior. The chapters are arranged as a sequential examination of each major element of an energy budget: (1) Body size, energetics and adaptive radiation; (2) Forage and range evaluation; (3) Foraging behavior: dynamics of dining out; (4) Regulation of forage intake; (5) Digestion; (6) Maintenance metabolism; (7) Incremental cost of activity; (8) Thermoregulation in ungulates; (9) Growth and development; (10) Pregnancy and lactation; with the last two chapters, (11) Assessment of nutritional status and (12) Computer simulation of energy budgets, focusing on techniques for determining nutritional status and the animal's probable response to a given environment. Each chapter is written by a researcher in that particular field. While it can be assumed that this contributes to the technical quality of the work, the continual change in tone and the variable levels of knowledge expected of the reader is disconcerting. At the extremes, the chapters range from chatty to abstruse and one wonders who the intended audience is. On the other hand, the flow of information within and between chapters is tightly organized with minimial overlap.

One cannot disagree with the basic premise of the book: that energy is the basic currency of ecosystems as well as individual organisms and that to understand how organisms capture and use energy is to go a long way in understanding how entire systems operate and how they can be managed. The authors have created an excellent entree into a voluminous body of literature. However, this is not casual reading. The reader is assumed to have a strong background in systematics, physiology, and mathematics. Apparently aimed at the researcher or advanced student, this book offers little of immediate use to the wildlife manager, and the advanced student or researcher would no doubt need to turn to the primary sources. One of the strongest features is the number of summary tables and figures, complete with references. The figures would be more useful, however, if they were labeled sufficiently to stand alone from the text.

The real disappointment is the lack of a summary chapter. Although the model presented in chapter 12 might be considered a synthesis of the preceding material, it really does not put the book into final focus. In the foreword, Prof. Reinhold Hofmann states that "...we are far from the final truth." A satisfying summary for this book would be some assessment of how far from the final truth we are, or how much closer this book has brought us, or at least, what needs to be done to close in on that truth.—**Linda Howell Hardesty,** Pullman, WA.

Seed Physiology Volume 1. Development. 1984. David R. Murray (Ed). Academic Press, Inc., Orlando, Florida 32887. 279 p. $54.50. Hard cover.

If you are interested in a good comprehensive update of the literature concerned mostly with the important storage molecules found in seeds, then I recommend purchasing Vol. 1 of *Seed Physiology*. The various authors of this volume do a good job of covering the accumulation of carbon, nitrogen, phosphorus, polysaccharides, lipids, and toxic compounds in developing seeds. For anyone with an interest in seeds, the relatively in-depth coverage of these subjects makes *Seed Physiology* a worthwhile addition to your reference library. However, such detailed coverage does make for some deadly reading in places. In addition, this book has a definite molecular orientation; and except for Murray's introductory chapter, there is very little coverage of seed anatomy or morphology.

Seed Physiology has both a subject and species index which includes both common and scientific names. Cross referencing both within and between the various chapters and even, to a degree, between volumes is relatively good. Good indexes improve the usefulness of any book and indicate the editor is doing his job. Also, the references are listed at the end of each chapter, which is preferable for a book of this type.

As with any book of this type, the continuity suffers somewhat from each chapter's having a different author. This fault is most evident in the treatment of future directions for research in the various chapters. For example, Bell's chapter on toxic compounds has an excellent section on suggestions for future research, whereas Matheson in his chapter on seed polysaccharides barely even mentions the subject. And, although J.S. Pate's chapter on nitrogen and carbon accumulation is well written and has good whole plant illustrations of the processes involved, he also makes seven references to unpublished data, which is somewhat disconcerting. In summary, although not without inconsistencies, the general quality of writing is consistently good throughout *Seed Physiology* and makes this book worthy of inclusion in any good reference library on seeds.—**Thomas L. Noland,** Pullman, WA.

Seed Physiology Volume 2. Germination and Reserve Mobilization. 1984. David R. Murray. (Ed). Academic Press, Inc., Orlando, Florida 32887. 295 p. $54.50. Hard cover.

Volume 2 of *Seed Physiology* attempts to cover dormancy and the processes of germination and mobilization of the major storage compounds, including nitrogen, phosphorus, lipids, and polysaccharides. Unfortunately, because of the erratic quality of various chapters in this book, good coverage of these topics is not always attained. The editor, however, has again done an admirable job of providing good indexes and encouraging good cross referencing.

Two of the better chapters of this book are "Structural aspects of dormancy" by Tran and Cavanaugh and "Mobilization of oil and wax reserves" by Trelease and Doman. Both chapters provide comprehensive coverage of their respective subjects. Tran and Cavanaugh provide a particularly detailed description, including SEMs and micrographs, of the various structures involved in dormancy of legume seeds. They also provide a good critical summary of the relative contribution the seed coat has to dormancy in other species and the various treatments used to alleviate this condition. The only questionable part of this chapter is: Why was it included in the book entitled *Seed Physiology?* Trelease and Doman provide the reader with useful and relatively comprehensive tables on both the liquid content of most commonly used oil seeds and the percent contribution of individual fatty acids to the lipid content. In addition, the authors present a good summary of the biochemical pathways involved in lipid mobilization and information on breakdown of wax esters. Finally, the authors finish their respective chapters with good summaries of the subject which include relevant suggestions for future research.

Two of the weaker chapters of *Seed Physiology* are Simon's chapter on "Early events in germination" and Ross' chapter on "Metabolic aspects of dormancy." In presenting the two hypotheses on leakage of solutes from seeds during imbibition, Simon defines them in peculiarly black-and-white fashion. Under the membrane rupture hypothesis he describes the solute leakage as a rapid process releasing nearly 100% of the solutes from the cell. Simon then describes solute leakage in the membrane repair hypothesis as a slow process releasing up to half the potassium present. However, these descriptions do not account for the possibility that partial membrane rupture could occur, allowing rapid release of some solutes and that subsequent membrane repair might cause a slowly decreasing rate of solute leakage. To Simon's credit, he does discuss the relative lack of plant data supporting his membrane repair hypothesis of solute leakage. However, the lack of a critical experiment to support the tenets of this thirteen-year-old hypothesis is particularly damning. Ross' chapter on "Metablic aspects of dormancy" is another weak chapter. Part of the problem with this chapter is the lack of coverage of the most current literature, as the latest citation is 1982 in a book that contains citations as recent as 1983 and 1984 in most chapters. For example, Ross only discusses De Klerk and Linskens' 1979 paper on differences in protein bands between dormant and after-ripened *Agrostemma* embryos and fails to mention three other important papers on the same subject published by De Klerk in 1981 and 1982. Another problem of this chapter is that it shows little imagination in suggesting new research directions.

In summary, some chapters of Volume 2 of *Seed Physiology* are worth reading but others are just a rehash of old work with little insight into the current research directions of the field. Unless you are particularly interested in the subjects of the better written chapters, you will probably be better off borrowing the library's copy of this book.—**Thomas L. Noland,** Pullman, WA.

The Background of Ecology: Concept & Theory. 1986. Robert P. McIntosh. Cambridge Univ. Press. paper.

This is a book of the history of ecology, written by an ecologist who loves history, or perhaps a historian who has an unusual understanding of ecology and its roots. I am convinced of the depth of his vision by the following statement taken from the first two sentences of chapter one: "Ecology in its early years was sometimes described as not a science at all, but merely a point of view. After nearly a century of trying to erect a conceptual, methodological and theoretical framework for the most complex phenomena encountered in nature, ecology was familiar only to a relatively small number of academic biologists and applied biologists, range managers, foresters, and fishery and game managers." That caught my attention immediately and I read on.

The author is a lucid and interesting writer, with numerous contributions to current ecological literature, in development and clarification of theory as well as historical research. I have long been impressed by his acquaintance with European literature and his ability to analyze and integrate this with the American scene. He lists an impressive 57 pages of references at the back of the book, to document his coverage of the field.

He begins his story looking at reports of "ecologists," of antiquity, in which he found a few exceptional individuals who noted organism/environment relationships that foretold of modern concepts, but failed to develop a continuing field of knowledge. He develops the claim that it was not until in the last decade of the 19th century "that several facets of natural history and physiology combined to emerge quite suddenly into a recognizable discipline of ecology." (Many biological historians have found difficulty defining this point.) He gives this special kind of biology the name "self-conscious ecology" to differentiate it from his "antecedents."

Historical aspects of ecology have mostly academic interest for me, but have an obvious value as background for today's concepts and theories. My interest jumped as the story picked up where I came in. And it was highly valuable to me to have the whole complex field in its present form outlined through developmental stages by a knowledgeable scientist, helping me to see where my fragments of knowledge fit into the big picture.

The discussion follows a somewhat chronological development, moving from early innovators through dynamic concepts in plant, marine, and animal ecology, to quantitative community ecology, population ecology, and ecosystems ecology, with final chapters on theoretical approaches and ecology in the conservation movement.

If you have been wondering what has been going on in the broad field of ecology while you have been busy with more mundane problems, I can recommend this book to you.—**Grant A. Harris,** Department of Forestry and Range Management, Washington State University, Pullman.

Landscape Ecology. 1986. By Richard T.T. Forman and Michel Godron. John Wiley & Sons, New York, N.Y. 619 p. $35.00.

Beginning in early 1970 a new lexicon began to enter professional jargon and the consciousness of the American public: the most famous or, to some, infamous "environmental impact" language of section 102 of the National Environmental Policy Act (NEPA) of 1969. NEPA required, in part, that we anticipate and predict the degree to which our natural environment would be affected or influenced by modification and use of the landscape. After almost 2 decades of trying, we continue to marvel at the complexity of natural systems, the complexity of predicting the consequences of our actions, and begin to understand the true difficulty in meeting the requirements of our own good intentions.

Landscape Ecology attempts to fill an historic gap between ecology and planning revealed by NEPA and other, more specialized, federal and state legislation. Scientifically based disciplines were not experienced in identifying the comprehensive impacts associated with aggressive human land use. Those who plan and design the built environment were equally at odds with analytical procedures that could incorporate ecological data and withstand a rigorous examination by our court system. An alliance was struck slowly as the ecological sciences began to fit pieces of the environmental puzzle into systematic, less capricious, and legally defensible planning processes. *Landscape Ecology* recognizes the need for a language that incorporates both quantitative and qualitative measurements of environmental disturbance.

Authors Forman and Godron have developed a very useful taxonomy of landscape descriptions. Their book begins by sketching the human perceptions and ecological concepts of landscapes. Landscapes are discussed as both a social and natural environment. A second section integrates the scattered ecological and qualitative characteristics of landscape patterns and spatial forms. Landscapes are viewed as having structure and spatial form through natural and man-induced patches, corridors, and networks composed of a "matrix" of heterogeneous parts.

Section three describes landscapes and landscape disturbances as dynamic and involving natural processes as well as human intervention. The section speaks directly to human-induced actions which precipitate environmental reactions among the flow of elements within and among landscapes. The last section aids the planner by describing methods of landscape typology as a means of assessing the sensitivity of environments to disturbance or changing land uses. The authors conclude by describing the importance of modelling complex interactions, among landscape characteristics, as a means of understanding disturbance and management practices.

Forman and Godron have enriched both ecologist and planners by synthesizing the work of each discipline into a single publication. The intended audience, students, may, however, find a degree of reading difficulty when the flow of text information is constantly interrupted by reference citations. On the other hand, the authors have highlighted important terms in bold-face, thus easing a student's search for definitions, and have provided a grand array of reference material. The book will also be valuable to the ecologist who wonders about what planners need to know and the planner who desires a clear image of what a landscape is all about.—**John Mack Roberts,** Pullman, WA.

Terrestrial Plant Ecology, Second Edition. 1987. By M.G. Barbour, J.H. Burk, and W.D. Pitts. The Benjamin/-Cummings Publishing Company, 2727 Sandhill Rd., Menlo Park, CA 94025. 634 p., Hardbound $39.95.

This is the best book available as a general plant ecology course textbook. It includes all aspects of plant ecology under one cover. Other books may discuss either traditional autecology or the more modern aspects of population biology, but this is usually not found in the same book. Odum wrote a good book on the subject of ecology, but it has an ecosystem approach that primarily uses animals to explain the concepts. If you want a fair representation of all aspects of modern plant ecology, then this is the only book to have. How many older textbooks have two chapters on species interactions, or include a discussion of ordination in the chapter on plant community classification? Many of the older, established plant ecologists, range scientists, and foresters that I know are purchasing this book just to read the chapter on plant communities ordination. Why? Because it is presented in a readable manner. Are we not all students of plant ecology regardless of our age? If we don't work with certain aspects of ecology, we might not understand some of the newer concepts and methods.

The figures and tables in this second edition are great. The authors have made a good effort to follow the current literature on plant ecology, and this is reflected in the updated edition. There are many references used that reflect current advances and concepts in plant ecology, such as frequent comments about mycorrhizal fungi associations. I talked to Dr. Bruce McCune, a professor who used this text book last summer for a field course in plant ecology, and he said that student feedback about the book was favorable. The students felt that the book was helpful and beneficial to them. Field courses are a brutal test for a textbook. Students taking summer field courses generally do not bother with one unless it is helpful to them in understanding concepts.

Terrestrial Plant Ecology is well written and organized. One can readily find sought-after information here by using either the Content Outline or the Index. I highly recommend this book to all people who work or are interested in plant ecology, for both yourself and for aiding those people who may seek your advice on a variety of ecological concepts. How nice it is to steer someone in a direction that leads them to understanding. In addition, you get 634 pages of text without paying a mint, as is often the case for an Academic Press reference book. This book is well bound, full sized, and on good quality paper, yet does not cost its weight in gold.—**Roger Rosentreter,** Boise, ID

Common Western Range Plants: Their Fundamental Structure, Growth and Value and Management (Third Ed.). 1986. John V. Stechman, Vocational Education Productions, Cal. Poly. State University, San Luis Obispo, CA 93407.

Ranchers and high school students (particularly FFA and 4-H) will find this manual filled with interesting and useful information, presented in language easily understood by nontechnical persons. It has many of the earmarks of a college range plants text, but pitched at a less technical level. It includes brief descriptions of the nature of rangelands, shows six major range regions, gives an elementary lesson in plant morphology useful in identification, explains botanical names, provides short lessons in plant phenology and physiology, forage palatability and nutritive values, range soils and stocking rates, all in 13 pages of text. It is presented in a heavy paper cover with plastic binding and 6 × 9 format, suitable for field travel.

Ninety of the 123 pages are devoted to line drawings and descriptions of range plant genera very reminiscent of the pages of Dayton's "Range Plant Handbook" of an earlier era. Line drawings are excellent, and include whole-plant as well as leaf, flower, and fruit detail on many of the plates. Description information, and illustrations, are mainly centered at the genus level, and are organized into traditional sections on grasses, grasslikes, forbs, and trees and browse, with an added poisonous plant section. Each section is preceded by a short discussion of importance to grazing. An interesting innovation is the addition of directions for conducting practical "range plant projects," and study questions, apparently for high school students.

Range managers, particularly those working with ranchers, will find this book useful for discussing problems in a general way with the public, and perhaps reviewing botanical names you have forgotten. An obvious exclusion is all but the western edges of the Great Plains region. The information appears to be based on sound technical references, and is complete enough for general use, though limited to a few of the most important range plants.—**Grant A. Harris,** Washington State University.

Books Received for Review

Complimentary copies available to volunteer reviewers, Contact Dr. Grant A. Harris, Department of Forestry and Range Management, WSU, Pullman, WA 99164.

Kangaroos; Their ecology and management in sheep rangelands of Australia. Graeme Caughley, Neil Shepherd and Jeff Short

To feed the Earth: Agro-ecology for sustainable development. Michael Dover and Lee M. Talbot

Cyprus; A chronicle of its forests, land, and people. J.V. Thirgood

Planning for drought; Toward a reduction of social vulnerability. D.A. Wilhite and W.E. Easterling, with D.A. Wood, (Eds.)