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Soil Depth and Changes in Dry Mass and Competitive Intensity of Two C_4 Grasses

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ABSTRACT

The presence of grassland biomes and species cannot be predicted by examining bottom up causes such as precipitation and temperature. Top down causes including herbivory and fire seem to be major controlling aspects with other factors secondary. We examined soil depth and competitive ability of two North American C_4 grasses in a greenhouse experiment. Changes in dry mass were determined and competitive intensity was calculated for both species. Species were grown separately or together in pots 30, 90, or 180 cm deep. When grown in monoculture, *Schizachyrium scoparium* total and belowground dry mass increased from the 30 to 90 cm depth, with no further significant increase from 90 to 180 cm. Aboveground dry mass did not increase significantly with depth. Total dry mass of *Buchloe dactyloides* increased significantly with depth when grown in monoculture. Aboveground dry mass increased from 30 to 90 cm depth but not from 90 to 180 cm. Belowground dry mass of *B. dactyloides* did not increase significantly with depth. In 180 cm pots, 53% of *S. scoparium* root dry mass was in the top 30 cm; 74% of *B. dactyloides* root dry mass was in the top 30 cm. Roots of *B. dactyloides* were not found deeper than 90 cm. Aboveground dry mass of *S. scoparium* was not different in mixture or monoculture at any depth. *Buchloe dactyloides* aboveground dry mass in mixture was significantly lower than monoculture at the 30 cm depth, but not at 90 or 180 cm. The greatest competitive intensity was in the shallow soil pots. Soil depth could partially explain mosaics found in C_4 grasslands where both species were found together with *S. scoparium* on deeper soils and *B. dactyloides* on shallower soils.

KEYWORDS

C_4 Grasses; Buffalo Grass; Little Bluestem; Dry Mass; Depth; Competitive Intensity; Semi-Arid Grasslands

1. Introduction

Native prairies in North America once covered almost four million km^2, but today only about one percent remains, with most converted to domestic use [1]. With changes, considerable encroachment and invasion of woody and herbaceous species have occurred [2]. On a large scale, grassland communities' seem relatively uniform, but on a small scale, they resemble a mosaic of miniature successions or patches and species composition may be controlled by different factors including resources [3,4]. These successions start with large or small scale disturbances creating patches or openings caused by fire, burrowing animals, large or small grazers, and drought [3]. These gaps or patches may serve as a reset mechanism [5] to reopen mature grasslands to early successional species [3] and then proceed in time toward a mature community. These patches may contain few or many species in various combinations and should be viewed both temporally and spatially [6].

Early successional species seem to require reduced competition or lower competitive intensity [7-9], increased soil surface light levels and soil resources for establishment [10-12]. These characteristics are found in disturbances, clearings, openings, or gaps. Many annuals

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are opportunistic, early successional species that could colonize grassland gaps and the characteristics of the gaps would determine the colonizing species [3]. As time passes, other species, with different characteristics and requirements, would establish in these gaps or patches. With the change in species composition, from early to mid or late, the community characteristics would also change. Late successional communities would not have the highly repetitive disturbance characteristics of early communities [9,13,14].

Grassland species and resources have patchy or heterogeneous distributions. In arid and semi-arid communities, water and soil nutrients are factors limiting the establishment and growth of many of these species [15-17]. In addition, soil depth and composition can directly determine water and nutrient availability and thus root depth and distribution [18]. In grasslands, 83% of the total belowground biomass is located in the upper 30 cm of soil [19]. However, differential rooting depth may allow partitioning of belowground resources leading to changes in growth and a reduction in belowground competition [20-23]. This partitioning may lead to spatial and temporal niche differentiation promoting coexistence of various species in grasslands [22-24].

In this paper, we examine the role of soil depth and how it influences aboveground, belowground and total dry mass of *S. scoparium* and *B. dactyloides*. In addition, we estimate how competitive intensity changes as a function of soil depth when the two species are grown together. We used three soil depths—30, 90, and 180 cm. We hypothesized that when grown in monoculture, above-, belowground and total dry mass of both species would increase from 30 to 90 cm depth, and that dry mass at 180 cm would be the same as at the 90 cm soil depth due to few roots in the deepest soil. We hypothesize that competitive intensity would be greatest in the shallowest soil depth examined (30 cm), but at the greater depths (90 and 180 cm) competitive intensity would decrease due to increasing soil resources and/or resource partitioning between the species.

2. Species Ecology, Characteristics and Distribution

Schizachyrium scoparium (Michx.) Nash. little bluestem, a mid-grass and *Buchloe dactyloides* (Nutt.) Engelm. buffalo grass, a shortgrass, can coexist in various grasslands [25-27]. *Schizachyrium scoparium* seems to increase on wetter-deeper soils and *B. dactyloides* increases on drier-shallower soils [28]. *Schizachyrium scoparium* and *B. dactyloides* can coexist on shallow-low nutrient soils in arid and semi-arid grasslands; but *B. dactyloides* would dominate on shallow-high nutrient soils [12]. However, effects of soil depth on competitive ability and distribution of these two species is not known. Thus, soil heterogeneity may play a role in determining the distribution and abundance of these two species.

The heterogeneity could be due to soil fertility, soil depth, or both; and could determine how the species compete and how they are distributed [12]. The ecological niche of these two species could be related to their rooting structure (shallow versus deep roots) or drought tolerance, and one species would usually be found on shallow-dry soils and the other on deep-wet soils. Thus, competition between the species could be reduced because of niche separation, which could explain their coexistence [29].

Schizachyrium scoparium occurs across North America, from Canada south to Mexico [30]. It has been found in all of the states in the continental United States, except Nevada and Alaska. *Schizachyrium scoparium* is an erect (0.5 to 2 m tall), C_4, native, warm-season, perennial grass that exhibits both a caespitose and sod-forming habit [31-33]. The mature root system is a network of finely branched rootlets to the third order [34]. The largest roots have a diameter of 0.5 to 1 mm, but root length shows considerable plasticity with length varying by soil type. Longer roots occur in sandy soils more than in silt loams, and may reach a length of 2.45 m. An example of the root distribution from a soil monolith taken from within a *S. scoparium* monoculture showed that 85.8% of the root biomass occurred in the top 15 cm soil depth, 5.3% in the next 15 cm, and 2.3%, 1.4%, and 2% in the next three 30 cm soil depths [34]. A comparison of *S. scoparium* root dry mass and distribution with depth in pastures under different grazing frequency showed that the depth distribution was the same across pastures, but there was a decrease in the dry mass with depth as grazing pressure increased [35].

Buchloe dactyloides occurs from Minnesota west to central Montana, and south to eastern Louisiana, Texas, New Mexico, eastern Arizona, and northern Mexico [36]. It is a C_4, warm-season, native, perennial, shortgrass which grows up to 30 cm in height [33]. *Buchloe dactyloides* is drought-, heat-, and cold-resistant. The roots of *B. dactyloides* are finer than those of most North American prairie grasses with a diameter < 1 mm. They tend to spread horizontally 15 to 46 cm in the top 15 cm of soil and to a depth of 180 cm [34]. The root dry mass taken from a soil monolith in a *B. dactyloides* monoculture showed the top 15 cm of soil contained 70% of the total dry mass, with 11.5% occurring in the next 15 cm, and 11, 4, and 3% of the dry mass in the next three 30 cm soil depth sequences [34,37].

3. Materials and Methods

Schizachyrium scoparium and *Buchloe dactyloides* seeds were obtained from a commercial seed company. A native Patrick soil which supports the growth of both spe-

cies was used in these experiments. Soil was the upper 20 cm of a clayey-over-sandy, carbonatic-thermic, typic calciustoll, with the "A" horizon depth from 25 to 41 cm [38] and was collected near the University of Texas at San Antonio (29˚34'55.55N, 98˚37'49.18W). Soil analysis indicated 7.5 $g \cdot kg^{-1}$ carbon, 11.6 $g \cdot kg^{-1}$ calcium, 1.3 $g \cdot kg^{-1}$ magnesium, 1.0 $mg \cdot kg^{-1}$ total nitrogen, 12.0 $mg \cdot kg^{-1}$ phosphorus, 138.0 $mg \cdot kg^{-1}$ potassium, and 196.0 $mg \cdot kg^{-1}$ sulfur. Plants were grown in a fiberglass greenhouse where daytime temperatures ranged from 26˚C to 38˚C. Photosynthetically active photon flux density (PPFD, 400 to 700 nm) in the greenhouse was 760 ± 96 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (mean ± 1 standard deviation), while outside mean PPFD was 2090 ± 139 $\mu mol \cdot m^{-2} \cdot s^{-1}$, with the sun at its zenith on a clear summer day. Light intensity was measured with a LI-Cor LI-88 integrating quantum sensor. Plants were watered as needed with deionized water, usually every day to maintain field capacity.

To examine effects of soil depth on above-, belowground and total dry mass of *S. scoparium* and *B. dactyloides* plants were grown in pots with three depths or lengths (30, 90, or 180 cm). There were five replications of each species and pot depth or length. To examine the effects of soil depth on aboveground dry mass and competitive intensity of the two species, a replacement experiment [39] was used. There were three main effects: species (2 levels; *S. scoparium* or *B. dactyloides*), soil depth (3 levels; 30, 90, or 180 cm), and planting combination (2 levels; alone [monoculture] or together [mixture]). There were five replications of each treatment, and density was held constant at two plants per pot. Thus, the proportion of *Schizachyrium*: *Buchloe* were 2:0, 1:1, and 0:2 plants per pot.

Seeds of both species were planted in the greenhouse on March 24 in 10-cm-diameter plastic pots (PVC pipe), with the bottom sealed with plastic bags (to prevent leaching of nutrients and water). Pots were 30, 90, and 180-cm-long and contained 2.4, 8.0, and 18.0 kg of air dried and sieved Patrick soil (described above), respectively. This resulted in the following nutrient amounts for the 30, 90 and 180 cm pots: N (2.4, 8.0, 18.0 $mg \cdot pot^{-1}$), P (28.8, 96.0, and 216.0 $mg \cdot pot^{-1}$), and K (331.2, 1,104.0, and 2484.0 $mg \cdot pot^{-1}$). No additional nutrients were added, and watering occurred *ad lib* to insure that water was not limiting and soil remained at field capacity. After 18 months and two growing seasons, plant tops were harvested by clipping at the soil surface. Tops were separated by species and dried at 110˚C to a constant mass. Ash-free belowground dry mass [40] of each monoculture pot was measured by carefully washing the soil from all the roots in each 30-cm segment, drying to a constant mass at 110˚C, weighing, ashing at 650˚C for 3-hr, reweighing, and subtracting. Roots of both species were fibrous and were not separated in pots containing mixtures, and not harvested. Thus, the effect of interspecific competition was only evaluated for aboveground dry mass.

Relative competitive intensity (RCI) [29] was calculated for each species in each depth treatment as follows:

$$RCI = (Ymono - Ymix)/Ymono$$

where: Ymono = dry mass of species in monoculture

Ymix = dry mass of species in mixture.

This measure of competitive intensity was equivalent to other common indices of competitive intensity (data not shown), [41].

To evaluate dry mass as a function of depth, only the data from monocultures were used. Above-, belowground, or total dry mass of the two species at the varying depths were appraised using two-way analyses of variance with species (2 levels) and soil depth (3 levels) as main effects, as well as the interaction term. The interaction term was not significant and removed from the model. To better understand how each species responded to depth, one-way analyses of variance of above-, belowground, or total dry mass of *S. scoparium* or *B. dactyloides* was used with depth (3 levels) as the main effect, followed by the Tukey-Kramer HSD multiple comparison test [42].

To compare the two species at each depth, one-way analyses of variance of above-, belowground, or total dry mass of *S. scoparium* or *B. dactyloides* at 30 cm, 90 cm, or 180 cm was conducted, with species (2 levels) as the main effect, followed by the Student's *t*-test [42]. To compare the distribution of roots with depth, one-way analyses of variance of belowground dry mass of *S. scoparium* or *B. dactyloides* from each of the 30 cm segments from the 90 cm or 180 cm pots were performed with segment number (90 cm = 3 levels; 180 = 6 levels) as the main effect. The distribution of roots between the two species was evaluated with one-way analyses of belowground dry mass for the 90 cm (3 segments) or 180 cm (6 segments) pots for each segment with species (2 levels) as the main effect. In some cases, data were either non-normal (Shapiro Wilk's Test) or the variances were not equal (Bartlett's Test). Data were logarithmically transformed which improved normality or corrected the heterschedasticity.

To estimate competition, three-way analyses of variance were performed on aboveground dry mass per plant of *S. scoparium* or *B. dactyloides*. Monoculture dry mass per pot was divided by two to obtain the mean dry mass per plant for the analyses. Main factors were species (2 levels), soil depth (3 levels), and planting combination (2 levels). All first and second order interactions were also entered into the model. To better evaluate the effects of soil depth and planting combination for each species, two-way analyses of variance were performed on aboveground dry mass per plant of *S. scoparium* or *B.*

dactyloides with soil depth (3 levels) and plant combination (2 levels) as main effects, as well as the interaction. For each species and at each soil depth, Student's *t*-tests of aboveground dry mass between planting combination (alone or mixture) were performed. In addition, for each species and within each planting combination, one-way analyses of variance of aboveground dry mass were performed with depth as the main effect, followed by the Tukey-Kramer Multiple Comparison test.

4. Results

4.1. Changes in Dry Mass across Soil Depths

No significant differences were found in aboveground dry mass plant^{-1} of *Schizachyrium scoparium* with increasing soil depth; however, aboveground dry mass doubled in the 90 cm pots and remained the same at 35.5 ± 7.1 g·plant^{-1} dry mass in the 180 cm pots (**Figure 1(a)**). Belowground dry mass of *S. scoparium* was significantly lower in the 30 cm deep pots at 4.1 ± 0.1 g·plant^{-1} compared to the 90 and 180 cm deep pots, which were not significantly different from one another (**Figure 1(b)**). Belowground dry mass in the 180 cm deep pots was 17.1 ± 1.8 g·plant^{-1}. Total dry mass for *S. scoparium* increased from 20 g·plant^{-1} to 42 g·plant^{-1} and then to 48 g·plant^{-1} as soil depth increased (**Figure 1(c)**), with dry mass being significantly different in the 90 and 180 cm pots compared to the 30 cm pots, but deeper pots were not significantly different from each other.

Aboveground dry mass of *Buchloe dactyloides* was significantly lower in the 30 cm deep pots (8.0 ± 0.2 g·pot^{-1}) than the 90 and 180 cm deep treatments, which were not significantly different from one another (**Figure 1(a)**). Aboveground dry mass increased from 8 g·plant^{-1} to 18 g·plant^{-1} and then to 25 g·plant^{-1} as soil depth increased. Belowground dry mass of *B. dactyloides* was not significantly different across the varying depths (**Figure 1(b)**), although dry mass was greatest at 6.0 ± 1.0 g·plant^{-1} in the 180 cm deep pots. Total dry mass of *B. dactyloides* increased significantly from 12 g·plant^{-1} to 22 g·plant^{-1} to 32 g·plant^{-1} with each increase in soil depth (**Figure 1(c)**).

Aboveground and total dry mass of *S. scoparium* was significantly greater than *B. dactyloides* at the 30 cm depth (**Figures 1(a)** and **(c)**); belowground and total dry mass of *S. scoparium* was significantly greater than *B. dactyloides* at the 90 cm depth (**Figures 1(b)** and **(c)**); and no differences in above-, belowground, and total dry mass were found in the 180 cm deep treatment (**Figure 1**), although *S. scoparium* had 29% more total dry mass than *B. dactyloides*.

4.2. Depth Distribution of Belowground Dry Mass

Changes in belowground dry mass as a function of depth

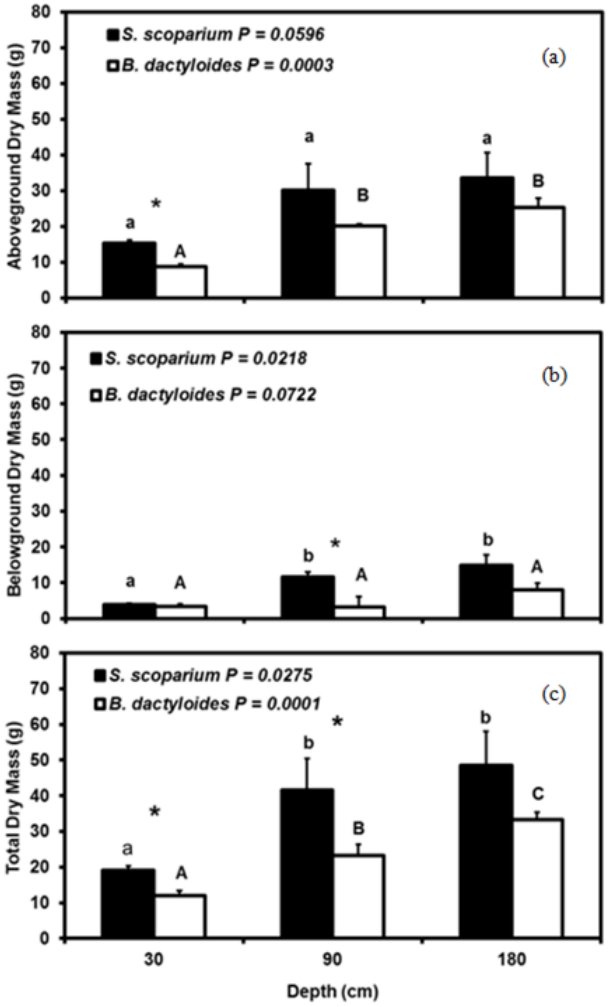

Figure 1. a) Aboveground; b) Belowground dry mass and c) Total dry mass per plant of *Schizachyrium scoparium* (■) and *Buchloe dactyloides* (□) when grown at a depth of 30, 90, and 180 cm. The probability values for the effects of depth for each species are presented. Bars with the same lower case letter indicate no significant differences in dry mass per plant for *S. scoparium* and bars with the same upper case letter indicate no significant differences in dry mass per plant for *B. dactyloides* (Tukey-Kramer HSD). An asterisk indicates significant differences between *S. scoparium* and *B. dactyloides* (Student's *t* test). Error bars represent one standard error of the mean for dry mass.

are presented in **Figure 2**. Regardless of the soil depth (90 or 180 cm), *S. scoparium* belowground dry mass was significantly greater than *B. dactyloides* in each of the 30 cm segments. In the 90 cm depth treatment, both *S. scoparium* and *B. dactyloides* belowground dry mass were significantly greater in the top 0 - 30 cm compared to the 30 - 60 cm segment or 60 - 90 cm segment, which were not significantly different from one another (**Figure 2(a)**). In the 90 cm pots, 7.5 g·plant^{-1} (65%) of *S. scoparium* root was found in the top 30 cm, followed by 1.6 g·plant^{-1} (14%) and 2.3 g·plant^{-1} (21%) in the next two 30

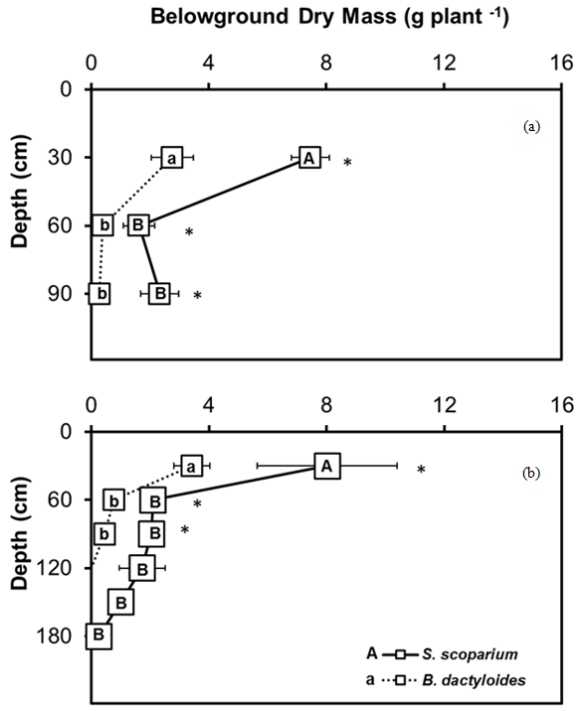

Figure 2. Belowground dry mass per plant for 30 cm segments for depths of A) 90 cm and B) 180 cm. Means with the same upper case letter (*S. scoparium*) or lower case letter (*B. dactyloides*) are not significantly different (ANOVA; Tukey-Kramer HSD). For each depth and segment, *S. scoparium* had a significantly higher belowground dry mass than *B. dactyloides* (Student's *t* test [*]). In the 180 cm depth, no *B. dactyloides* roots were found in the bottom three segments, and the data were not included in the analysis. Error bars represent one standard error of the mean. If not shown, standard errors of the mean are smaller than the symbol.

cm segments. For *B. dactyloides* in the 90 cm pots, 2.76 g·plant^{-1} (81%) was found in the top 30 cm segment, followed by 0.39 g·plant^{-1} (11%) and 0.28 (8%) in the next two 30 cm segments.

Changes in belowground dry mass in the 180 cm deep pots were similar to the 90 cm deep pots (Figures 2(a) and (b)). Both *S. scoparium* and *B. dactyloides* belowground dry mass was significantly greater in the first 30 cm depth segment than all other depth segments (Figure 2(b)). For *S. scoparium*, belowground dry mass was not significantly different in any of the deeper 30 cm depth segments. In the 180 cm pots, 8.0 g·plant^{-1} (53%) of *S. scoparium* root dry mass was found in the top 30 cm, followed by 2.1 (14%), 2.0 (13%), 1.7 (11%), 1.0 (7%), and 0.3 (2%) g·plant^{-1} in the deeper, sequential 30 cm segments. For *B. dactyloides* in the 180 cm pots, there was 3.4 g·plant^{-1} (73%) in the upper 30 cm depth segment, followed by 0.8 (17%) and 0.5 g·plant^{-1} (10%) in the next two 30 cm segments. For *B. dactyloides*, no roots were found in the bottom three soil segments. The belowground dry mass in the 30 - 60 cm segment and 60 - 90 cm segment were significantly lower than the top 30 cm segment, but they were not significantly different from one another.

4.3. Differences in Competition with Soil Depth

Competition of the two species was significantly different across the soil depth treatments. Soil depth and planting combination (alone [monoculture] or together [mixture]) had no significant effect on aboveground dry mass of *S. scoparium* (Table 1). Conversely, both soil depth and planting combination had significant effects on aboveground dry mass of *B. dactyloides* (Table 1). No significant differences were found in aboveground dry mass of *S. scoparium* with increasing soil depth, regardless of whether grown alone or in mixture (Figure 3(a)). In addition, aboveground dry mass in mixture was the same as dry mass when grown alone in all depth treatments (although dry mass increased from approximately 17 g·plant^{-1} in the 30 cm pots to approximately 27 g·plant^{-1} in the 90 and 180 cm deep pots, Figure 3(a)).

For *B. dactyloides*, aboveground dry mass was significantly lower in the 30 cm deep pots, compared to the 90 and 180 deep ones (approximately 5 g·plant^{-1} versus about 20 g·plant^{-1}), regardless of whether it was grown alone or in mixture with *S. scoparium* (Figure 3(b)). Significant differences were found in the 30 cm deep pots with a 59% reduction in *B. dactyloides* aboveground dry mass when it was grown with *S. scoparium* (Figure 3(b)). No significant differences in *B. dactyloides* aboveground dry mass were found in the 90 and 180 cm deep pots when mixture and monoculture dry mass were compared. In all depth treatments, aboveground dry mass of *B. dactyloides* was reduced when grown with *S. scoparium*, but differences were 9% - 14% in the deeper pots compared to about 5 g·plant^{-1} or about 59% reduction in the 30 cm deep pots (Figure 3(b)).

Relative aboveground competitive intensity was calculated for the two species at all three depths (Figure 4). Competitive intensity was greatest in the 30 cm depth treatments for *S. scoparium* (−0.46) and for *B. dactyloides* (+0.58) and was lower in the 90 or 180 cm soil depths (Figure 4). In the 90 cm deep pots, relative aboveground competition intensity for *S. scoparium* was very close to zero at −0.02 and for *B. dactyloides* it was +0.11. In the 180 cm deep soil pots relative aboveground competition intensity was low, but higher than in the 90 cm treatments at +0.12 for *S. scoparium* and +0.22 for *B. dactyloides*.

5. Discussion

Changes in dry mass and competitive intensity of *S. scoparium* and *B. dactyloides*, two C_4 grasses, were studied. This was done as a function of soil depth in the green

Table 1. *F*-ratio and *P*-value for two-way analysis of variance of aboveground dry mass for *Schizachyrium scoparium* and *Buchloe dactyloides*, with depth (3 levels, 30, 90, and 180 cm) and planting combination (2 levels, alone [monoculture] or mixture) as the main effects. The interaction terms was not significant and removed from the model. The error term degrees of freedom was 24.

	Source	DF	*F*-ratio	*P*-value
Species				
	Depth	2	1.61	0.2218
Schizaciryrium	Planting			
scoparium	Combination	1	0.05	0.8175
	Depth	2	29.87	0.0001
Buchioe	Planting			
dactvloides	Combination	1	10.39	0.0036

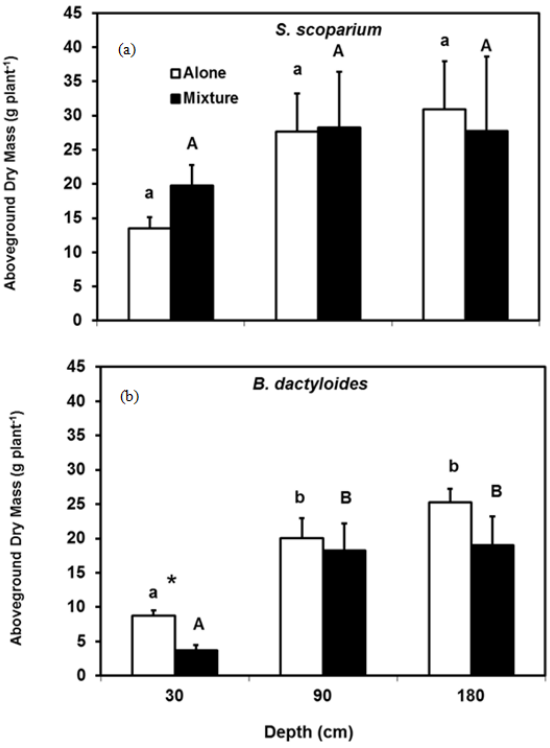

Figure 3. Aboveground dry mass per plant when grown alone (□) and in mixture (■) for each depth for a) *Schizachyrium scoparium* and b) *Buchloe dactyloides*. Bars with the same lower case letter indicate no significant differences in aboveground dry mass when grown alone and bars with the same upper case letter indicate no significant differences aboveground dry mass when grown in mixture (ANOVA; Tukey-Kramer HSD). An asterisk indicates significant differences between growth alone and in mixture (Student's T-test). Error bars represent one standard error of the mean.

house to better understand the association and interaction of these two species. *Schizachyrium scoparium* and *B. dactyloides* coexist in some grasslands [25,27], nevertheless *S. scoparium* seems to increase on wetter-deeper

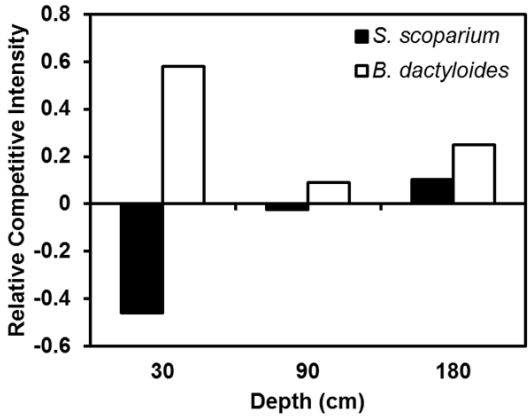

Figure 4. Relative competitive intensity (RCI = [Ymono – Ymix]/Ymono) for *Schizachyrium scoparium* (■) and *Buchloe dactyloides* (□) at three soil depths (30, 90, and 180 cm) was calculated using aboveground dry mass. Dry mass at a proportion of 1:1 was used for Ymix.

soils and *B. dactyloides* increases on drier-shallower soils [28]. It is not clear if biotic or abiotic factors promote the habitat selectivity. Thus, soil heterogeneity including depth and nutrient level could play a role in determining the association, distribution, abundance and overlap of these two species. Many studies have documented increases in grass biomass with increased soil volume [43], soil depth [21], and gap sizes [44,45]. Biomass changed disproportionally with neighbor root densities, but for some species biomass increased and with other species biomass decreased [46]. Further, successional patterns and species distributions in time and space have been shown to be highly dependent upon soil depth patterns within some grasslands [47].

The root niche differentiation hypothesis [48] suggests that water reaching below the grass root zone would be accessible to deep rooted woody plants suggesting niche separation and therefore reduced competition and facilitation of co-existence of these two very dissimilar plant types. This does not seem to be the factor that allows woody plants to establish and exist with grasses in C_4 grasslands and savannas which seems to be controlled by top down factors including fire and herbivory [13]. However, it seems that soil depth reduces competition and promotes co-occurrence of some grassland species including the two C_4 species in the current study.

A previous study showed that root dry mass of *S. scoparium* was equally distributed through the soil column when growth was limited to a soil depth of 90 cm. However, when the soil depth was increased to 180 cm 80% of the root dry mass was found in the top 30 cm of soil [21]. The results of root distribution of *S. scoparium* in the current experiment are similar to those reported from soil monoliths collected in the field [34]. Other factors which have been shown to influence the growth and dis-

tribution of *S. scoparium* roots are soil type and past land use, with dry mass decreasing with grazing intensity but depth distribution being relatively constant [34,35]. Two other studies found approximately 80% of the root dry mass of *S. scoparium* in the top 30 cm in a silt loam soil monolith of 120 cm total depth [34,37].

It has been suggested that community structure can be determined by the level of competitive intensity [49], but this contention appears equivocal [50,51]. Competitive intensity appears lower in environments where growth is limited by abiotic factors [39]. We reported here that competitive intensity was reduced for both species when soil depth increased (**Figure 4**). *Schizachyrium scoparium* was able to reduce the growth of *B. dactyloides* in the shallow soil, but with increased soil depth and increased soil resources, competitive intensity decreased and the two species performed the same in mixture as in monoculture at the same depth. The plants in the current study were started from seed; consequently extrapolation should be limited to establishment in disturbances or gaps. In addition, we did not compare competition between seedlings and adults *per se*. Gaps or disturbances are important for creating mosaics in vegetation and have a wide range of spatial scales [5,6,52,53].

The importance of soil resources in determining competitive outcomes between plants in arid, shortgrass prairies is unclear. In some studies, nutrient levels had no effect on competition or community composition [54]. In others, changes in community composition occurred with increases in soil nutrients [55-57]. *Buchloe dactyloides* was a better competitor than B. gracilis, regardless of the level of soil fertility [57] and *B. dactyloides* has also been shown to reduce the growth of seedlings of a woody plant, *Prosopis glandulosa* (mesquite) [58]. A previous study with *S. scoparium* and *B. dactyloides* in shallow pots showed that soil resources were important, with *B. dactyloides* reducing the growth of *S. scoparium* when soil nutrients were high [12].

Results of other experiments concerning the role of soil resources in determining the growth and competitive ability of *S. scoparium* are equivocal. In monoculture, increased levels of nitrogen did not affect the growth rate of *S. scoparium* [51]. Other studies indicated that added nitrogen increased the dry mass of *S. scoparium* [59]; and there is a suggestion that the response of *S. scoparium* to soil nitrogen may be water dependent [60]. In the current study, we found that increased soil depth (volume and concomitantly the amount or availability of soil resources) increased the dry mass of *S. scoparium* in monoculture from 20 $g \cdot plant^{-1}$ in 30 cm deep soil to 48 $g \cdot plant^{-1}$ in the deepest soil tested. When in competition with a southern mid-grass (*Paspalum plicatulum*) at various soil depths, *S. scoparium* was an equal competitor at a depth of 30 cm, but *P. plicatulum* out-competed *S. scoparium* at depths of 90 and 180 cm [21], probably because *P. plicatulum* could access deeper soil resources.

When *S. scoparium* was examined in common garden competition experiments, it was one of the strongest competitors [51], however, in field experiments it was one of the most suppressed species [51,61]. In unfertilized plots, belowground competition limited *S. scoparium*; while in fertilized field plots, both above- and belowground competition limited *S. scoparium* [51]. Further, tilling or disturbance decreased the cover of *S. scoparium* in a mixed prairie [51]. *Schizachyrium scoparium* can reduce soil nitrate at shallow soil depths and in the middle of the growing season, thus deeper rooted and earlier growing species are more likely to be co-dominants [22]. Apparently *S. scoparium* is restricted to low productivity habitats or deeper soils [61-63].

The findings from the current greenhouse experiment between *S. scoparium* and *B. dactyloides* suggest that increased depth either 1) allows resource partitioning or 2) increases soil nutrients so that they are not limiting due to soil volume. However, based on previous experiments, we would expect *B. dactyloides* to be the better competitor when soil resources are higher [12]. This, and the root distribution pattern presented in **Figure 2**, lead to the conclusion that the increased depth and differential root growth patterns of these two species allows resource partitioning.

We examined the effects of soil depth on the dry mass production and distribution in the soil column and the competitive intensity between *S. scoparium* and *B. dactyloides* two C_4 grasses. However, competition for light or light levels could also be a factor in determining the competitive interaction and community structure in arid and semiarid grasslands, especially for seedlings. Based on morphology, it might be expected that *S. scoparium* could shade the shorter *B. dactyloides*. Above- and belowground competition were not separated in this current experiment, and we suggest that aboveground competition could have been a factor in our experiment reducing the dry mass of *B. dactyloides* and could also be important in the field.

Ideally, field experiments would give a more realistic view of the growth and interaction of these two species, but conducting experiments in the field to evaluate soil depth is difficult at best. Our results indicated soil depth could play an important role in determining community structure in North American grasslands where these two species co-occur especially in arid or semiarid communities, particularly during the plant establishment phase. Plants segregate along a variety of niche axes, including light, soil moisture, rooting depth, partitioning of soil nutrients and combinations of these factors [24]. This segregation seems to facilitate coexistence. In a previous study with these two species [12], we reported that in

shallow soil, partitioning of soil resources does not occur. During the establishment phase in shallow, low soil nutrient patches, *B. dactyloides* and *S. scoparium* would coexist, while in shallow, high soil nutrient patches, *B. dactyloides* would be the dominate species. From the current experiment, *S. scoparium* reduced the aboveground dry mass of *B. dactyloides* at the shallower depth, but in 90 or 180 cm deep soils, resources were no longer limiting or resource partitioning seemed to occur with a reduction of competition and therefore coexistence of the species.

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