

THE IMPORTANCE OF NEIGHBORS, SOIL pH, PHOSPHORUS, AND NITROGEN FOR THE GROWTH OF TWO C₄ GRASSES

O. W. VAN AUKEN¹ AND J. K. BUSH

Division of Life Sciences, University of Texas at San Antonio, San Antonio, Texas 78249-0662

In the coastal prairies of Texas, C₄ grasses dominate. However, reasons for spatial differences in composition of these prairies are uncertain, and the reasons for codominance of *Schizachyrium scoparium* and *Paspalum plicatulum* are unexplained. We completed a greenhouse experiment that examined the effects of neighbors, soil pH, added P, and N on the growth of *P. plicatulum* and *S. scoparium*, two C₄ grasses. Intraspecific competition was essentially equal to interspecific competition, and soil factors seem to control dry mass of these two species. For *P. plicatulum*, addition of P to native soil increased above- and belowground dry mass 1.8–2.5 times, while P and N together increased dry mass 2.9–6.5 times. The response was pH dependent, with the greatest dry mass at low pH. Root:shoot ratios changed from 0.3 to ca. 1.0 as the pH decreased in native soil regardless of the P level. When N was added, ratios were ca. 0.3 across all pH and P treatments. For *S. scoparium* in native soil, there was little change in aboveground dry mass when P was added; however, belowground dry mass was augmented 1.5–1.9 times, with the greatest dry mass at pH 7.0. Additions of P and N increased aboveground dry mass 2.2–2.7 times, with the greatest dry mass at pH 7.0. N additions caused reductions of 79%–89% in belowground dry mass compared with that of native soil, at all levels of P and pH. Root:shoot ratios were 5–10 times higher in the native soil compared with N addition treatments and increased to 1.0 as pH decreased. Ratios were about 15% higher with P added to native soil and remained constant at ca. 0.1 in all the N addition treatments. These two C₄ grasses seem to be competitively equal. Their growth was not determined by the presence of neighbors but by levels of soil resources and soil pH.

Introduction

In pre-Columbian central North America, grasslands were essentially continuous from Manitoba, Canada, through Texas, to the Gulf of Mexico (Gould 1968; Risser et al. 1981). Tallgrass prairies were located in the eastern part of this grassland biome, but only remnants remain (Kuchler 1964; Samson and Knopf 1994). These prairies include various geographic subdivisions, including the true prairies in the north and the coastal prairies in Texas just inland from the Gulf of Mexico (Estes et al. 1982; Diamond and Smeins 1988; Smeins et al. 1991). In the tallgrass prairies, species composition changes from north to south, with C₃ grasses dominant in the north and C₄ grasses in the south (Terri and Stowe 1976; Diamond and Smeins 1988). The native coastal prairies of Texas are dominated by *Schizachyrium scoparium* (Michx.) Nash (little bluestem), *Paspalum plicatulum* Michx. (brownseed paspalum), and *Sorghastrum nutans* (L.) Nash (Indian grass), all C₄ grasses (Diamond and Smeins 1983, 1984, 1988).

In the coastal prairies of Texas, *S. scoparium* and *S. nutans* are found on soils with pH values of 5.2–7.4 (Diamond and Smeins 1983, 1985). Both species had frequency values of 50%–100%, and frequency was positively correlated with soil pH. *Paspalum plicatulum* occurred over the same pH range but only had high frequency values on the low-pH soils (5.2–6.4). These low-pH soils also had a lower clay content, which indicates a possible nutrient gradient; but, on low-phosphate soils, optimum pH for growth was the same for both species (Jurena and Van Auken 1996).

We found *S. scoparium*, *P. plicatulum*, and *S. nutans* as community dominants on the coastal prairies of Texas with relatively constant dry mass over several years (Diamond and Smeins 1984; Van Auken et al. 1992a). In addition, adding N, shading, lack of grazing, and burning caused *S. nutans* dry mass to increase. In greenhouse experiments, growth of *P. plicatulum* was favored over *S. scoparium* at low N levels regardless of light level, but adding N increased *S. scoparium* dry mass when the two species were grown together (Van Auken et al. 1992b). In addition, *P. plicatulum* dry mass was four times greater than *S. scoparium* in 180-cm compared with 30-cm deep pots, which demonstrates that soil depth was important in defining the species' niche (Van Auken et al. 1994).

In addition to these studies demonstrating the importance of light levels, pH, and soil resources for the growth of these C₄ prairie species, we have measured significant interspecific competition between *S. scoparium* and *P. plicatulum*, but only in a few cases. Competition between species is constantly cited as one of the major factors determining community composition and structure (Harper 1977; Grime 1979; Grace and Tilman 1990; Bazzaz 1990), but it is not the only factor (Callaway et al. 1996; Pugnaire et al. 1996), and it is a consistently debated topic (Grace 1993, 1995; Goldberg 1994; Twolan-Strutt and Keddy 1996). If interspecific competition is so important in determining community composition and structure, it seems we should be able to detect it more frequently. Competition has been reported in a large number of studies (reviewed in Schoener 1983), but intraspecific competition was as strong or stronger than interspecific competition in 75% of the examples evaluated (Connell 1983). Thus, greater interspecific compared with intraspecific competition has not been found as often as one might expect.

¹Author for correspondence and reprints. Fax 210-458-5658; E-mail oauken@post3.utsa.edu.

Manuscript received May 1996; revised manuscript received December 1996.

Although previous studies demonstrated some of the factors that determine the growth and interaction of these C_4 grasses, they do not explain the codominance of the two species on acidic soils or the disappearance of *P. plicatulum* in more basic soils of the coastal prairies. Here we examined the effect of soil pH, added P, and N on the growth of *P. plicatulum* and *S. scoparium* in monocultures. In addition, we examined the interaction of these species in mixtures when soil pH, P, and N were altered. We hypothesized that *P. plicatulum* dry mass would be highest in low-pH soil, whereas *S. scoparium* would have equal dry mass across the pH range tested. We also hypothesized that the two species would be equal competitors in low-pH soils and that *S. scoparium* would be competitively superior in more basic soils. Finally, we hypothesized that the addition of P would alter the interaction between the two species because of changes in solubility as a function of pH.

Material and methods

A fiberglass greenhouse was used for plant growth, in which daytime temperatures ranged from 26° to 38°C. Photosynthetically active photon flux density (PPFD, 400–700 nm) in the greenhouse was $562 \pm 135 \mu\text{mol m}^{-2} \text{s}^{-1}$ (outside PPFD = $1542 \pm 18 \mu\text{mol m}^{-2} \text{s}^{-1}$, $\bar{X} \pm \text{SD}$ averaged over the experiment). Light level was measured with a LI-COR LI-188 integrating quantum sensor.

A factorial experiment was used to evaluate the effects of soil pH (three levels), soil P (two levels), soil N (two levels), and competition (two levels) on the above- and belowground dry mass of *Paspalum plicatulum* and *Schizachyrium scoparium*. There were five replicates of each treatment for a total of 240 pots in the experiment. The three soil pH levels tested were 5.6, 7.0, and 8.2. These values span the range of soil pH in which these two species are found in the field. Soil P levels included native soil (3.67 mg kg^{-1}) and P additions in the form of Na_2HPO_4 to increase the P level by 100 mg kg^{-1} . Soil N levels included native soil (1.67 mg kg^{-1}) and N additions in the form of NH_4NO_3 to increase the N level by 100 mg kg^{-1} . These concentrations of P and N have been used in other studies with similar soil type and with *S. scoparium* and other C_4 grasses (Hossner et al. 1992). Competitive levels consisted of each species grown alone at a density of two plants/pot or in mixture at a proportion of 1:1, *P. plicatulum*:*S. scoparium*. Previous experiments showed that two of these C_4 perennials per pot caused a 40%–50% reduction in per-plant dry mass, and four caused an additional, similar decrease. Further increases in density have smaller effects on dry mass per pot or per plant. The per-plant relationship is a reciprocal function for both species.

Rhizomes of *P. plicatulum* collected from a site in Bastrop County, Texas (30°2'N, 97°25'W), and seedlings of *S. scoparium* germinated from commercial seeds were transplanted into 15 cm deep \times 15 cm diameter pots lined with plastic bags (to prevent nutrient loss) containing 1700 g of native soil. Initial dry mass of *P. plicatulum* and *S. scoparium* was $0.39 \pm 0.03 \text{ g}$ and $0.27 \pm 0.05 \text{ g}$, respectively ($\bar{X} \pm \text{SD}$; $n = 5$). The soil was the upper 20 cm of a Lilbert Variant Series, classified as loamy fine sand, siliceous, thermic Arenic Plinthic Paleudult (Dolezel 1980). Soil was air dried, sieved (6.44-mm mesh), and mixed for uniformity. Analysis of three independent soil samples indicated that mean soil

pH was 6.1 (Texas Agricultural Extension Service Soil Testing Laboratory). A series of soil titrations were completed to determine the amount of HCl or $\text{Ca}(\text{OH})_2$ to add to each pot to obtain the experimental soil pH values ($\text{pH} = -17.78 \times \text{mL of } 0.1 \text{ N HCl per g of soil} + 6.15$, $r = 0.98$, $P \leq 0.0001$; $\text{pH} = 540 \times \text{g of } \text{Ca}(\text{OH})_2 \text{ per g of soil} + 6.59$, $r = 0.97$, $P \leq 0.0001$). After transplanting, soil was thoroughly wetted with deionized water, and then plants were watered as needed, usually everyday with ca. 150 mL. Soil pH was measured at the end of the experiment and found to be within approximately 0.2 pH units of the starting value.

Four and one-half months after planting, plant tops were harvested by clipping at the soil surface, separated by species, and dried at 100°C to a constant mass. Ash-free belowground dry mass (Böhm 1979) was measured by carefully washing the soil from all roots, separating by species, drying to a constant mass at 100°C, weighing, ashing at 650°C for 3 h, reweighing, and subtracting the inorganic component. Absolute competition intensity was calculated as monoculture dry mass per plant minus mixture dry mass per plant (Grace 1995). A positive value indicated higher monoculture dry mass, and a negative value indicated a higher mixture dry mass.

Separate ANOVAs were performed on above- and belowground dry mass of each species grown in monoculture. Main factors included pH (three levels), soil P (two levels), and soil N (two levels). Also included in the model were all first- and second-order interactions (Steel and Torrie 1980; SAS Institute 1985). Cell variances were homogeneous within each ANOVA (by the F_{max} test; Tietjen and Beckman 1972).

To examine competitive effects, four-way ANOVAs were performed on above- and belowground *P. plicatulum* or *S. scoparium* dry mass per plant (monoculture dry mass per pot was divided by two, to obtain the mean dry mass per plant). Main factors were soil pH, soil P, soil N, and competition. Interactions included all first-, second-, and third-order interactions among the four main factors. Competition was a significant factor for *S. scoparium*; therefore, further analyses of competition included a comparison of monoculture and mixture *S. scoparium* dry mass within each treatment using one-way ANOVAs, with competition (monoculture or mixture) as the factor.

Results

For *Paspalum plicatulum*, aboveground dry mass in monoculture, all main factors (pH, P, and N) were significant, as were the two- and three-way interactions (fig. 1). For belowground dry mass, pH and phosphate, as well as their interaction, were significant. There was no significant pH effect for aboveground dry mass in the native soil treatment, but there was a 1.8–2.5-fold increase in dry mass at each pH tested as a result of P additions (fig. 1A). If N was added but not P (fig. 1B), there was no significant pH effect and no significant difference in aboveground dry mass when compared with native soil (fig. 1A). When both N and P were added (fig. 1B), there was a significant pH-dependent increase in aboveground dry mass, with the pH 5.6 treatment having 2.9 times more dry mass than the pH 8.2 treatment. Similar significant trends were seen with belowground dry mass (fig. 1C, D). In the native soil, belowground dry mass was pH dependent, increasing to the highest levels in the pH 5.6 treatment

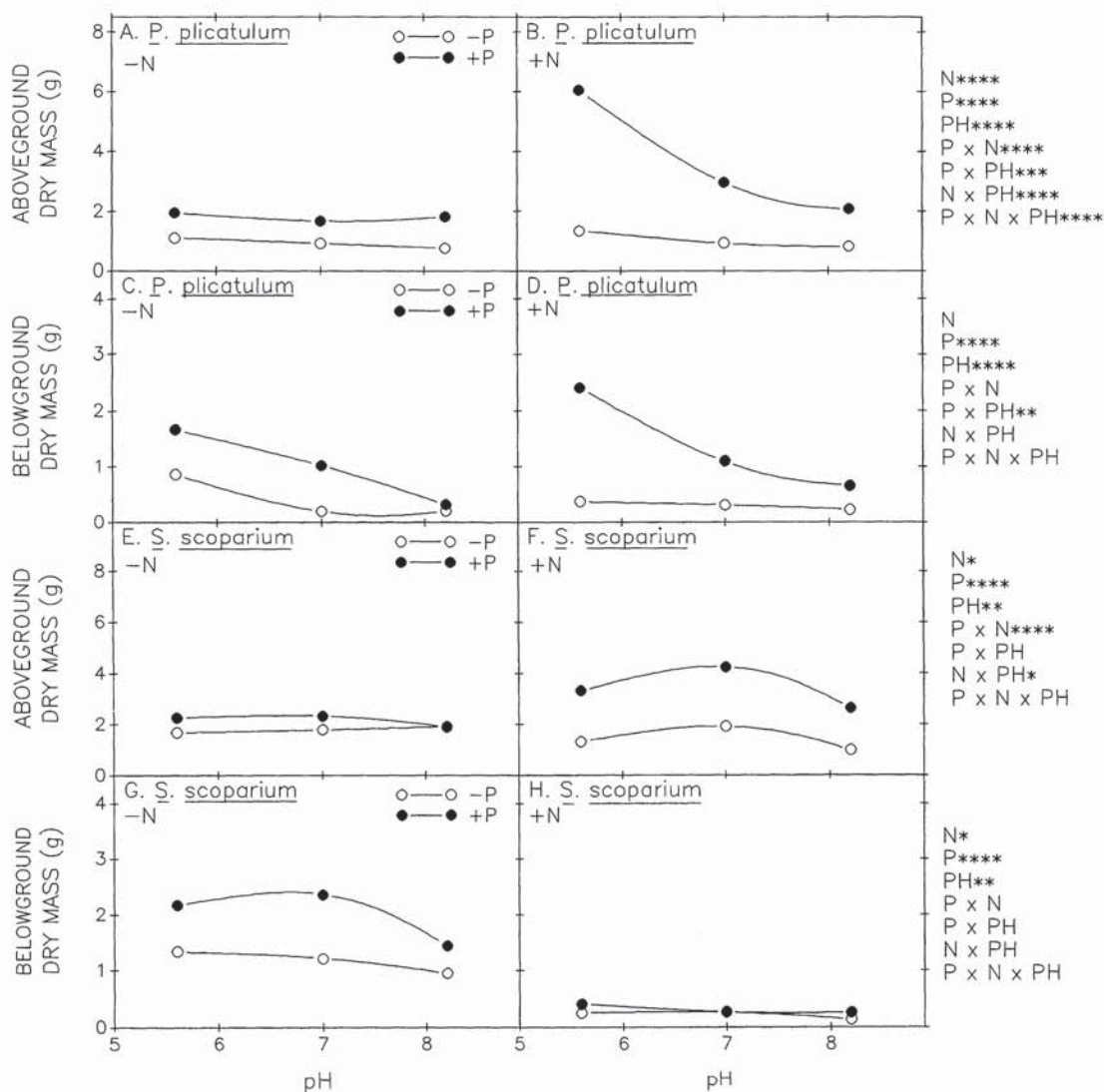


Fig. 1 Aboveground and belowground dry mass of *Paspalum plicatulum* (A–D) and *Schizachyrium scoparium* (E–H) grown in monocultures at soil pH's from 5.6 to 8.2. Soil was a siliceous loamy fine sand containing 3.67 mg kg⁻¹ P and 1.67 mg kg⁻¹ N. The –N–P indicates native soil with no added N or P. The +N+P indicates the soil was amended with 100 mg kg⁻¹ N and P. Each pair of panels (e.g., A, B) represent a three-way interaction between pH, N, and P for that variable. Results of the ANOVA are found to the right of each pair of panels; N, nitrogen effects; P, phosphate effects; and pH, pH effects. Interaction between these effects are shown as adjacent letters (NP, e.g.). Significance levels: **P* < 0.05, ***P* < 0.01, ****P* < 0.001, and *****P* < 0.0001.

and raised 1.9 times with added P (fig. 1C). In the N addition treatments, P additions elevated belowground dry mass 2.9–6.5 times and was pH dependent with the highest value at pH 5.6 (fig. 1D).

For *Schizachyrium scoparium*, aboveground and belowground dry mass, all main factors (pH, P, and N) were significant, as were the two-way interactions between N and P, and pH and N for aboveground dry mass (fig. 1). In native soil, there was no pH effect and little increase in aboveground dry mass as a result of P additions (fig. 1E). If N was added but P was not (fig. 1F), there was no pH effect and no difference in aboveground dry mass compared with the native soil treatment (fig. 1E). When both N and P were added (fig. 1F), there was a significant increase in aboveground dry mass (2.2–2.7 times), and it was pH-dependent, with the pH 7.0 treatment having 22%–38%

more dry mass than either the pH 5.6 or 8.2 treatments. In the native soil (fig. 1G), the additions of P augmented belowground dry mass 1.5–1.9 times, with the greatest increase at pH 7.0. With the additions of N (fig. 1H), belowground dry mass was reduced 79%–89% compared with native soil (fig. 1G), and the effect was independent of pH and P.

For *P. plicatulum* root : shoot ratios, pH was the only significant main factor, and none of the interactions were significant (fig. 2). Ratios increased from 0.3 to ca. 1.0 as the pH decreased in the native soil (fig. 2A). When N was added, the ratio was ca. 0.3 regardless of the P levels or pH (fig. 2B). For *S. scoparium* root : shoot ratios, soil N was the only significant main factor, and none of the interactions were significant (fig. 2). Ratios were ca. 15% higher in the native soil when P was added and increased to 1.0 as the pH decreased

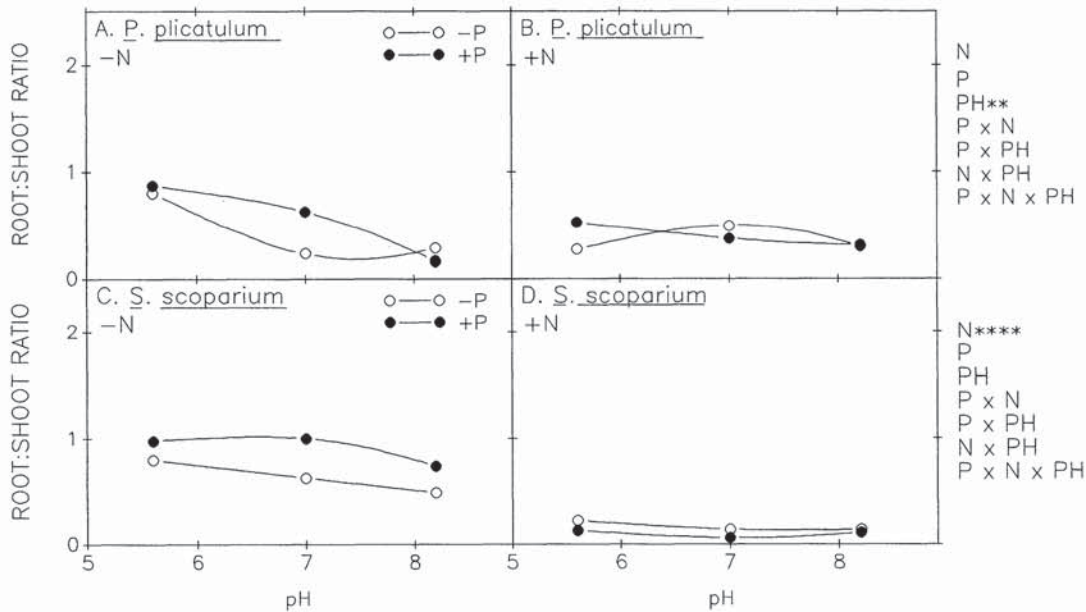


Fig. 2 Root:shoot ratios for *Paspalum plicatulum* (A, B) and *Schizachyrium scoparium* (C, D) grown in monoculture at soil pH's from 5.6 to 8.2. The -N-P was native soil, and the +N+P was amended with 100 mg kg⁻¹ of N and P. Results of the ANOVA are found to the right of each pair of panels; N, nitrogen effects; P, phosphate effects; and pH, pH effects. Interaction between these effects are shown as adjacent letters (NP, e.g.). Significance levels: *P < 0.05, **P < 0.01, ***P < 0.001, and ****P < 0.0001.

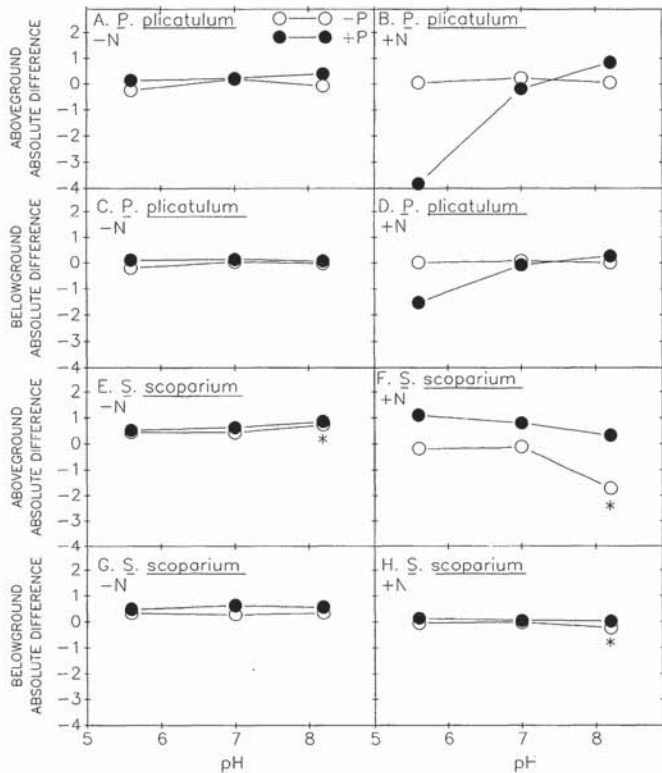


Fig. 3 Absolute competition intensity for *Paspalum plicatulum* and *Schizachyrium scoparium* is presented in grams dry mass (monoculture dry mass - mixture dry mass) as a function of soil pH. Positive values indicate monocultures produced more dry mass than did mixtures, whereas negative values indicate the reverse. The -N-P is native soil, and +N+P is native soil amended with 100 mg kg⁻¹ N and P. An asterisk indicates a significant difference between monoculture and mixture dry mass for that specific treatment.

(fig. 2C). When N was added, the ratios were reduced and remained constant at ca. 0.1 in all pH treatments, with or without added P (fig. 2D).

For *P. plicatulum* above- or belowground dry mass, absolute competitive intensity was not significant (four-way ANOVA, P > 0.05). The pH did not have an effect on competition in the native soil with or without added P (fig. 3A,C) or when N was added but P was not (fig. 3D). When N and P were added together (fig. 3B,D), there was an increase in above- and belowground dry mass in mixture (negative value) at pH 5.6 (not significantly different).

For *S. scoparium* above- and belowground dry mass, absolute competitive intensity was significant (four-way ANOVA P < 0.05). There was one significant difference in aboveground dry mass in the native soil treatment with slightly more dry mass in monoculture than in mixture at pH 8.2 (fig. 3E). Aboveground dry mass in mixture was significantly greater in the N addition treatment without added P at pH 8.2 (fig. 3F). Belowground dry mass in the native soil treatment, with or without added P, was similar to aboveground dry mass, with slightly more dry mass in monocultures. In the N addition treatments, there was only one significant difference between mixture and monoculture at pH 8.2 without P addition (fig. 3H).

Of the 24 comparisons of *S. scoparium* competition, there were three examples of significant differences in mixture and monoculture dry mass per plant. One showed greater monoculture than mixture dry mass, two showed greater mixture than monoculture dry mass, and all were at pH 8.2. Significant differences between mixture and monoculture dry mass were dem-

onstrated in 12.5% of the treatments. There were no examples of a significantly greater dry mass in mixture of one species coupled to a concomitant significantly lower dry mass of the second species.

Discussion

Previously, we reported fairly constant dry mass of *Schizachyrium scoparium* and *Paspalum plicatulum* in the coastal prairies of Texas over several years without manipulation, which indicates codominance and possibly equal interspecific competition (Van Auken et al. 1992a). Declines in dry mass of these species occurred when N was added to plots. Coupled with this was an increase in *S. nutans* dry mass, which indicates some type of interaction, possibly competition. We expected that *S. scoparium* and *P. plicatulum* were able to maintain their position in the coastal prairies of Texas because of their competitive abilities. Community composition measurements (Diamond and Smeins 1983) implied that *S. scoparium*'s dominance on more neutral soils could result from competitive dominance over *P. plicatulum*. Earlier, we found that *P. plicatulum* produced greater dry mass at lower N, regardless of the light levels tested (Van Auken et al. 1992b). *Schizachyrium scoparium* grew very little in mixture or in monoculture; thus, when *P. plicatulum* was grown with *S. scoparium* in low-N soil, it was effectively growing at a reduced density (compared with monoculture) and was able to use additional available resources for growth (Van Auken et al. 1992b). Growth in higher light levels and elevated N levels demonstrated true interference, but there was only one significant reciprocal effect on the second species in the three densities tested.

We also examined competitive effects between these two species in a series of depth experiments, but the results were equivocal (Van Auken et al. 1994). In shallow soils, intraspecific and interspecific competition were equal. In deeper soils, *P. plicatulum* had greater growth than *S. scoparium* because of root proliferations and acquisition of deeper soil resources. Thus, we have been able to detect significant differences in dry mass production between *P. plicatulum* and *S. scoparium* but not strong interspecific interference. Therefore, we hypothesize that they are relatively equal competitors in many cases and probably exist as community codominants by being able to equally acquire and use soil and/or other resources.

Differences in growth were detected with various P and N additions in the present study, but the greatest increases were when both N and P were added together, and then growth was pH dependent. *Paspalum plicatulum* dry mass was greatest at pH 5.6, and *S. scoparium* dry mass was greatest at pH 7.0. Consequently, differences in community composition between these species in the coastal prairies in some cases is probably caused by environmental heterogeneity (Werner and Platt 1976; Grubb 1977). That is, soils are deeper or shallower, have higher or lower pH, have more or less clay, and thus different nutrient levels, which allows

one species or the other to increase or decrease. Superimposed on these slight environmental differences in soil depth and fertility are slight functional differences between the species, which would allow one species an advantage in gaining resources and producing greater dry mass. Thus, community composition differences can be amplified by environmental heterogeneity and functional niche differences between species (van den Bergh and Braakhekke 1978; van den Bergh 1979; Cody 1986; Braakhekke 1988).

Coexistence of species is easy to detect, but mechanisms responsible for coexistence are not. Niche differences may be temporal and disappear as species become adults (Davis 1991). Differential resource utilization (de Wit et al. 1966), use of microsites (Jackson and Caldwell 1989; Van Auken et al. 1992c; Black et al. 1994), ability to take up resources at low concentration (Tilman 1988, 1990), and accessibility of deep resources (Phillips 1963; Berendse 1979, 1981, 1982; Bush and Van Auken 1991) are all mechanisms to reduce competition and define niche differences.

Plant growth is dependent on available N and P, which is dependent on soil pH (Russell 1973). Most soil P is bound to Ca or Mg (Gahoonia et al. 1992), especially in neutral or basic soils (Meharg and Killham 1990). In spite of finding differential pH-dependent growth of the two species, we detected little evidence of differences in interspecific competition. Where significant interspecific competition was found in one species, it was not discovered in the other. In addition, changes in competitive intensity can be explained by changes in monoculture dry mass at the various soil pH and N and P levels rather than by interspecific competition. If a species does not grow well in a given treatment in monoculture while a second species does, when the two species are grown together, the better-growing species is effectively growing at a reduced density and is potentially released from nutrient limitation as a result of the lack of growth of the poorer-growing species. Thus, in mixture it may take up the available resources not used by the poorer-growing species, which indicates a significant competitive intensity; however, there is really no interference with the second species. Thus, we have the appearance of competition, but it is asymmetrical or measured in only one species.

The pH- and nutrient-dependent growth of these two species is probably regulated by presently undetermined physiological or biochemical characteristics of their absorptive organs. *Paspalum plicatulum* may be limited in its ability to pump or exchange protons with the soil; thus, it may be limited in its ability to create areas of low pH along the root where P can be solubilized and taken up (Thibaud et al. 1986, 1988). Therefore, *P. plicatulum* growth may require a slightly more acidic soil if appropriate soil resources are going to be absorbed. *Schizachyrium scoparium*, on the other hand, may have roots or absorptive organs with a greater ability to extrude protons into more neutral or basic soil, which thus solubilizes P for uptake but only

for certain microsites along the root. However, if *S. scoparium* is grown in a slightly acidic soil, it may lose the advantage it has in slightly basic soils.

Biomass of species growing together may be reduced by the presence of neighbors (Harper 1977), and

if the species are ecological equivalents, the reciprocal negative effects may be equal. This could result in the species being codominants in a community and perhaps over a significant range of resources, as is apparently the case for these two C_4 grasses.

Literature cited

- Bazzaz FA 1990 Plant-plant interactions in successional environments. Pages 239–263 in JB Grace, D Tilman, eds. Perspectives on plant competition. Academic Press, New York.
- Berendse F 1979 Competition between plant populations with different rooting depths. I. Theoretical considerations. *Oecologia* 43: 19–26.
- 1981 Competition between plant populations with different rooting depths. II. Pot experiments. *Oecologia* 48:334–341.
- 1982 Competition between plant populations with different rooting depths. III. Field experiments. *Oecologia* 53:50–55.
- Black RA, JH Richards, JH Manwaring 1994 Nutrient uptake from enriched soil microsites by three Great Basin perennials. *Ecology* 75:110–122.
- Böhm W 1979 Methods of studying root systems. Pages 1–188 in WD Billings, F Golley, OW Lange, JS Olson, eds. Ecological studies. No. 33. Springer, New York.
- Braakhekke WG 1980 On coexistence: a causal approach to diversity and stability of grassland vegetation. *Versl Lanbouwkond Onderz Ned* 902:1–134.
- Bush JK, OW Van Auken 1991 Importance of time of germination and soil depth on growth of *Prosopis glandulosa* (Leguminosae) seedlings in the presence of a C_4 grass. *Am J Bot* 78:1732–1739.
- Callaway RM, EH DeLucia, D Moore, R Nowak, WH Schlesinger 1996 Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. *Ecology* 77:2130–2141.
- Cody ML 1986 Structural niches in plant communities. Pages 381–405 in J Diamond, TJ Case, eds. Community ecology. Harper & Row, New York.
- Connell JH 1983 On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696.
- Davis SD 1991 Lack of niche differentiation in adult shrubs implicates the importance of the regeneration niche. *Trends Ecol & Evol* 6:272–274.
- de Wit CT, GP Tow, GC Ennik 1966 Competition between legumes and grasses. *Versl Lanbouwkond Onderz Ned* 687:1–30.
- Diamond DD, FE Smeins 1983 Remnant grasslands of the Fayette Prairie, Texas. *Am Midl Nat* 110:1–13.
- 1984 Remnant grassland vegetation and ecological affinities of the Upper Coastal Prairie of Texas. *Southwest Nat* 29:321–334.
- 1985 Composition, classification and species response patterns of remnant tallgrass prairies in Texas. *Am Midl Nat* 113: 294–308.
- 1988 Gradient analysis of remnant True and Upper Coastal Prairie grasslands of North America. *Can J Bot* 66:2152–2161.
- Dolezel R 1980 Soil survey of Nacogdoches County, Texas. USDA Soil Conservation Service and Forest Service Survey. Washington, D.C. 146 pp.
- Estes JR, RJ Tyril, JN Brunden 1982 Grass and grassland: systematics and ecology. University of Oklahoma Press, Norman. 312 pp.
- Gahoonia TS, N Clasassen, A Jungk 1992 Mobilization of phosphates in different soils by ryegrass supplied with ammonium or nitrate. *Plant Soil* 140:241–248.
- Goldberg DE 1994 Influence of competition at the community level: an experimental version of the null models approach. *Ecology* 75:1503–1506.
- Gould FW 1968 Grass systematics. McGraw-Hill, New York. 382 pp.
- Grace JB 1993 The effects of habitat productivity on competition intensity. *Trends Ecol & Evol* 8:229–230.
- 1995 On the measurements of plant competition intensity. *Ecology* 76:305–308.
- Grace JB, D Tilman 1990 Perspective on plant competition: some introductory remarks. Pages 3–7 in JB Grace, D Tilman, eds. Perspective on plant competition. Academic Press, New York.
- Grime JP 1979 Plant strategies and vegetation processes. Wiley, New York. 222 pp.
- Grubb PJ 1977 The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol Rev* 52: 107–145.
- Harper JL 1977 Population biology of plants. Academic Press, New York. 892 pp.
- Hossner LR, HJ Woodward, J Bush 1992 Growth and selenium uptake of range plants propagated in uranium mine soil. *J Plant Nutr* 15:2743–2761.
- Jackson RB, MM Caldwell 1989 The timing and degree of root proliferation in fertile-soil microsites for three cold-desert perennials. *Oecologia* 81:149–153.
- Jurena PN, OW Van Auken 1996 Effects of phosphate concentration and soil pH on the growth of *Schizachyrium scoparium* and *Paspalum plicatulum*, two co-occurring C_4 grasses. *Bull Torrey Bot Club* 123:93–99.
- Kuchler AW 1964 Potential natural vegetation of the coterminous United States. American Geographical Society Special Publication 36. American Geographical Society, New York. 156 pp.
- Meharg AA, K Killham 1990 The effect of soil pH on rhizosphere carbon flow of *Lolium perenne*. *Plant Soil* 123:1–7.
- Phillips WS 1963 Depth of roots in soil. *Ecology* 44:424–429.
- Pugnaire FI, P Haase, J Puigdefabregas 1996 Facilitation between higher plant species in a semiarid environment. *Ecology* 77:1420–1426.
- Risser PG, EC Birney, HK Blockers, SW May, WJ Parton, JA Wiens 1981 The true prairie ecosystem. Dowden Hutchinson Ross, Stroudsburg, Pa. 557 pp.
- Russell EW 1973 Soil conditions and plant growth. Longman, London. 298 pp.
- Samson F, F Knopf 1994 Prairie conservation in North America. *BioScience* 44:418–421.
- SAS Institute 1985 SAS user's guide: statistics. SAS Institute, Cary, N.C. 956 pp.
- Schoener TW 1983 Field experiments on interspecific competition. *Am Nat* 122:240–285.
- Smeins FE, DD Diamond, CW Hanselka 1991 Coastal prairie. Pages 269–290 in RT Coupland ed. Ecosystems of the world. 8A. Natural grasslands: introduction and Western Hemisphere. Elsevier, New York.
- Steel RGD, JH Torrie 1980 Principles and procedures of statistics: a biometric approach. McGraw-Hill, New York. 633 pp.
- Terri JA, LG Stowe 1976 Climatic patterns and the distribution of C_4 grasses in North America. *Oecologia* 23:1–12.
- Thibaud JB, JC Davidian, H Sentenac, A Soler, C Grignon 1988 H^+ cotransport in corn roots as related to the surface pH shift induced by active H^+ excretion. *Plant Physiol* 88:1469–1473.
- Thibaud JB, A Soler, C Grignon 1986 H^+ and K^+ electrogenic exchanges in corn roots. *Plant Physiol* 81:847–853.
- Tietjen GF, RJ Beckman 1972 Tables for use of the maximum F -ratio in multiple comparison procedures. *J Am Stat Assoc* 67:581–583.
- Tilman D 1988 Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J. 361 pp.
- 1990 Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. Pages 117–141 in JB Grace, D Tilman, eds. Perspectives on plant competition. Academic Press, New York.

- Twolan-Strutt L, PA Keddy 1996 Above- and belowground competitive intensity in two contrasting wetland plant communities. *Ecology* 77:256–270.
- Van Auken OW, JK Bush, DD Diamond 1992a Changes in species dry mass in the upper Coastal Prairie when light and nutrient levels are altered. *Can J Bot* 70:1777–1783.
- 1992b Competition between Coastal Prairie species: *Paspalum plicatulum* and *Schizachyrium scoparium*. *Bull Torrey Bot Club* 119:401–406.
- 1994 Changes in growth of two C₄ grasses (*Schizachyrium scoparium* and *Paspalum plicatulum*) in monoculture and mixture: influence of soil depth. *Am J Bot* 81:15–20.
- Van Auken OW, JH Manwaring, MM Caldwell 1992c Effectiveness of P acquisition by juvenile cold-desert perennials from different patterns of fertile-soil microsites. *Oecologia* 91:1–6.
- van den Bergh JP 1979 Changes in the composition of mixed populations of grassland species. Pages 59–80 in MJA Werger, ed. *The study of vegetation*. Junk, The Hague.
- van den Bergh JP, WG Braakhekke 1978 Coexistence of plant species by niche differentiation. Pages 126–137 in AHJ Freyden, JW Woldendorp, eds. *Structure and functioning of plant populations*. North Holland, Amsterdam.
- Werner PA, WJ Platt 1976 Ecological relationships of co-occurring goldenrods (*Solidago: Compositae*). *Am Nat* 97:959–971.