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Root traits associated with nutrient exploitation following defoliation in three coexisting perennial grasses in a semi-arid savanna

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Experiments were conducted to evaluate root traits associated with nutrient exploitation following defoliation in three coexisting perennial grasses in a semi-arid savanna. Root length density was determined within soil cores directly beneath plants, nitrogen uptake was evaluated by excised-root assay with $(^{15}NH_4)_2SO_4$, and mycorrhizal root colonization was estimated by observation of root segments. Root length density was lowest for *Bouteloua curtipendula*, intermediate for *Eriochloa sericea*, and highest for *Aristida purpurea* indicating that root length density was a more important trait for the mid-seral than the late-seral species. Rates of ^{15}N uptake were greatest in the least grazing tolerant late-seral species, *E. sericea*, intermediate in the mid-seral species, *A. purpurea*, and lowest in the most grazing tolerant late-seral species, *B. curtipendula*. Two successive defoliations reduced ^{15}N uptake 60% in the late-seral species with the greatest uptake rate (*E. sericea*), but not in species with lowest uptake rates (*B. curtipendula*). Root length colonization was consistently high (33–61%) in all three species suggesting that these C_4 perennial grasses may function as obligate mycotrophs. Contrasting responses among the two late-seral species indicate that the least grazing tolerant species, *E. sericea*, appears best adapted for nutrient exploitation while the most grazing tolerant species, *B. curtipendula*, appears best adapted for efficient nutrient retention. Contrasting responses of nitrogen uptake to short-term defoliation parallel the population responses of these two coexisting late-seral species to long-term herbivory. These data indicate that herbivory may shift interspecific competitive interactions by mediating nutrient exploitation and that a trade-off may exist between nutrient exploitation and herbivory tolerance in these species.

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Numerous physiological and morphological traits have been associated with effective resource acquisition and competition in plants. Plants in unproductive environments are often characterized by low rates of nutrient absorption, effective nutrient retention and slow growth rates to maintain a balance between resource demand and availability (Grime 1979, Chapin 1980). In contrast, plants in productive environments are often characterized by rapid rates of nutrient absorption and growth to exploit greater resource availability. However, the ability to predict competitive outcomes on the basis of plant traits becomes more difficult as the competing plants become more similar in form and function (Keddy and Shipley 1989). Functional similarity has been hypothesized to promote species coexistence by minimizing the intensity of interspecific

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competition (Aarssen 1983, Goldberg and Werner 1983). These interpretations justify the need for additional research to identify plant traits contributing to resource acquisition and competitive ability among dominant species possessing similar life history strategies (e.g., Tilman and Wedin 1991, van der Werf et al. 1993, Ryser and Lambers 1995).

Prediction of competitive outcomes and insight into mechanisms of species coexistence is further constrained by uncertainty regarding the intensity of plant competition along productivity gradients (Casper and Jackson 1997, Goldberg and Novoplansky 1997). However, competition is generally assumed to be greatest for belowground resources in less productive environments. Consequently, high root length densities (Nye and Tinker 1977, Teo et al. 1995), efficient nutrient uptake kinetics (Jackson and Caldwell 1991) and high frequencies of mycorrhizal infection (Hetrick et al. 1990, Gehring and Whitham 1994) are common root traits of many perennial grasses. However, simple linear relationships should not necessarily be expected between root traits and resource acquisition (Caldwell 1994) and these relationships are often difficult to identify in natural systems (Sanders and Fitter 1992, Diaz and Honrubia 1995). In addition, roots of various species may exhibit considerable morphological and physiological plasticity to enhance exploitation of heterogeneously distributed resources (Jackson et al. 1990, Caldwell 1994, Hetrick et al. 1994a, b).

Most grasslands and savannas are characterized by intensive herbivory capable of modifying nutrient acquisition within and between plant species (Berendse 1985, Caldwell et al. 1987). A reduction in whole-plant photosynthesis and preferential carbon allocation to shoot growth following defoliation reduces root growth and function as root carbohydrates are depleted (Briske and Richards 1995, Briske et al. 1996). Various investigators have documented reductions in nutrient absorption rates of both fast- and slow-growing grasses in response to one or more defoliations (Davidson and Milthorpe 1966, Poorter et al. 1991), but increased rates of nutrient absorption have also been reported (Chapin and Slack 1979, McNaughton and Chapin 1985). Similarly, a reduction in root elongation may occur within 24 h after removal of greater than 50% of the canopy (Crider 1955, Davidson and Milthorpe 1966) and root mortality may occur following severe defoliation (Allsopp 1998).

A series of experiments were designed to investigate root length density, nitrogen absorption rate, and mycorrhizal colonization of roots of three perennial grasses in an attempt to explain the mechanism of coexistence and relative species abundance in a semi-arid savanna. *Bouteloua curtipendula*, *Eriochloa sericea*, and *Aristida purpurea* are all C_4 perennial, caespitose grasses that are widely distributed on the Edwards Plateau Resource Region of west-central Texas (Gould 1975, Smeins et al. 1976). *E. sericea* and *B. curtipendula* are both late-seral midgrasses (0.5–1.0 m in height) that have shown large reductions in abundance to long-term intensive grazing by domestic herbivores (Fuhlendorf and Smeins 1997). However, *B. curtipendula* has recovered more rapidly than *E. sericea* when grazing has been eliminated and *B. curtipendula* has greater population densities than *E. sericea* in moderately grazed communities indicating that it is the more herbivory tolerant of the two late-seral grasses (Fuhlendorf and Smeins 1997, Hendon and Briske 1997, Briske and Hendrickson 1998). In contrast, *A. purpurea* is a smaller statured (0.25–0.70 m in height) mid-seral species that has maintained a low, but relatively constant, population density in response to grazing (Fuhlendorf and Smeins 1997). We reasoned that the coexistence of two late-seral species with distinct responses to herbivory and a herbivory resistant, subordinate species would provide a valuable comparison of root traits associated with effective nutrient exploitation and species coexistence. Early seral grasses have been shown to be inferior competitors compared to late-seral grasses based on their ability to reduce soil nitrogen to low concentrations (Tilman and Wedin 1991).

We evaluated four specific hypotheses: 1) late-seral species would have greater root length densities than the mid-seral species, 2) late-seral species would have greater nitrogen absorption rates per unit root mass than the mid-seral species, 3) late-seral species would have greater frequencies of mycorrhizal infection than the mid-seral species, and 4) severe defoliation would suppress nitrogen absorption rate and mycorrhizal infection to a greater extent in late-seral than in the mid-seral species. Research protocol involved four destructive harvests of selected plants of all three species from the field following the imposition of severe defoliation at three frequencies.

Materials and methods

Study site

Research was conducted at the Texas A&M University Agricultural Research Station 56 km south of Sonora, Texas, USA (31°18′N; 100°28′W). The station is located in the southwestern portion of the Edwards Plateau Land Resource Area at an elevation of approximately 735 m. The area is potentially a midgrass grassland with individuals and clustered trees of *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei* and *J. pinchotii* (Smeins and Merrill 1988, Fuhlendorf and Smeins 1997). This investigation was conducted in a community that had been protected from domestic, but not native herbivores, since 1948, because it contained abundant populations of late-seral grasses.

Topography of the research station is highly dissected and soils contain large amounts of limestone fragments, stones and gravel (Wiedenfeld and McAndrew 1968, Smeins and Merrill 1988). The dominant soils are Tarrant stony clays that formed over fractured limestone and are classified as Lithic Haplustolls. These soils are relatively shallow with a depth of 15 to 30 cm. Specific soil characteristics are as follows: pH 8.04, 35.5 g kg^{-1} organic carbon, 3.2 g kg^{-1} total nitrogen, 10.7% $CaCO_3$, with a textural distribution of 3.0, 50.5, and 46.5% sand, silt and loam, respectively (Marshall 1995).

Median long-term precipitation is 439 mm, but it is highly erratic (Smeins and Merrill 1988). May and September are typically the wettest months while November and January tend to be the driest. Mean annual precipitation was 73.6, 98.1, and 94.3% of the long-term mean for 1993, 1994, and 1995, respectively. Precipitation during the study period (15 May–15 July 1995) was 192.5 mm.

Procedures and variables

Plant defoliation and growth

Forty-eight established plants of *B. curtipendula*, *E. sericea* and *A. purpurea* Nutt. var. *wrightii* (Nash) were identified and permanently marked on 12 May 1995. Plant basal circumference was measured and half of the plants were defoliated to a 4-cm stubble height while the other half remained undefoliated to serve as controls. One half of the defoliated plants received a second defoliation on 13 June. Six plants per species and defoliation treatment were destructively harvested at each of the following times: 3–5 (16–18 May) and 33–34 (14 and 15 June) d after the first defoliation and 2–4 (15–17 June) and 28–30 (11–13 July) d after the second defoliation.

At each sampling date, shoot biomass above defoliation height was collected for each plant and oven-dried at 65°C until a constant weight was attained. Regrowth biomass was collected after the first and second defoliation and total biomass was based on cumulative biomass production above defoliation height from the beginning of the growing season for both defoliated and undefoliated plants. Current years live and recent dead biomass was separated, weighed and ground in a Wiley mill to pass a 40-mesh screen. After harvesting plant shoots, two soil cores (4.8 cm diameter) were taken on opposite sides of each plant to a depth of 17 cm. The corer was placed at the edge of the plant and driven into the soil at an angle toward the plant center to sample areas of high root density without damaging the plant shoots. Core placement beneath plants located at a minimum distance of 30 cm from the nearest neighbor decreased the probability of including roots from adjacent species. One of the soil cores was used to determine VAM spore populations and the other was used to determine root length density and frequency of mycorrhizal infection.

Roots were extracted from soil cores with a hydropneumatic elutriation system (Smucker et al. 1982), floated in water to remove organic debris and they were then stored in an FAA solution at 4°C. Root length was initially measured with a graduated planimeter and the line intercept method of Tennant (1975) on 26 root samples that had been floated and pressed between two Plexiglas plates. The intent was to initially compare the speed and accuracy of these two procedures and then use the most effective procedure. Linear regression analysis indicated that root lengths obtained by both methods were highly correlated (measured length $= -6.7 + 0.766$ estimated length, $R^2 = 92.4$, $P < 0.001$, $n = 26$), but the procedure of Tennant was more rapid. Consequently, we used this procedure to estimate root length in the remaining samples, but estimated values were corrected using the regression equation based on the planimeter measurements. Root length density (cm of roots per cm^3 of soil) was calculated from total root length and total core volume (311.2 cm^3).

Rate of ^{15}N absorption

Roots for the ^{15}N absorption experiment were harvested after the root cores had been taken by excavating the entire plant including a block of soil approximately 25 × 25 cm to the depth of the fractured limestone (15 to 30 cm). Although these soil samples did not capture the entire root system, they did contain many fine lateral roots. Roots were manually washed from the soil, floated in water and retained if they were ≤ 1 mm in diameter and had a light color characteristic of young roots. Roots from individual plants were separated into two or three subsamples of 0.69 ± 0.02 g ($n = 341$) dry weight, wrapped in cheese cloth bags, and equilibrated for 1 h in a 0.5-mM $CaCl_2$ solution at 25°C (Jackson et al. 1990, Vucinic and Vuletic 1995). Roots were immersed in solutions of $(^{15}NH_4)_2SO_4$ which contained 1, 10 or 25 mM $^{15}NH_4$. Native soils at this site contained a mean of 5.29 ppm NH_4 (range 3.45–10.91; 1 mM $(^{15}NH_4)_2SO_4 = 36$ ppm) as measured with a Carlo-Erba NA-1500 elemental analyzer (Marshall 1995). Higher concentrations were developed to represent enriched soil patches.

All solutions were well mixed and aerated, adjusted to pH 7.5, and contained both 0.01 M sucrose as an energy source and 0.5 mM $CaCl_2$ to maintain membrane integrity (Jackson et al. 1990, Vucinic and Vuletic 1995). Root subsamples were immersed in the ^{15}N labeled solutions for 10 min and then rinsed three times for a minimum of 2 min in unlabeled 50-mM $(NH_4)_2SO_4$ solutions at 5°C. The rinse solutions were designed to replace any ^{15}N adsorbed to the root surfaces. The ^{15}N absorption experiments were completed within 2–2.5 h after plant collection in the field

to minimize the effect of root excision on ammonium absorption (Bloom and Caldwell 1988). Roots were blotted dry, oven-dried at 60°C, weighed, ground to pass a 40-mesh screen, and approximately 7.5 mg of biomass was loaded into tin capsules for analysis of ^{15}N content by mass spectrometry (Boutton 1991). Analysis of ^{15}N atom percent was conducted with a Carlo-Erba NA-1500 elemental analyzer interfaced with a VG-Isomass mass spectrometer (Isotope Services Inc., Los Alamos NM).

Mycorrhizae

Roots were cut into 20 mm segments, cleared and stained for determination of mycorrhizal colonization at 100–400 × magnification (Giovannetti and Mosse 1980). Two fields on each of thirty root segments were scored for presence or absence of hyphae, vesicles and arbuscules for each plant, and the percentage of colonized root length was calculated by multiplying root length density by percentage colonization.

Soil for spore counts was air dried, sieved with a 2-mm screen and stored in plastic bags at 4°C. Spores were extracted from 100-g subsamples by wet sieving through 500-, 250- and 38-µm sieves (McKenney and Lindsey 1987). Spores in the 38-µm portion of the sievate were placed on filter paper and counted at 10 × magnification.

Statistical analyses

Plant growth and mycorrhizal variables were analyzed using three-way ANOVA (2 defoliation treatments × 3 species × 4 sampling dates). The ^{15}N root absorption data were analyzed using four-way ANOVA (2 defoliation treatments × 3 species × 4 sampling dates × ^{15}N solution concentrations). Absorption rates of ^{15}N at 1 and 25 mM $(NH_4)_2SO_4$ were analyzed for all defoliation treatments, species and sampling dates. The only exception was that ^{15}N uptake data were not collected for undefoliated plants of any species at the second sampling period because a comparable set of data was collected 2–3 d later (15–17 June). Consequently, uptake data for this sampling date was excluded from the analysis. LSD was utilized for mean separation when F tests indicated that a variable was significant at the 0.05 level. Mycorrhizal colonization data (arcsine square-root), spore count data [$\ln(x+1)$] (St. John and Koske 1988), and ^{15}N uptake data [$\log_{10}(x)$] were transformed before statistical analyses, but nontransformed values are presented in figures, tables and text. Linear regression analysis was used to investigate relationships between the following variables: mycorrhizal colonization percentages, spore numbers, root length density, shoot regrowth production and total shoot production/unit basal area. Within each species, the regression lines for defoliated and undefoliated plants were first compared and pooled if they were not significantly different ($P > 0.05$, $P \geq 0.20$ for 35 of 44 comparisons). If this was the case, regression lines were then compared among dates within each species, and data were again pooled if treatment means were not significant ($P > 0.05$). Slopes of two or more regression lines were tested following the procedure of Neter et al. (1985).

Results

Plant growth

Plant basal area was significantly different among species at the outset of the investigation with the largest values for *B. curtipendula* (163.2 cm^2), intermediate values for *E. sericea* (123.3 cm^2), and smallest values for *A. purpurea* (99.2 cm^2). Plant basal area was not measured as a response variable because of the short duration of the investigation. Total shoot biomass production is expressed on a unit area basis to standardize for this inherent variation in species stature. Total shoot biomass production per unit basal area was 61% lower ($P < 0.05$) for *B. curtipendula* than for *E. sericea* and *A. purpurea*. Total biomass production per unit plant basal area significantly increased from the first to the second harvest date in all species for both defoliated and undefoliated plants (Tables 1, 2). Defoliated plants of all three species produced a similar ($P > 0.05$) amount of total shoot production compared to undefoliated plants at the end of the investigation. Shoot regrowth per unit basal area was similar ($P > 0.05$) for defoliated plants of all three species.

Root length density was similar among harvest dates and between defoliation treatments, but differed among species (Tables 1, 2). Averaged across sampling dates, *A. purpurea* had 29 and 46% greater ($P < 0.05$) root length density than *E. sericea* and *B. curtipendula*, respectively. *E. sericea* had a 25% greater ($P < 0.05$) root length density than *B. curtipendula*. A positive correlation ($P < 0.05$, $y = 54.3 + 16.0x$, $r = 0.49$, $n = 24$) existed between root length density and total biomass production on undefoliated plants of *A. purpurea*. Regrowth production averaged across all three species of defoliated plants also showed a positive correlation ($P < 0.05$, $y = 8.68 + 2.73x$, $r = 0.49$, $n = 18$) with root length density on 14–15 June.

Mycorrhizal infection

Percent VAM colonization was similar for all three species and did not significantly differ between defoliated and undefoliated plants (Table 1). Percent VAM colonization and colonized root length density (data not shown) significantly decreased (9%), in both defoliated and undefoliated plants, from mid-May to mid-June or mid-July. Colonized root length density was 150% greater ($P < 0.05$) for *A. purpurea* than for *B.*

Table 1. Results of a three-way analysis of variance examining the effects of harvest date, plant species and defoliation treatment on total shoot biomass production (g/cm^2), shoot regrowth production (mg/cm^2), root length density (cm/cm^3), percentage VAM colonization, and mycorrhizal spore number/100 g dry soil for *Bouteloua curtipendula*, *Eriochloa sericea* and *Aristida purpurea* in a semiarid savanna near Sonora, TX, USA. Data are presented in table 2.

Source	df	Mean sums of squares and significance level					
		Total shoot production (g/cm^2)	Shoot regrowth production (mg/cm^2)	Root length density (cm/cm^3)	% VAM colonization	df	Spore number
Date	3	0.0342***	12466**	12.667	0.0467*	3	0.089
Species	2	0.1333***	29803***	94.488***	0.0312	2	0.639*
Def. trt.	1	0.0011	388345***	2.901	0.0014	1	0.436
Date × Species	6	0.0085	2391	2.107	0.0126	6	0.081
Date × Def. trt.	3	0.0037	4086	3.962	0.0304	3	0.460*
Species × Def. trt.	2	0.0009	29208***	0.351	0.0283	2	0.236
Date × Species × Def. trt.	6	0.0041	1790	2.506	0.0133	6	0.136
Error	120	0.0064	2758	6.379	0.0166	46	0.116
Total	143					69	

* $P<0.05$, ** $P<0.01$, *** $P<0.001$.

curtipendula or *E. sericea* because of a significantly greater root length density (Table 2).

Fungal spores were identified as *Glomus geosporum* (Nicolson and Gerdemann), *Sclerocystis sinuosom* (Gerdemann and Baksin), *Gigaspora margarita* (Becker and Hall) and several additional *Glomus* species. Spore number showed a significant date × defoliation treatment interaction (Table 1). Mean spore number was similar ($P > 0.05$) among sampling dates for undefoliated plants of all species, but was lower ($P < 0.05$) in mid-June than mid-May or mid-July for defoliated plants (Table 2). However, defoliated plants had a greater ($P < 0.05$) mean spore number than undefoliated plants at the beginning (mid-May) and end (mid-July) of the investigation. Mean spore number for *B. curtipendula* plants was 32 and 38% lower ($P < 0.05$) than for *E. sericea* or *A. purpurea*, respectively, for defoliated plants.

Rate of ^{15}N absorption

The rate of ^{15}N uptake showed a significant interaction among species, defoliation treatment and date (Table 3). Mean rates of ^{15}N uptake were similar ($P > 0.05$) between defoliated and undefoliated plants for all species within 3 d of the initial defoliation on 16 May (Fig. 1). However, undefoliated plants of *E. sericea* had a 113% greater ($P < 0.05$) rate of ^{15}N uptake compared to undefoliated *B. curtipendula* plants in mid-June. The second defoliation significantly reduced the rate of ^{15}N uptake after 3 (17 June) and 29 d (13 July) for *E. sericea* and *A. purpurea*, respectively, compared to undefoliated plants at these dates. The rate of ^{15}N uptake was reduced by 60% by the second defoliation in *E. sericea* while uptake rate was unaffected in *B. curtipendula*. The rate of ^{15}N uptake subsequently increased by approximately 25% in defoliated *E. sericea* and *A. purpurea* plants, but values did not attain uptake rates of undefoliated plants by the end of the experiment.

Soil-plant-mycorrhizal relationships

Percentage VAM colonization was positively correlated with root length density for *B. curtipendula* in mid-July ($P < 0.01$, $r = 0.98$, $n = 6$) (data not shown). Percentage VAM colonization was not significantly correlated with total biomass or regrowth for any species, harvest date or defoliation treatment (data not shown).

Spore numbers and percentage VAM colonization were positively correlated for *A. purpurea*, but not for *B. curtipendula* and *E. sericea* ($P = 0.05$, $r = 0.41$, $n = 24$)(data not shown). Within each species, there was no significant correlation between spore numbers and root length density at any harvest date or defoliation treatment.

Table 2. Mean (± 1 s.e., $n = 6$) plant basal area (cm^2), total shoot biomass production (g/cm^2), shoot regrowth production (mg/cm^2), root length density (cm/cm^3), percentage VAM colonization, and mycorrhizal spore number/100 g dry soil for *Bouteloua curtipendula*, *Eriochloa sericea* and *Aristida purpurea* in a semiarid savanna near Sonora, TX, USA. One-half of the plants were initially defoliated on 12 May and one-half of these received a second defoliation on 13 June 1995.

Trait / Species	Harvest date and defoliation treatment							
	16–18 May		14–15 June		15–17 June		11–13 July	
	Defoliated	Undefoliated	Defoliated	Undefoliated	Defoliated	Undefoliated	Defoliated	Undefoliated
Plant basal area								
B. curtipendula	123.3 ± 21.3	137.5 ± 32.8	196.6 ± 24.1	149.7 ± 18.8	209.0 ± 23.9	145.4 ± 15.5	146.16 ± 9.35	197.5 ± 20.2
E. sericea	150.1 ± 12.6	131.3 ± 18.6	123.8 ± 17.1	102.9 ± 12.8	125.4 ± 21.6	130.1 ± 18.8	99.3 ± 13.1	123.9 ± 20.2
A. purpurea	115.2 ± 11.6	74.06 ± 6.95	128.3 ± 24.6	120.2 ± 13.2	110.0 ± 27.0	83.0 ± 14.0	78.4 ± 8.63	84.3 ± 12.4
Shoot production								
B. curtipendula	0.043 ± 0.005	0.026 ± 0.003	0.037 ± 0.004	0.053 ± 0.009	0.081 ± 0.078	0.064 ± 0.010	0.058 ± 0.003	0.077 ± 0.011
E. sericea	0.085 ± 0.011	0.091 ± 0.012	0.168 ± 0.038	0.208 ± 0.054	0.090 ± 0.013	0.114 ± 0.018	0.201 ± 0.057	0.125 ± 0.030
A. purpurea	0.113 ± 0.019	0.110 ± 0.032	0.205 ± 0.072	0.171 ± 0.050	0.117 ± 0.013	0.137 ± 0.027	0.212 ± 0.060	0.167 ± 0.041
Regrowth production								
B. curtipendula	01.450 ± 00.40		12.75 ± 01.23		01.68 ± 00.32		14.57 ± 02.47	
E. sericea	0.556 ± 0.151		23.41 ± 07.03		00.88 ± 00.24		14.95 ± 06.40	
A. purpurea	0.658 ± 0.208		20.75 ± 07.02		00.77 ± 00.29		5.00 ± 00.57	
Root length density								
B. curtipendula	3.87 ± 0.58	3.64 ± 0.26	2.50 ± 0.70	2.95 ± 0.97	3.38 ± 0.70	3.13 ± 0.87	3.23 ± 1.28	2.77 ± 0.55
E. sericea	5.15 ± 0.71	5.24 ± 0.74	3.90 ± 0.84	4.02 ± 0.87	5.85 ± 1.63	3.65 ± 0.46	2.60 ± 0.37	3.51 ± 0.35
A. purpurea	6.37 ± 0.72	6.25 ± 1.23	4.88 ± 1.37	5.67 ± 0.60	7.04 ± 1.23	6.06 ± 1.19	6.49 ± 1.89	4.95 ± 1.63
% colonization								
B. curtipendula	55.19 ± 05.59	46.39 ± 02.87	43.53 ± 05.17	41.03 ± 05.98	51.29 ± 05.90	44.30 ± 09.39	50.79 ± 09.99	40.38 ± 03.04
E. sericea	55.00 ± 05.64	41.40 ± 07.03	36.56 ± 07.28	45.50 ± 10.30	39.72 ± 03.64	61.00 ± 07.80	34.06 ± 05.04	33.89 ± 02.18
A. purpurea	53.89 ± 06.61	54.72 ± 04.38	41.74 ± 05.89	47.50 ± 05.25	44.72 ± 05.22	51.11 ± 04.63	53.65 ± 08.56	44.23 ± 03.67
Spore number								
B. curtipendula	5661 ± 2003	3972 ± 250	2461 ± 235	4306 ± 1046	2267 ± 448	4156 ± 1117	3939 ± 933	2661 ± 463
E. sericea	5861 ± 2068	3544 ± 742	4289 ± 589	4450 ± 1257	4489 ± 1093	4856 ± 580	6567 ± 741	3222 ± 209
A. purpurea	6339 ± 755	3739 ± 327	3717 ± 593	4956 ± 951	6961 ± 993	3561 ± 540	6139 ± 1150	3761 ± 1093

Discussion

An evaluation of root traits indicates that all three C_4 perennial grasses possess unique variations for nutrient exploitation and coexistence in this semi-arid savanna. Our hypotheses addressing the expression of root traits between mid- and late-seral species and the response of these traits to defoliation were inconsistent with the results so all four hypotheses were rejected. The mid-seral species, *A. purpurea*, had a greater root length density than both of the late-seral species (hypothesis one), late-seral species possessed the highest and lowest nitrogen absorption rate per unit root mass while the mid-seral species had an intermediate absorption rate (hypothesis two), the frequency of mycorrhizal infection was comparably high among all three species (hypothesis three), and severe defoliation suppressed nitrogen absorption in the least grazing tolerant late-seral species and in the mid-seral species, but not in the most grazing tolerant late-seral species (hypothesis four).

Similar amounts of shoot growth following one or two severe defoliations indicate that all three species possess comparable short-term herbivory tolerance. Comparable regrowth among species was unexpected because they all show unique responses to long-term grazing in this savanna (Smeins et al. 1976, Fuhlendorf and Smeins 1997). *E. sericea* is considered least resistant to long-term herbivory followed by *B. curtipendula* and *A. purpurea* which is most resistant. Similar expression of short-term herbivory tolerance supports the interpretation that the herbivore-induced replacement of *E. sericea*, and to a lesser extent, *B. curtipendula*, is driven by selective herbivory, rather than by unequal herbivory tolerance among species (Anderson and Briske 1995, Hendon and Briske 1997, Briske and Hendrickson 1998; but see Augustine and McNaughton 1998).

Root length density was lowest for *B. curtipendula* and highest for *A. purpurea* which suggests that root length density is a more important root trait for the mid-seral than the late-seral species. *B. curtipendula* has been reported to have a greater root hair density per unit root length for most depths above 0.6 m compared to an associated mid-seral shortgrass, *Hilaria belangeri* (Yoder et al. 1995). Greater root hair density would contribute to a greater absorptive surface per unit root length, but this trait was apparently insufficient to increase the rate of nitrogen uptake relative to the other two species with higher root length densities. Defoliation did not reduce root length density in any species

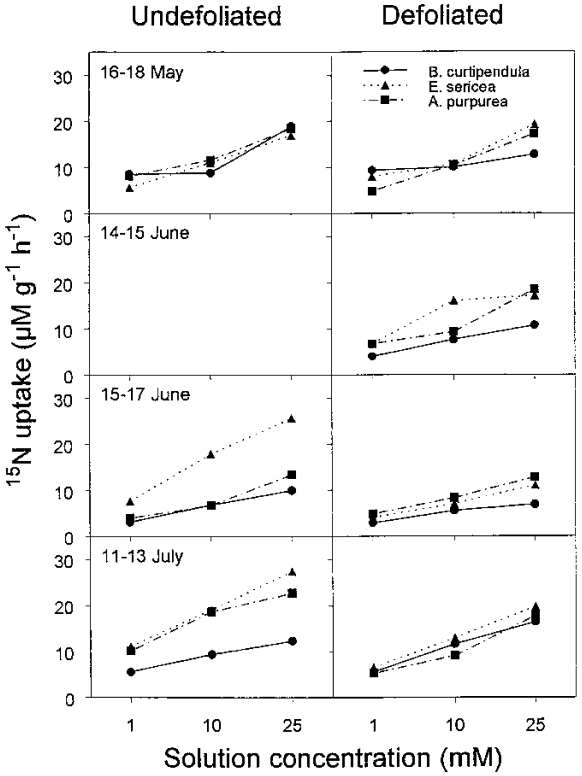

Fig. 1. Rates of ^{15}N uptake ($n = 2$ to 6) for undefoliated and defoliated plants of *Bouteloua curtipendula* (circles), *Eriochloa sericea* (triangles) and *Aristida purpurea* (squares) in a semiarid savanna near Sonora, TX, USA. Roots were subsampled and immersed in $(^{15}NH_4)_2SO_4$ solutions containing 1, 10 or 25 mM of labeled ammonium on the following dates: 3–5 (16–18 May) and 33–34 (14–15 June) d after the first defoliation, and 2–4 (15–17 June) and 28–30 (11–13 July) d after the second defoliation. Anova results are presented in table 3.

Table 3. Results of a four-way analysis of variance examining the effects of harvest date, plant species, defoliation treatment and concentration of $(^{15}NH_4)_2SO_4$ solutions on ^{15}N uptake rate for *Bouteloua curtipendula*, *Eriochloa sericea* and *Aristida purpurea* in a semiarid savanna near Sonora, TX, USA. Uptake data for the second sampling date were excluded from the analysis. Data are presented in Fig. 1.

Source	Mean sums of squares and significance level	
	df	^{15}N uptake rate (μmol g^{-1} h^{-1})
Date	2	0.980***
Species	2	0.761***
Def. trt.	1	0.609***
^{15}N conc.	2	5.632***
Date × Species	4	0.123*
Date × Def. trt.	2	0.054
Date × ^{15}N conc.	4	0.016
Species × Def. trt.	2	0.090
Species × ^{15}N conc.	4	0.019
Def. trt. × ^{15}N conc.	2	0.001
Date × Species × Def. trt.	4	0.232***
Date × Species × ^{15}N conc.	8	0.020
Date × Def. trt. × ^{15}N conc.	4	0.030
Species × Def. trt. × ^{15}N conc.	4	0.011
Date × Species × Def. trt. × ^{15}N conc.	8	0.014
Error	242	0.044
Total	295	

* $P<0.05$, ** $P<0.01$, *** $P<0.001$.

because of the short-term nature of the experiment and the existence of an extensive root system prior to defoliation (Becker et al. 1997).

Mycorrhizal fungi may not contribute to the disproportionate rates of nitrogen uptake among these three species because all species had similar levels of VAM colonization. Consistent, high percentages (33–61) of VAM colonization in all three species support the interpretation that C_4 perennial grasses may function as obligate mycotrophs in semi-arid as well as in mesic environments (Hetrick et al. 1990, Hartnett et al. 1994, Wilson and Hartnett 1997). Mean spore number per 100 g dry soil was within the range previously reported for grassland soils (Allen et al. 1989). Defoliated plants had a higher mean spore number than undefoliated plants at the first and last sampling dates in contrast to reports of decreasing spore number associated with intensive plant defoliation (Bethlenfalvay and Dakessian 1984, Bethlenfalvay et al. 1985). However, defoliation-induced reductions in root growth have previously been demonstrated to stimulate VAM spore production and it has been hypothesized that sporulation may be negatively correlated with root growth (Hayman 1982, Wallace 1987, Allen et al. 1989). Apparently, defoliation did not remove sufficient photosynthetic tissue to reduce substrate availability to fungi for sufficient periods to reduce infection rates or induce mortality in this investigation (Trent et al. 1988; but see Hetrick et al. 1990, Allsopp 1998).

Spore density was positively correlated with VAM colonization in *A. purpurea*, but not in the two late-seral species. Absence of a significant correlation between spore number and infection frequency indicates that a substantial portion of VAM colonization may be caused by propagules other than spores and that spore density is sufficiently high to occupy all colonization sites on the root systems (Jakobsen and Heidmann 1989).

Roots of *E. sericea* and, to a lesser extent, *A. purpurea*, possess a high V_{max} that enables them to effectively exploit nitrogen over the range of concentrations found in these soils as evidenced by the proportional rate of ^{15}N uptake with increasing nitrogen concentrations. In contrast, physiological root plasticity implies that absorption kinetics increase more rapidly than solution concentration in nutrient rich patches (Jackson and Caldwell 1991, Derner and Briske 1999). Consequently, physiological plasticity does not appear to be an important mechanism contributing to nutrient exploitation in these species. This interpretation may have been influenced by the relatively high solution concentrations utilized and the relatively short incubation times imposed.

Rates of ^{15}N absorption decreased rapidly in *E. sericea* and *A. purpurea* following the second defoliation, but inherently lower absorption rates of *B. curtipendula* remained relatively constant. Reductions in the rate of nutrient absorption following defoliation have previously been reported and are attributed to a depletion of root carbohydrates that suppress this energy dependent process (Davidson and Milthorpe 1966, Poorter et al. 1991). The physiological basis for maintenance of a constant rate of nitrogen absorption following severe defoliation of *B. curtipendula* plants is uncertain. We can only assume that a low rate of nitrogen uptake was maintained by carbon allocation to the root system from current photosynthesis, storage carbon, or a combination of these two sources (Chapin and Slack 1979, McNaughton and Chapin 1985, Thornton et al. 1993). Rapid increases in rates of nitrogen uptake at the end of the investigation establish that *E. sericea* and *A. purpurea* plants were reestablishing a positive carbon balance following the second defoliation (e.g., Clement et al. 1978).

The relative expression of root length density, nitrogen absorption rates, and frequency of VAM infection among species can be interpreted within the established strategies characterizing the ability of plants to exploit resources along productivity gradients (Grime 1979, Chapin 1980). *E. sericea*, one of the late-seral species, appears best adapted for effective nutrient exploitation based on rapid rates of nitrogen uptake with intermediate root length density. The capacity for rapid nitrogen absorption coupled with its ability to initiate growth several weeks earlier than associated C_4 grasses may enable this species to effectively preempt soil resources and attain competitive dominance on productive sites (Hendon and Briske 1997). *E. sericea* occupies sites with deeper soils and presumably greater nutrient availability than does *B. curtipendula* which supports this interpretation (Fuhlendorf and Smeins 1998). The associated late-seral species, *B. curtipendula*, appears less well adapted for rapid nutrient exploitation based on possession of a low root length density and a low rate of nitrogen absorption. These traits correspond with a strategy of efficient nutrient retention (Chapin 1980, Thornton et al. 1993, Aerts 1999) and support the interpretation that rapid nutrient acquisition is not a prerequisite for species dominance in unproductive environments (Tilman and Wedin 1991, Theodose et al. 1996). The mid-seral species, *A. purpurea*, appears to rely on construction and maintenance of a large root length density coupled with an intermediate rate of nitrogen uptake for coexistence in this community. However, the construction and maintenance costs associated with a large root length density may compromise its competitive ability relative to the two late-seral species and partially contribute to its subordinate position within the community.

An evaluation of root traits contributing to nutrient exploitation and species coexistence in this savanna must consider the role of intensive grazing by domestic herbivores. Herbivore-induced population reductions in *E. sericea* suggest that traits associated with effective

nutrient exploitation may be rapidly suppressed by intensive herbivory. Effective nutrient exploitation may increase the concentration and display of nutrients in foliage that may increase the probability of selective herbivory in this species (Hendon and Briske 1997). Chronic leaf removal may suppress the competitive advantage of this species by reducing root carbohydrates necessary for nutrient uptake. In contrast, traits associated with effective nutrient retention, rather than nutrient exploitation, may maintain or potentially enhance herbivory tolerance (Berendse 1985, Derner et al. 1997). For example, the more herbivory tolerant, late-seral species *B. curtipendula* displayed the lowest rate of nitrogen uptake, but it was the only species to maintain predefoliation nitrogen uptake rates following two severe defoliations. The large root sink associated with the construction and maintenance of a large root length density in the mid-seral species *A. purpurea* may contribute to the limited expression of herbivory tolerance in this species (Briske et al. 1996). This species has been shown to increase carbon allocation to roots, rather than shoots, immediately following defoliation which is counter to the allocation pattern of herbivory tolerant species. Grazing resistance in *A. purpurea* is assumed to result from the effective expression of herbivory avoidance, rather than herbivory tolerance (Heitschmidt et al. 1990).

These C_4 perennial grasses express varied root traits for nutrient exploitation and coexistence in this grazed, semi-arid savanna. The uniform expression of mycotrophy was the only trait consistently expressed among all three species. Contrasting responses of nitrogen uptake to short-term defoliation parallel the population responses of these two coexisting late-seral grasses to long-term herbivory. These data indicate that herbivory may shift interspecific competitive interactions by mediating nutrient exploitation and that a trade-off may exist between nutrient exploitation and herbivory tolerance in these species.

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References

Aarssen, L. W. 1983. Ecological combining ability and competitive combining ability in plants: an experimental approach. – Am. Nat. 122: 707–731.

Aerts, R. 1999. Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. – J. Exp. Bot. 50: 29–37.

Allen, M. F., Richards, J. H. and Busso, C. A. 1989. Influence of clipping and soil water status on vesicular-arbuscular mycorrhizae of two semi-arid tussock grasses. – Biol. Fertil. Soils. 8: 285–289.

Allsopp, N. 1998. Effect of defoliation on the arbuscular mycorrhizas of three perennial pasture and rangeland grasses. – Plant Soil 202: 117–124.

Anderson, V. J. and Briske, D. D. 1995. Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? – Ecol. Appl. 5: 1014–1024.

Augustine, D. J. and McNaughton, S. J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. – J. Wildl. Manage. 62: 1165–1183.

Becker, G. F., Busso, C. A., Montani, T. et al. 1997. Effects of defoliating *Stipa tenuis* and *Piptochaetium napostaense* at different phenological stages: root growth. – J. Arid Environ. 35: 269–283.

Berendse, F. 1985. The effect of grazing on the outcome of competition between plant species with different nutrient requirements. – Oikos 44: 35–39.

Bethlenfalvay, G. J. and Dakessian, S. 1984. Grazing effects on mycorrhizal colonization and floristic composition of the vegetation on a semiarid range in northern Nevada. – J. Range Manage. 37: 312–316.

Bethlenfalvay, G. J., Evans, R. A. and Lesperance, A. L. 1985. Mycorrhizal colonization of crested wheatgrass as influenced by grazing. – Agron. J. 77: 233–236.

Bloom, A. J. and Caldwell, R. M. 1988. Root excision decreases nutrient absorption and gas fluxes. – Plant Physiol. 87: 794–796.

Boutton, T. W. 1991. Stable carbon isotope ratios of natural materials. I. Sample preparation and mass spectrometric analysis. – In: Coleman, D. C. and Fry, B. (eds), Carbon isotope techniques. Academic Press, pp. 155–171.

Briske, D. D. and Richards, J. H. 1995. Plant responses to defoliation: a physiological, morphological and demographic evaluation. – In: Bedunah, D. J. and Sosebee, R. E. (eds), Wildland plants: physiological ecology ad developmental morphology. Soc. Range Manage., Denver, CO, pp. 635–710.

Briske, D. D. and Hendrickson, J. R. 1998. Does selective defoliation mediate competitive interactions in a semiarid savanna? A demographic evaluation. – J. Veg. Sci. 9: 611–622.

Briske, D. D., Boutton, T. W. and Wang, Z. 1996. Contribution of flexible allocation priorities to herbivory tolerance in C_4 perennial grasses: an evaluation with ^{13}C labeling. – Oecologia 105: 151–159.

Caldwell, M. M. 1994. Exploiting nutrients in fertile soil microsites. – In: Caldwell, M. M. and Pearcy, R. W. (eds), Exploitation of environmental heterogeneity by plants. Academic Press, pp. 325–347.

Caldwell, M. M., Richards, J. H., Manwaring, J. H. and Eissenstat, D. M. 1987. Rapid shifts in phosphate acquisition show direct competition between neighbouring plants. – Nature 327: 615–616.

Casper, B. B. and Jackson, R. B. 1997. Plant competition underground. – Annu. Rev. Ecol. Syst. 28: 545–570.

Chapin III, F. S. and Slack, M. 1979. Effect of defoliation upon root growth, phosphate absorption and respiration in nutrient-limited tundra graminoids. – Oecologia 42: 67–79.

Chapin III, F. S. 1980. The mineral nutrition of wild plants. – Annu. Rev. Ecol. Syst. 11: 233–260.

Clement, C. R., Hopper, M. J., Jones, L. H. P. and Leafe, E. L. 1978. The uptake of nitrate by *Lolium perenne* from flowing nutrient solution: II. Effect of light, defoliation, and relationship to CO_2 flux. – J. Exp. Bot. 29: 1173–1183.

Crider, F. J. 1955. Root growth stoppage resulting from defoliation of grasses. – USDA Tech. Bull. 1102.

Davidson, J. L. and Milthorpe, F. L. 1966. The effect of defoliation on the carbon balance in *Dactylis glomerata*. – Ann. Bot. 30: 185–198.

Derner, J. D. and Briske, D. D. 1999. Does a tradeoff exist between morphological and physiological root plasticity? A comparison of grass growth forms. – Acta Oecol. 20: 519–526.
Derner, J. D., Briske, D. D. and Boutton, T. W. 1997. Does grazing mediate soil carbon and nitrogen accumulation beneath C_4, perennial grasses along an environmental gradient? – Plant Soil 191: 147–156.
Diaz, G. and Honrubia, M. 1995. Effect of native and introduced arbuscular mycorrhizal fungi on growth and nutrient uptake of *Lygeum spartum* and *Anthyllis cytisoides*. – Biol. Plant. 37: 121–129.
Fuhlendorf, S. D. and Smeins, F. E. 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. – J. Veg. Sci. 8: 819–828.
Fuhlendorf, S. D. and Smeins, F. E. 1998. The influence of soil depth and plant species response to grazing within a semi-arid savanna. – Plant. Ecol. 138: 89–96.
Gehring, C. A. and Whitham, T. G. 1994. Interactions between aboveground herbivores and the mycorrhizal mutualists of plants. – Trends Ecol. Evol. 9: 251–255.
Giovannetti, M. and Mosse, B. 1980. An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infection in roots. – New Phytol. 84: 489–499.
Goldberg, D. E. and Werner, P. A. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. – Am. J. Bot. 70: 1098–1104.
Goldberg, D. and Novoplansky, A. 1997. On the relative importance of competition in unproductive environments. – J. Ecol. 85: 409–418.
Gould, F. W. 1975. The grasses of Texas. – Texas A&M Univ. Press.
Grime, J. P. 1979. Plant strategies and vegetation processes. – Wiley.
Hartnett, D. C., Samenus, R. J., Fischer, L. E. and Hetrick, B. A. D. 1994. Plant demographic responses to mycorrhizal symbiosis in tallgrass prairie. – Oecologia 99: 21–26.
Hayman, D. S. 1982. Influence of soils and fertility on activity and survival of vesicular-arbuscular mycorrhizal fungi. – Phytopathology 72: 1119–1125.
Heitschmidt, R. K., Briske, D. D. and Price, D. L. 1990. Pattern of interspecific tiller defoliation in mixed-grass prairie grazed by cattle. – Grass Forage Sci. 45: 215–222.
Hendon, B. C. and Briske, D. D. 1997. Demographic evaluation of a herbivory-sensitive perennial bunchgrass: does it possess an Achilles heel? – Oikos 80: 8–17.
Hetrick, B. A. D., Wilson, G. W. T. and Owensby, C. E. 1990. Mycorrhizal influences on big bluestem rhizome regrowth and clipping tolerance. – J. Range Manage. 43: 286–290.
Hetrick, B. A. D., Hartnett, D. C., Wilson, G. W. T. and Gibson, D. J. 1994a. Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie grasses. – Can. J. Bot. 72: 168–176.
Hetrick, B. A. D., Wilson, G. W. T. and Schwab, A. P. 1994b. Mycorrhizal activity in warm- and cool-season grasses: variation in nutrient-uptake strategies. – Can. J. Bot. 72: 1002–1008.
Jackson, R. B. and Caldwell, M. M. 1991. Kinetic responses of *Pseudoroegneria* roots to localized soil enrichment. – Plant Soil 138: 231–238.
Jackson, R. B., Manwaring, J. H. and Caldwell, M. M. 1990. Rapid physiological adjustment of roots to localized soil enrichment. – Nature 344: 58–60.
Jakobsen, I. and Heidmann, T. 1989. MPN estimates of VAM diaspores in cultivated soils. – Agric. Ecosyst. Environ. 29: 199–203.
Keddy, P. A. and Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. – Oikos 54: 234–241.
Marshall, S. B. 1995. Biogeochemical consequences of livestock grazing in a juniper-oak savanna. – M.S. thesis, Texas A&M Univ., College Station, TX.
McKenney, M. C. and Lindsey, D. L. 1987. Improved method for quantifying endomycorrhizal fungi spores from soil. – Mycologia 79: 779–782.
McNaughton, S. J. and Chapin III, F. S. 1985. Effects of phosphorus nutrition and defoliation on C_4 graminoids from the Serengeti Plains. – Ecology 66: 1617–1629.
Neter, J., Wasserman, W. and Kutner, M. H. 1985. Applied linear statistical models: regression, analysis of variance, and experimental designs. – R.D. Irwin.
Nye, P. H. and Tinker P. B. 1977. Solute movement in the soil-root system. – Univ. of California Press.
Poorter, H., van der Werf, A., Atkin, O. K. and Lambers, H. 1991. Respiratory energy requirements of roots vary with the potential growth rate of a plant species. – Physiol. Plant. 83: 469–475.
Ryser, P. and Lambers, H. 1995. Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. – Plant Soil 170: 251–265.
Sanders, I. R. and Fitter, A. H. 1992. The ecology and functioning of vesicular-arbuscular mycorrhizas in co-existing grassland species. II. Nutrient uptake and growth of vesicular-arbuscular mycorrhizal plants in a semi-natural grassland. – New Phytol. 120: 525–533.
Smeins, F. E. and Merrill, L. B. 1988. Longterm change in a semiarid grassland. – In: Amos, B. B. and Gehlbach, F. R. (eds), Edwards Plateau vegetation: plant ecological studies in central Texas. Baylor Univ. Press, pp. 101–114.
Smeins, F. E., Taylor, T. W. and Merrill, L. B. 1976. Vegetation of a 25-year exclosure on the Edwards Plateau, Texas. – J. Range Manage. 29: 24–29.
Smucker, A. J. M., McBurney, S. L. and Srivastava, A. K. 1982. Quantitiative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. – Agron. J. 74: 500–503.
St. John, T. V. and Koske, R. E. 1988. Statistical treatment of endogonaceous spore counts. – Trans. Br. Mycol. Soc. 91: 117–121.
Tennant, D. 1975. A test of a modified line intersect method of estimating root length. – J. Ecol. 63: 995–1001.
Teo, Y. H., Beyrouty, C. A., Norman, R. J. and Gbur, E. E. 1995. Nutrient uptake relationship to root characteristics of rice. – Plant Soil 171: 297–302.
Theodose, T. A., Jaeger III, C. H., Bowman, W. D. and Schardt, J. C. 1996. Uptake and allocation of ^{15}N in alpine plants: implications for the importance of competitive ability in predicting community structure in a stressful environment. – Oikos 75: 59–66.
Thornton, B., Millard, P., Duff, E. I. and Buckland, S. T. 1993. The relative contribution of remobilizatin and root uptake in supplying nitrogen after defoliation for regrowth of laminae in four grass species. – New Phytol. 124: 689–694.
Tilman, D. and Wedin, D. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. – Ecology 72: 685–700.
Trent, J. D., Wallace, L. L., Svejcar, T. J. and Christiansen, S. 1988. Effect of grazing on growth, carbohydrate pools, and mycorrhizae in winter wheat. – Can. J. Plant Sci. 68: 115–120.
van der Werf, A., van Nuenen, M., Visser, A. J. and Lambers, H. 1993. Contribution of physiological and morphological plant traits to a species' competitive ability at high and low nitrogen supply: a hypothesis for inherently fast- and slow-growing monocots. – Oecologia 94: 434–440.
Vucinic, Z. and Vuletic, M. 1995. The effect of addition of sucrose on the energy status and the trans-root electric potential difference of excised maize roots. – Plant Cell Physiol. 36: 45–52.

Wallace, L. L. 1987. Effects of clipping and soil compaction on growth, morphology and mycorrhizal colonization of *Schizachyrium scoparium*, a C_4 bunchgrass. – Oecologia 72: 423–428.

Wiedenfeld, C. C. and McAndrew, J. D. 1968. Soil survey of Sutton County, Texas. – Soil Conservation Service, U.S. G.P.O., Washington, DC.

Wilson, G. W. T. and Hartnett, D. C. 1997. Effects of mycorrhizae on plant growth and dynamics in experimental tallgrass prairie microcosms. – Am. J. Bot. 84: 478–482.

Yoder, C. K., Thurow, T. L., Carlson, D. H. and Caesar, B. L. 1995. Root distribution patterns of common curly-mesquite and sideoats grama on two Texas rangeland sites. – Southwest. Nat. 40: 273–280.