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INFLUENCE OF SOIL AND PLANT-PLANT INTERACTIONS ON GROWTH AND FLOWERING OF TWO POTENTIALLY DOMINANT BUNCHGRASSES IN THE LONGLEAF PINE ECOSYSTEM

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INFLUENCE OF SOIL AND PLANT-PLANT INTERACTIONS ON GROWTH AND FLOWERING OF TWO POTENTIALLY DOMINANT BUNCHGRASSES IN THE LONGLEAF PINE ECOSYSTEM

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By James Cory Groover

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ABSTRACT

Neighborhood interactions and edaphic conditions can help predict the distribution of species and the composition and structure of plant communities. The longleaf pine ecosystem of the southeastern U.S. provides an ideal setting in which to study interactions among dominant members of the understory community. Bunchgrasses provide the structure and fuel that enable frequent fires to mediate succession and maintain the extremely diverse understory community characteristic of the imperiled longleaf pine ecosystem. I investigated responses to bunchgrass neighborhood composition by wiregrass (*Aristida stricta* Michx.) and little bluestem (*Schizachyrium scoparium* [Michx.] Nash), two competing and potentially dominant C_4 bunchgrasses occurring in north Florida longleaf pine savannas. I conducted (1) a reciprocal transplant experiment and (2) a multi-factorial greenhouse experiment to better understand how these two species influence each other in the context of their neighborhoods and their native soils. I asked: (1) What is the effect of these two species interacting with each other in neighborhoods in determining the performance of both species? (2) What is the effect of edaphic conditions in determining the performance of the two species? And lastly, (3) how do neighborhood composition and edaphic conditions interact to influence bunchgrass performance and potential dominance of the two species? Overall, bluestem individuals grew faster, produced more total biomass, more aboveground biomass and more flowering culms than wiregrass, although wiregrass produced more belowground biomass. In the greenhouse, conspecific competition was more intense for both species. The two species responded differently to conspecific crowding in terms of biomass production, with bluestems decreasing in aboveground biomass with additional conspecific neighbors, while wiregrass decreased in terms of belowground biomass production with additional conspecific neighbors. Overall our findings suggest that wiregrass may compete more in terms of belowground biomass production, while bluestems respond competitively in terms of aboveground resource allocation. A lack of variation in soils among sites indicates that the edaphic condition we assessed does not determine bunchgrass dominance in these sites.

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INTRODUCTION

Explaining the distribution of species is a central goal of plant community ecology. Plant communities often have an unequal distribution of species, with a few dominant species representing the majority of the communities' biomass (Volkov et al. 2003). Dominant plant species are important to ecosystem productivity and community assembly and invasibility (Smith and Knapp 2003, Smith et al. 2004). Changes in dominant species can have drastic effects on community dynamics, causing alterations in species composition, species diversity, and disturbance patterns (Ellison et al. 2005). Grime (1987) specifies that plant dominance studies are imperative to our understanding of community dynamics because "the struggle between dominants provides a potent driving force for successional change and is a major determinant in the fate of subordinate species."

Plant-plant interactions are a central focus of plant community ecology because interactions among plants may influence species distributions, community composition, succession, and evolution (Hacker and Gaines 1997, Tielborger and Kadmon 2000, Keddy et al. 2006, Holmgren and Scheffer 2010, Pugnaire 2010, Fajardo and McIntire 2011, Gagnon et al. 2012, Richardson et al. 2012). Plant-plant interactions are either negative (competition) or positive (facilitation) and can be looked at from both inter- and intra-specific perspectives (Roughgarden 1983). To grow and succeed, plants require certain amounts of water, nutrients, and space. Competition decreases the individual fitness of those plants involved, while facilitation promotes a plant's survival, growth, or reproduction (Pugnaire 2010). Much early research on plant-plant interactions, such as work by Grime (1973) and Tilman (1982), focused only on competition. Ecology now broadly accepts that both competition and facilitation are common, influential, and co-occurring phenomena in most communities and ecosystems (Menge and Sutherland 1987). Numerous studies show that positive and negative interactions work simultaneously in structuring communities (Bertness and Callaway 1994, Tielborger and Kadmon 2000, Holmgren and Scheffer 2010).

Edaphic conditions are fundamentally important in determining plant community composition and can greatly influence the interactions among species (Clark et al. 1998, Tuomisto et al. 2002). Soils vary in moisture regime, texture, and nutrients in important ways (Drewa et al. 2002, Peet 2006, and Garcia-Palacios et al. 2012). Parent material, topography, solar radiation, and precipitation patterns all influence the edaphic conditions upon which plant communities establish (Birkeland 1999, Peet 2006). The influence of soil properties on neighborhood interactions can differ temporally, regionally, or locally, depending on the ecosystem under study (Tilman 1989, Bertness and Callaway 1994).

Comprising some 40% of the earth's land surface, grasslands are the most extensive, possibly the most economically valuable, and the most threatened biome (World Resources 2001, Gibson 2009). A grassland can be defined as having a graminoid dominated understory with infrequent to no woody vegetation (Riser 1988). The composition of grasslands can be related to soil nutrients, local climate, topography, bedrock and soil, soil nutrients, soil moisture, disturbance, age, and management (Gibson 2009). Although typically overlooked as a grassland, the longleaf pine (*Pinus palustris*) ecosystem in the southeastern U.S. possesses a diverse understory dominated by C_4 bunchgrasses (Noss et al. 2014).

Since the European conquest of the New World, the longleaf pine (LLP) ecosystem has been reduced to less than 3% of its original, 37-million-hectare extent across the southeastern U.S., making it one of the most threatened ecosystems (Frost 1993, Earley 2004, Keddy et al. 2006, Peet 2006, Noss et al. 2014). Frequent (every 1-3 years), low to moderate intensity, lightning- and human-ignited fires maintain the sparse overstory, absent mid-story, and extremely diverse understory characteristic of LLP (Christensen 1981, Platt 1999, Veldman et al. 2013). By providing both the matrix in which these diverse LLP understory communities form and the fine fuels needed for fire continuity, C_4 bunchgrasses are an integral part of this imperiled system. Two of the most dominant and widespread species account for a clear division in longleaf understory communities. One is wiregrass (*Aristida stricta* Michx.), which tends to dominate the eastern portion of the longleaf range along the Atlantic coastal plain (Rogers and Provencher 1999). The other is little bluestem (*Schizachyrium scoparium* [Michx.] Nash), which is most often the dominant bunchgrass in the western gulf coastal plain of Louisiana and Texas as well as the more northerly reaches of longleaf in Alabama and Georgia (Frost 1993).

Wiregrass, or three-awn grass, is a long-lived perennial bunchgrass occurring exclusively in frequently burned coastal pine communities of the southeastern U.S. Wiregrass is adapted to frequent fire, only producing viable seeds in years following growing season fires, and quickly decreasing in abundance with fire exclusion (Clewell 1989, Glitzenstein et al. 1995, Maliakal et al. 2000). Wiregrass root structure helps maintain longleaf ecosystem function by improving soil structure and increasing its water holding capacity (Outcalt and Lewis 1988). Studies involving wiregrass and plant-plant interactions have demonstrated both competitive and facilitative interactions with inter- and intraspecific neighbors (Mulligan et al. 2002, Mulligan and Kirkman 2002, Espeleta et al. 2004, Aschenbach et al. 2010, Wallet 2016).

S*chizachyrium scoparium* var. *scoparium* (i.e., little bluestem, henceforth referred to as 'bluestem') has a much more continental distribution, occurring in all U.S. states except Alaska, Nevada, and Oregon. It occurs in the understory of open pine and oak stands across the country and is also an important structural component in the tall and mixed grass prairies of the central U.S. (Steinberg 2002). Within the historic range of the LLP ecosystem, bluestem tends to be the dominant bunchgrass on sites with higher clay and silt content, and inland within the Gulf Coastal Plain (Steinberg 2002). Research in longleaf and prairie ecosystems has documented little bluestem outcompeting other C_4 bunchgrasses (Wedin and Tilman 1993, West 2002). Little bluestem has also been found to be a better colonizing species compared to wiregrass; for example, Grelen (1962) found disturbed LLP sites in NW Florida that previously contained wiregrass and found these sites being re-colonized by bluestem but not wiregrass. Unlike wiregrass, bluestem hosts arbuscular mycorrhizae, which are most important for the species' performance under moisture stress (Anderson and Roberts 1993). In testing for ecosystem functionality between little bluestem and wiregrass, West (2002) found that wiregrass retained nitrogen better than bluestem, which suggests wiregrass is more adapted to the excessively well drained soils of the coastal plain where available nitrogen is more often limiting. In the same study, West demonstrated bluestem's ability to quickly absorb and use pulses of nutrients compared to wiregrass, which further supports the competitive nature of bluestem, as well as its tendency to dominate LLP sites with higher silt and clay concentrations (Bridges and Orzell 1989, Peet 2006).

The central focus of my research is the influence of bluestem and wiregrass on one another within the context of their native soils. I designed a combination field experiment and greenhouse study to examine how the two species affect one another. I asked: (1) what is the effect of neighborhood composition in determining the performance of these two species? I expected intraspecific interactions would be more influential in the performance of study individuals than interspecific interactions. (2) What is the effect of edaphic conditions in determining the performance of the two species? I expected little variation in the performance of wiregrass in response to varying edaphic conditions; by contrast, I expected that bluestem would perform better as edaphic conditions improved (e.g., increases in silt/clay or nutrients). Lastly, I asked: (3) how would varying neighborhood composition and edaphic conditions interact to influence bunchgrass performance and potential dominance of the two species?

METHODS

Site description

I conducted my experiments at Eglin Air Force Base (AFB) in Santa Rosa, Okaloosa, and Walton counties, Florida, USA (30°N; 86°W). Eglin AFB is geographically positioned in a major transitional zone of eastern and western longleaf community types, with eastern sites being primarily wiregrass dominated and western sites being primarily bluestem dominated (Harcombe et al. 1993). Within the Choctaw East, Choctaw West, Metts, and Sikes hunting units of Eglin AFB, I chose six sites based on the dominant species of bunchgrass present. Half the sites were dominated by wiregrass (n=3) and the other half were dominated by bluestem (n=3). Each site was a circle with a radius of 50 m (0.78 ha) in relatively open longleaf pine habitat with a bunchgrass dominated understory at least 100 meters from any road. I established six, 4 × 4 m subsites within each site based on vegetative characteristics (bunchgrass dominated understory). I used these sites to carry out both: (i) the reciprocal transplant study and (ii) the greenhouse study described below. I collected and numbered 30 parent tussocks of each species at each of the six sites and brought them to the greenhouse at Hancock Biological Station (HBS) in western Kentucky. I subdivided these parent tussocks into multiple smaller individuals that I used in both the reciprocal transplant and greenhouse studies. All resulting individuals had at least 10 vegetative tillers and an initial mass of approximately 1.0 g (mass calculated following root rinsing individuals and patting dry with towel). I also collected 400 liters of soil at each site. To comply with Eglin AFB permits, I limited my collection to the top 20 cm of soil. In an effort to maintain some integrity of soil horizonation, I collected soils from 0-10 cm and 10-20 cm separately.

Soils

Soils underlying all bluestem dominated sites belonged to the Lakeland soil series and were classified as sandy thermic, coated Typic Quartzipsamments (Soil Survey Staff USDA-NRCS). Soils in one wiregrass dominated site belonged to the Pactolus series described as thermic, coated Aquic Quartzipsamments (Soil Survey Staff USDA-NRCS). Soils of the two remaining wiregrass dominated sites belonged to the Blanton soil series classified as loamy siliceous, semiactive, thermic Grossarenic Paleudults (Soil Survey Staff, USDA-NRCS).

In May 2014, I extracted 6 composite soil samples (6 cores of 2.54 – 4.445 cm diameter) at each sub-site within each of my 6 sites (n = 36). I collected all soil samples in the same way from each sub-site at a depth of 0 – 20 cm (Fig. 1B). The University of Kentucky soil testing lab in Lexington, Kentucky analyzed the chemical properties of soil samples. The laboratory measured extractable nutrients using the Mehlich-3 extraction procedure (Mehlich 1984) and analyzed them by ICP (Lab Fit AS-3010D Dual pH Analyser, Labfit Pty Ltd Perth, Australia). The lab calculated soil pH using 1 M KCl and analyzed samples using Lab Fit AS-30100 Dual pH Analyser (Labfit Pty Ltd Perth, Australia). The Waters Agricultural Laboratories Inc. in Owensboro, Kentucky analyzed soil physical properties; the lab used the Bouyoucos hydrometer method (Bouyoucos 1962) to determine particle size distribution of soils, reported as percent sand, silt, and clay.

Greenhouse study

I designed a factorial experiment in the greenhouse to evaluate the effects of plant-plant interactions (5 levels) and soil (2 levels: soil collected from wiregrass-dominated sites and soil from bluestem-dominated sites) on wiregrass and bluestem under more controlled conditions. Using the soils collected from the field, I filled the bottom half of each 7.5 L round black flower pot with soil collected from the depth of 10-20 cm, then added soil collected from 0-10 cm to fill pots completely. I used a total of 90 pots in the greenhouse experiment (N = 5 ratios of competition × 2 soil dominance types × 3 sub-sites × 3 replicates of each = 90 pots). Each pot contained 4 study individuals, with ratios of wiregrass and bluestem individuals representing the 5 levels of competition as follows: (1) four wiregrass tussocks, (2) three wiregrass tussocks and one of bluestem,

(3) two wiregrass tussocks and two of bluestem, (4) one wiregrass tussocks and 3 of bluestem, and (5) four bluestem tussocks (Fig. 1).

In June 2014, I used a random number generator to select study individuals from the pool of parent tussocks collected from the field. I rinsed plant roots thoroughly to avoid contaminating pots with foreign soils. I then removed any senescent material, blotted excess moisture with a towel, weighed, photographed, and immediately planted each in its designated pot. I randomly determined the location of study pots within my array in the greenhouse. I removed pots in October 2015, rinsed soil from roots, and divided roots by hand using a rinsing hose and a comb. I towel-dried study individuals and then allowed them to air dry for 10 minutes before weighing (wet weight) and photographing them. I then dried samples at 55°C for 24 hours before measuring dry mass (total, above-, and belowground). To assess each individual's growth performance, I used total biomass, aboveground biomass, belowground biomass, and root:shoot ratio as response variables.

Field study

The reciprocal transplant experiment examined differences in performance between wiregrass and bluestem individuals planted in differing LLP understory conditions. Specifically, the dominant C_4 bunchgrass and edaphic conditions differed by site, as did associated interactions among individual bunchgrass tussocks resulting from these differences in dominance. Each study site (N=6; for wiregrass-dominated sites n=3, and for bluestem sites n=3; Fig. 1) served as both origin site (from which study individuals were taken) and destination site (where study individuals were planted). I procured study individuals for this experiment by subdividing the 30 parent tussocks from each of my six sites. I established study individuals in standard 10 cm round planting pots in the HBS greenhouse prior to planting them at field sites in March of 2015. I chose only individuals greater than 1 cm in basal diameter with at least 10 vegetative tillers. At each of the 6 study sites I established 6, 4 × 4 m subplots, in each of which I planted 6 focal tussocks (one apiece originating from the 6 study sites; N = 6 sites × 6 subplots × 6 transplants/subplot = 216 total transplants; Fig. 1). At each site I planted 36 study individuals (Fig. 1); half were wiregrass, and half were bluestem.

I measured individual growth performance in two ways. One was change in the number of vegetative culms (which I will henceforth refer to as 'tiller growth' to avoid confusion with flowering culms). The second was change in basal diameter (basal growth). I calculated both as the initial measurement subtracted from the harvest measurement at study end, divided by the initial measurement. I calculated basal diameter as the average of 2 diameter measurements (diameter 1 – maximum diameter, diameter 2 – diameter perpendicular to diameter 1). I estimated reproductive output as the number of flowering culms produced by each individual at the end of the study in October 2015. For each study individual I took one reading during the morning (between 8:00am and 12:00pm) and one during the afternoon (between 1:00pm and 5:00pm) in an attempt to capture changes in PAR availability throughout the day.

Statistical Analyses

To check soil data for normality, I both visually assessed variables using quantile-quantile (Q-Q) plots and used Shapiro-Wilk tests. I log transformed the soil chemical properties Ca, Mg, and Zn to achieve approximate normality. I used Levene's tests and residual boxplots to assess equality of variances. I used linear mixed models to assess differences in chemical and physical soil properties between sites dominated by wiregrass and bluestem (α=0.05). I performed all statistical analyses using R 3.2.5 (R Core Team 2016).

My first step in analyzing my greenhouse data was evaluating normality, which I did using both Shapiro-Wilk tests and quantile-quantile (Q-Q) plots. To achieve approximate normality I used square root transformations for the growth performance variables: total biomass, root:shoot ratio, and aboveground biomass, as well as for the reproductive response variable: number of flowering culms. To achieve approximate normality for the response variable belowground biomass, I added the same quantity to all values so that the lowest value equaled 1, then log transformed. To formally check for heteroscedasticity, I used Levene's test. To graphically assess for heteroscedasticity, I examined residual boxplots for each parameter. To determine how plant-plant interactions and soils influenced the performance of wiregrass and bluestem, I used mixed effects models for each fitness parameter. To identify best fit models, I used a backwards model selection procedure following Zuur et al. (2009) using restricted maximum likelihood (REML) estimation and Akaike Information Criterion (AIC) values. I used Tukey's HSD test to identify significant differences among the levels of model effects.

I assessed transplant data for normality and heteroscedasticity similarly to the greenhouse data. Both tiller growth and basal growth required log transformations to meet assumptions of normality. For transformations to work properly, I added the same quantity to all values so that the lowest was equal to 1. Similarly, to achieve approximate normality, I added the same quantity to the number of flowering culms so that the lowest was equal to 1 prior to square root transformation. To determine how origin (i.e., the species of the study individual, wiregrass or bluestem) and destination (where an individual was planted, wiregrass or bluestem dominated sites) affected the performance of study individuals, I used mixed effects models for each response variable. I used backwards model selection following Zuur et al. (2009) to identify best fit models using restricted maximum likelihood (REML) and Akaike Information Criterion (AIC) values. I used Tukey's HSD tests to compare and identify significant differences between the levels of model effects.

RESULTS

Soil properties

For all results F-values and P-values are reported from linear models; mean values are reported for each species along with standard error values. Wiregrass-dominated sites had significantly more silt than bluestem-dominated sites ($F_{1,24}$= 5.65, P= 0.025; Fig. 2). Despite this, percent clay and percent sand were not different. Soil phosphorus differed between sites, with wiregrass-dominated sites having significantly more phosphorus than bluestem sites ($F_{1,34}$= 6.73, P= 0.014). Among the other soil extractable nutrients assessed (K, Ca, Mg, Zn), none differed. Soils at all sites were acidic (4.89 ± 0.17 versus 4.97 ± 0.13 for bluestem and wiregrass-dominated sites, respectively) and not statistically different ($F_{1,34}$= 1.70, P= 0.207).

Greenhouse study

The model selection process led to the same subset of predictors for each greenhouse response variable. Response variables included: total biomass, root:shoot ratio, flowering culms, and above- and belowground biomass. Fixed effects in the preferred model included species, species ratio (number of conspecifics per pot), their interaction, and initial (wet) mass as a covariate. The random term "pot number" served as a random covariate to account for my array within the greenhouse. The preferred model also used origin site as a random term that accounted for variation in edaphic conditions and among parent tussocks collected from the six sites used in the experiment. A large decrease in AIC values (greater than 10) with the removal of soil type (wiregrass or bluestem) led me to exclude this factor from the model.

The main effect of species was highly significant in predicting the total biomass of study individuals ($F_{1,327}$= 16.41, $P < 0.001$, Fig. 3). On average, bluestems produced more biomass than wiregrass individuals (total biomass: bluestem = 13.3 ± 9.36, wiregrass = 11.9 ± 7.13). The effect of species ratio also significantly influenced total biomass produced, with individuals of both species tending to produce less total biomass with every additional conspecific sharing the pot ($F_{4,327}$= 5.17, P= 0.002, Fig. 4). Initial mass of study individuals was a significant predictor of total biomass produced ($F_{1,327}$= 21.91, $P < 0.001$). The interaction between the main effects of species and species ratio was significant in predicting the total biomass of individuals ($F_{2,327}$= 2.97, P= 0.03, Fig. 3). According to Tukey's HSD, the total biomass of bluestems was more when grown in pots with all wiregrass (T_{120}=4.03, $P < 0.001$, Fig. 3). As the number of bluestem individuals per pot increased, the total biomass per bluestem decreased. The total biomass of wiregrass individuals did not differ across the varying species ratios.

Wiregrass individuals had a larger average root:shoot ratio than bluestem individuals (mean root:shoot ratio: wiregrass = 0.75 ± 0.51, bluestem = 0.27 ± 0.35; $F_{1,266}$= 158.79, $P < 0.001$, Fig. 4). Initial biomass was not significant in predicting root:shoot ratio ($F_{1,318}$= 3.15, P= 0.077). The interaction between the main effects of species and species ratio was a significant predictor of the root:shoot ratio of study individuals ($F_{4,97}$= 4.54, P= 0.004, Fig. 4). Tukey's post-hoc analysis indicated that for wiregrass study individuals, root:shoot ratio decreased as the number of wiregrass individuals per pot increased, with pots containing all wiregrass having a significantly lower root: shoot ratio compared to pots with mixed ratios of study individuals (T_{120}= 3.41, P= 0.005, Fig. 4).

For aboveground biomass, all main effects were significant in predicting the performance of study individuals. Species predicted aboveground biomass of individuals ($F_{1,327}$= 47.45, P < 0.001, Fig. 5); bluestem individuals produced significantly more aboveground biomass than wiregrass individuals (mean aboveground biomass: bluestem = 10.9 ± 8.4, wiregrass = 7.4 ± 5.2). Species ratio in pots predicted aboveground biomass of individuals ($F_{3,327}$= 4.05, P = 0.008, Fig. 5). The interaction between species and species ratio was significant in predicting the above ground biomass study individuals produced ($F_{3,327}$= 4.86, P = 0.003, Fig. 5). According to post-hoc analysis, bluestem individuals grown with no conspecifics produced significantly more aboveground biomass than those grown with any number of conspecifics (T_{327}= 4.12, P= 0.003, Fig. 5). Conversely for wiregrass, aboveground biomass was significantly more in pots grown in monoculture (T_{327}= 2.61, P= 0.04, Fig. 5).

For belowground biomass, species predicted the performance of study individuals ($F_{1,327}$= 13.44, P < 0.001, Fig. 6). Wiregrass individuals had significantly more belowground biomass than bluestem individuals (mean belowground biomass: bluestem = 2.4 ± 2.11, wiregrass = 4.3 ± 3.43). Species ratio influenced belowground biomass, in that individuals of both species tended to produce less belowground biomass as the number of conspecifics sharing a pot increased ($F_{4,327} = 3.51$, $P < 0.001$, Fig. 6). Individuals of both species had significantly more belowground biomass when grown with all interspecific neighbors compared to when grown with all conspecific neighbors (wiregrass: $T_{327} = 2.81$. P=0.026, bluestem: T_{327}= 3.14, P= 0.009). Initial mass predicted belowground biomass of study individuals ($F_{1,327}$= 32.81, $P < 0.001$, Fig. 6).

Species was a significant predictor of reproductive effort. Bluestem individuals on average produced more flowering culms per individual than wiregrass (mean number flowering culms: bluestem = 5.3 ± 3.51, wiregrass = 4.95 ± 9.19; $F_{1,262}$= 34.4, $P < 0.001$, Fig. 7). Neither the main effect of species ratio nor the initial mass of individuals predicted the reproductive effort of study individuals. The interaction of species and species ratio was significant in predicting reproductive effort of individuals ($F_{3,162}$= 5.23, P= 0.002, Fig. 7). The post-hoc analysis revealed that wiregrass individuals grown in monoculture produced more flowering culms per individual than did wiregrass grown in mixtures of species (T_{85}= 3.72, P= 0.003, Fig. 7). Although the reproductive effort of bluestem individuals tended to decrease as the number of conspecifics per pot increased, the difference was not significant.

Transplant study

According to the model selection process, the best-fit model was the same subset of predictors for all response variables in the transplant study. The preferred model contained the main effects of origin (species of study individual), destination (wiregrass- or bluestem-dominated site where an individual was planted), and their interaction. It also contained the random effect of burn unit. Available light (PAR) between wiregrass-and bluestem-dominated sites was not a useful covariate, so I eliminated it from subsequent analyses.

Origin was a significant predictor of tiller growth, with bluestem individuals producing significantly more tillers than wiregrass individuals (mean tiller growth: bluestem = 5.7 ± 5.68, wiregrass = 2.63 ± 2.07; $F_{1,194}$= 35.14, $P < 0.001$, Fig. 8). The interaction between origin and destination was a significant predictor of tiller growth ($F_{1,194}$= 10.9, $P = 0.002$, Fig. 8). According to the post hoc analysis, bluestem individuals had significantly more tiller growth in bluestem-dominated destinations ($T = 6.51_{194}$, $P < 0.001$), while wiregrass showed no preference of destination site.

For the response variable basal growth, origin (i.e., species) was the only fixed effect that influenced growth performance. Bluestems demonstrated a greater increase in basal diameter than wiregrass (mean basal growth: bluestem = 0.41 ± 0.52, wiregrass = 0.21 ± 0.19, $F_{1,195}$= 11.41, $P < 0.001$, Fig. 9). Although, on average, bluestem individuals exhibited increased basal growth in bluestem-dominated destinations compared to wiregrass-dominated destinations, these differences were not statistically significant.

Origin was a significant predictor of reproductive performance, with bluestem individuals producing significantly more flowering culms than wiregrass individuals (mean number flowering culms: bluestem = 3.05 ± 3.81, wiregrass = 0.79 ± 1.87, $F_{1,179}$=52.76, $P < 0.001$, Fig. 10). The interaction between the main effects of origin and destination was significant in predicting number of flowering culms ($F_{1,179}$=4.71, P= 0.031). Tukey's HSD tests indicated that both species produced more flowering culms when planted in sites dominated by conspecifics (wiregrass: $T=_{179}$ -3.44, $P = 0.004$, bluestem: $T_{179} = 7.03$, $P < 0.001$, Fig. 10).

DISCUSSION

Growth Performance

In the greenhouse study, neighborhood interactions strongly influenced growth of both wiregrass and bluestem tussocks, whereas all measured soil influences were unimportant. For both species, intraspecific competition was more intense than interspecific competition. Bluestem tussocks produced more aboveground biomass when growing without conspecific neighbors, whereas wiregrass tussocks produced more belowground biomass in the same scenario. Classic ecological theory on the coexistence of species predicts that competition with conspecific neighbors should be more intense than interspecific competition (Tilman 1982, Tilman 1989). Results from the greenhouse study support this competition theory, in that competition was most intense for both species when grown in monocultures. Curiously, results from the transplant study would seem to contradict this: bluestem tussocks grew larger in bluestem-dominated sites, suggesting some other influence at play.

In all treatments within the greenhouse, bluestems allocated more resources to the production of aboveground biomass, whereas wiregrass produced more belowground biomass. Individually, plants respond differently to resource availability and edaphic conditions by changing morphology, altered root proliferation or variation in biomass allocation (Hutchings and Kroon 1994, West et al. 2004, Espeleta et al 2009). These findings are consistent with West (2002), who also reported that wiregrass individuals allocated more resources to belowground performance and that bluestems allocated more to aboveground growth. The greater belowground biomass of wiregrass across all treatments in the greenhouse study reflects their growth form with extensive root systems adapted to the frequently burned coastal plain (Clewell 1989). The decreased belowground biomass of wiregrass monocultures coupled with no response of aboveground biomass suggests that wiregrass stands become limited by belowground space. Such competition for belowground space might explain why bunchgrass tussocks in the longleaf ecosystem are more evenly patterned on the landscape than would be expected by chance (Hovanes et al. *in press*).

Reproductive Output

Wiregrass reproduction is tightly linked to the intensity, seasonality, and occurrence of fire and to the environmental conditions (soil temperature, increased light availability, modification to soil microbial community) that fire creates (Platt et al. 1988, Outcalt 1994, Certini 2005). Although occurrence of fire explains flowering in one wiregrass site, it does not explain why wiregrass individuals from all sites produced at least some flowering culms. The tendency of wiregrass individuals to flower more when grown in monoculture in the greenhouse could explain why some wiregrass flowered without a fire cue. I postulate that wiregrass individuals grown in monoculture were limited by belowground resources (space and nutrients) and thus responded by allocating resources to reproductive effort. Wallett et al. (in review) found increased reproductive effort of wiregrass when grown with conspecific neighbors in a less stressful North Florida LLP seepage slope habitat, which could also support our drought- and fire-free greenhouse findings of increased flowering of wiregrass in monocultures. I expect this increased reproductive effort of wiregrass monocultures contributed to their significant increase in aboveground biomass since there was no response in terms of vegetative tiller growth by wiregrass. This suggests that a limiting of belowground resources is a cue for wiregrass to allocate more resources to reproduction. Similar to the greenhouse findings, wiregrass individuals in the transplant study exhibited increased reproductive effort when grown on sites dominated by wiregrass, which further suggests mechanisms controlling wiregrass community structure are predominantly belowground.

The Role of Soils

The physical and chemical properties of soils (more silt and phosphorus in wiregrass-dominated sites) across the understory communities assessed contradict other work in LLP (e.g., Bridges and Orzell 1989, Peet 2006). This result also contradicts our hypothesis that bluestem-dominated sites would be higher in silt and soil nutrients. Individually, plants respond differently to resource availability and edaphic conditions by changing morphology, e.g., altered root proliferation or variation in biomass allocation (Hutchings and Kroon 1994, West et al. 2004, Espeleta et al 2009). The increased soil phosphorus observed in wiregrass-dominated sites may have been confounded by a number of factors. Prescribed fire is often associated with temporary pulses of increased soil nutrients (Schmalzer and Hinkle 1987, Schmalzer and Hinkle 1991, Robins and Myers 1992). Two of the three wiregrass-dominated sites burned 5 weeks prior to collecting soils samples, which could have led to an overall increase in mean soil phosphorus in wiregrass sites. Studying nutrient pulses from fire in central Florida, Schmalzer and Hinkle (1991) found post-fire increases in soil nutrients, especially phosphorus. Their findings used samples that were taken in May following a March fire, which mirrors the time frame of our fires (Schmalzer and Hinkle 1991).

Some parameters known to influence LLP edaphic conditions that we did not measure include soil moisture, soil Nitrogen, and fungal associations with arbuscular mycorrhizae (AM fungi). Any or all might have explained results of the transplant study that contradicted those from the greenhouse. Soil moisture may have better explained variation among sites since water is known to be the primary limiting factor in the LLP ecosystem (Mitchell et al. 1999, Kirkman et al. 2001). Soil moisture can directly and indirectly influence soil properties including chemical reactivity, temperature, bulk density, rates of decomposition, microbial activity, and nutrient cycling (Outcalt and Lewis 1988, Brady and Weil 2010). Mitchell and colleagues (1999) demonstrated the ability of wiregrass to improve soil moisture through shading and hydrologic uptake. Nitrogen content also may have influenced the edaphic environment in which study individuals grew. The performance of bluestem individuals in the greenhouse study are consistent with the findings of West (2002), who demonstrated the competitive ability of little bluestem to quickly utilize available resources. The subtle changes observed in the total dry mass of wiregrass individuals across treatments in the greenhouse further support the research of West (2002). That study suggested that the tendency of wiregrass individuals to retain available nutrients instead of quickly using them was an adaption of wiregrass to the often nutrient limited, excessively well drained soils of the coastal plain. West (2002) provided evidence for increased performance of little bluestem when grown with higher nitrogen concentrations, and conversely a lack of growth response by wiregrass to the same nitrogen additions. In a greenhouse experiment, Van Auken and Bush (1997) reported increases in little bluestem dry mass in response to nitrogen additions when grown with heterospecific neighbors.

Another potentially important soil parameter not evaluated was the soil microbial community. Most research suggests no symbiotic relationships occur between wiregrass and AM fungi, while studies have found strong associations between little bluestem and AM fungi (Anderson and Roberts 1993, Anderson et al. 1994, Anderson and Menges 1997, Koide 2010). Anderson and colleagues (1993, 1994) demonstrated the relationship between AM fungi and little bluestem and predicted these associations were most important during periods of drought stress, or when little bluestems were growing on nutrient poor sites, especially soil phosphorus (Anderson and Menges 1997). This could in part explain why bluestem individuals in the transplant study experienced increased growth in bluestem-dominated sites despite the presence of conspecific competition and decreased silt and phosphorus.

LIST OF FIGURES

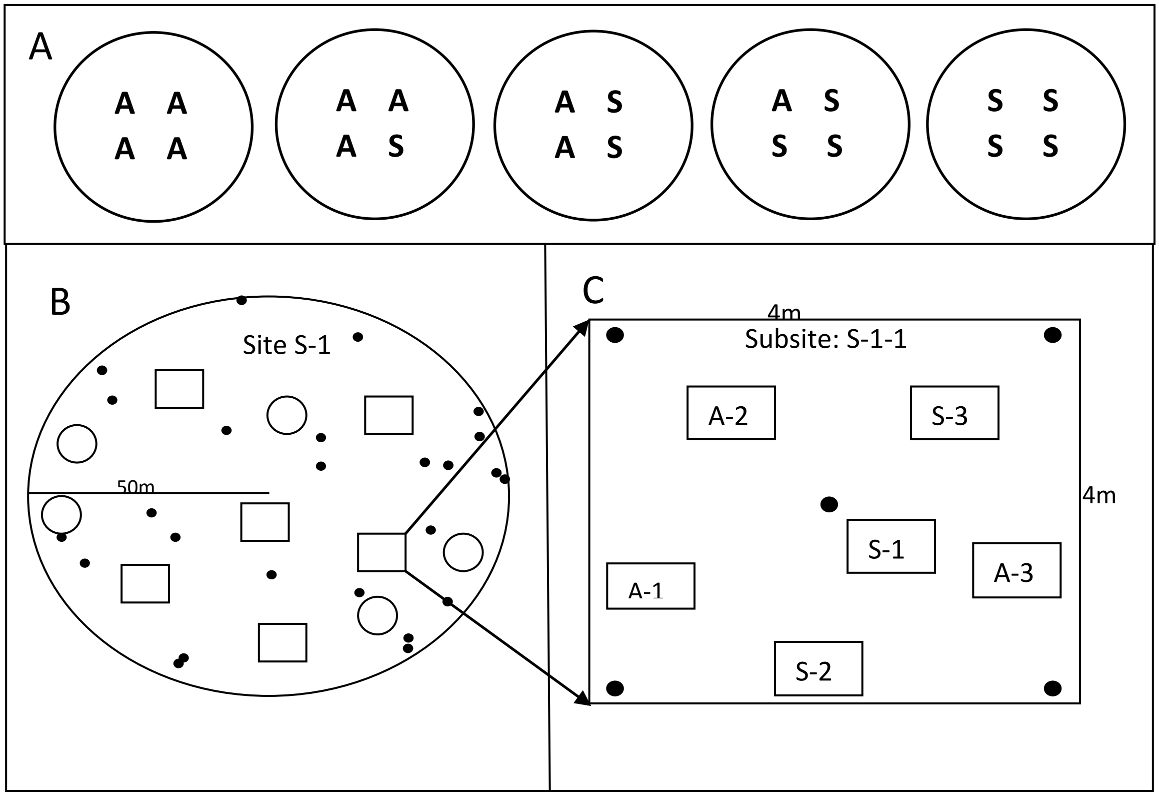

Figure 1. Frame A represents the five different ratios of species growing in pots in the greenhouse. Circles represent pots. Letters represent individual bunchgrass tussocks (A = wiregrass, S = bluestem). The lower frames are a diagram of the transplant study at Eglin AFB. Frame B represents one of six study sites, with the small circles representing soil collection areas, dots representing bunchgrass collection sites, and squares representing the subsites used in transplanting. Frame C depicts one of six subsites in each site, with black dots indicating soil sampling locations and the alpha-numeric rectangles designating study individuals.

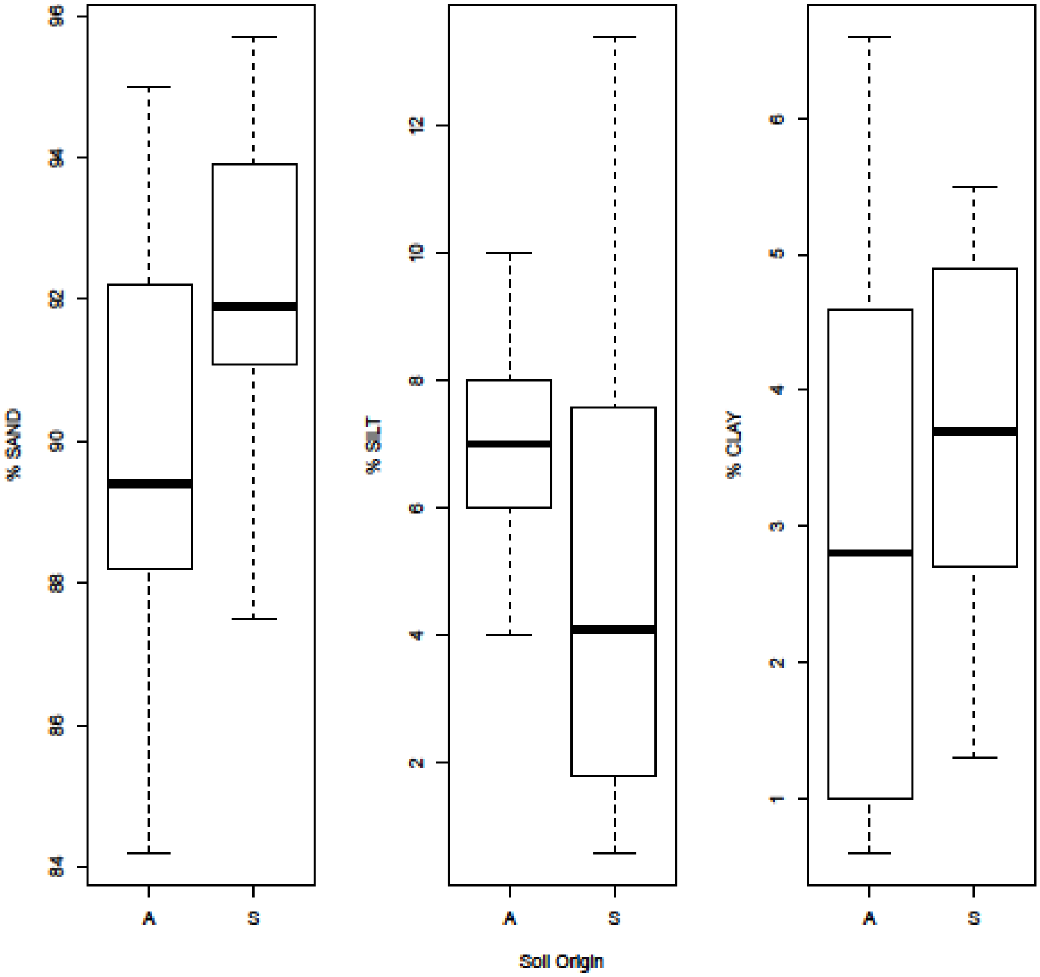

Figure 2. Percent soil particle size of sand, silt, and clay in wiregrass-dominated (A) and bluestem-dominated (S) study sites at Eglin Air Force Base.

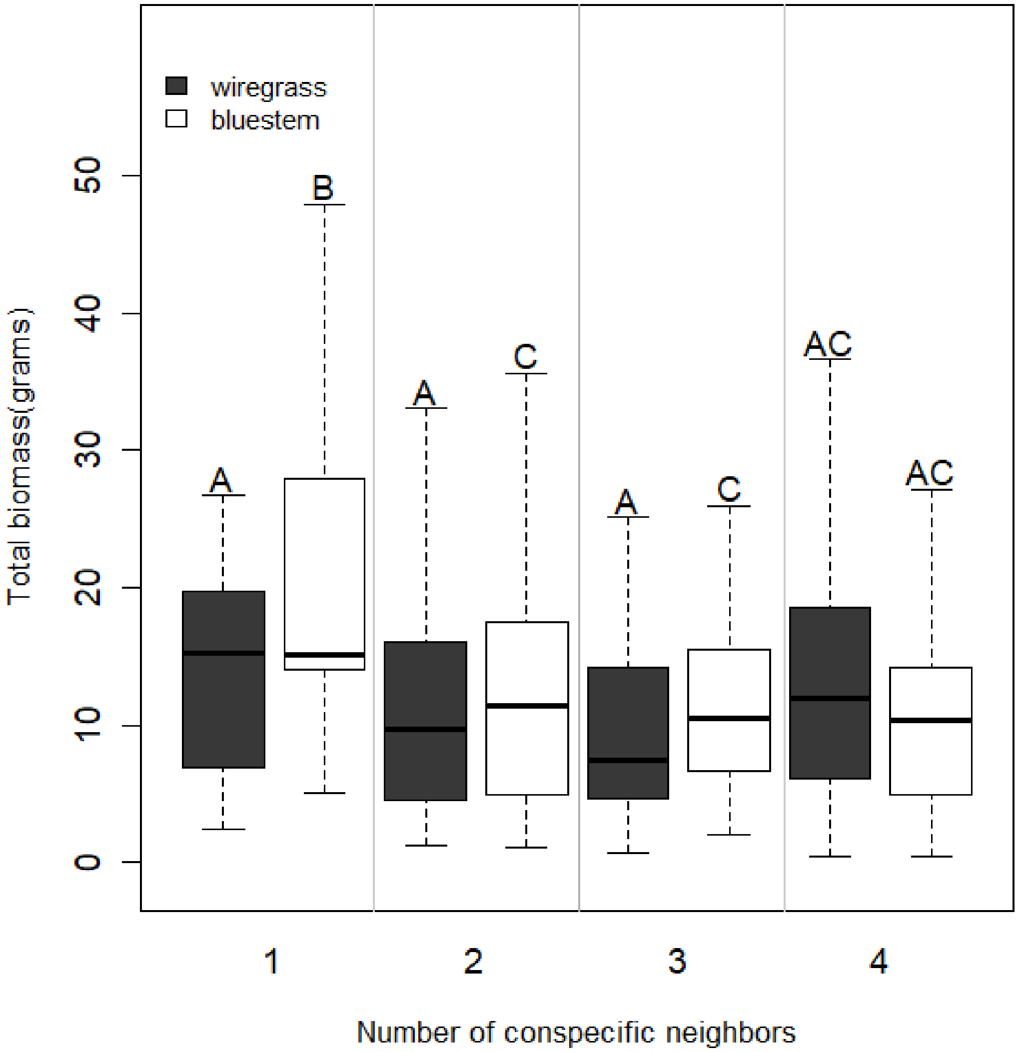

Figure 3. Total biomass produced by wiregrass and little bluestem tussocks in response to different ratios of heterospecific and conspecific neighbors in pots in the greenhouse. Number of conspecific neighbors was complementary to the number of heterospecific neighbors, with all pots containing four study individuals. Error bars represent 1 SE. Letters indicate significant differences in the response of each species at $P < 0.05$ based on pairwise Tukey post-hoc tests.

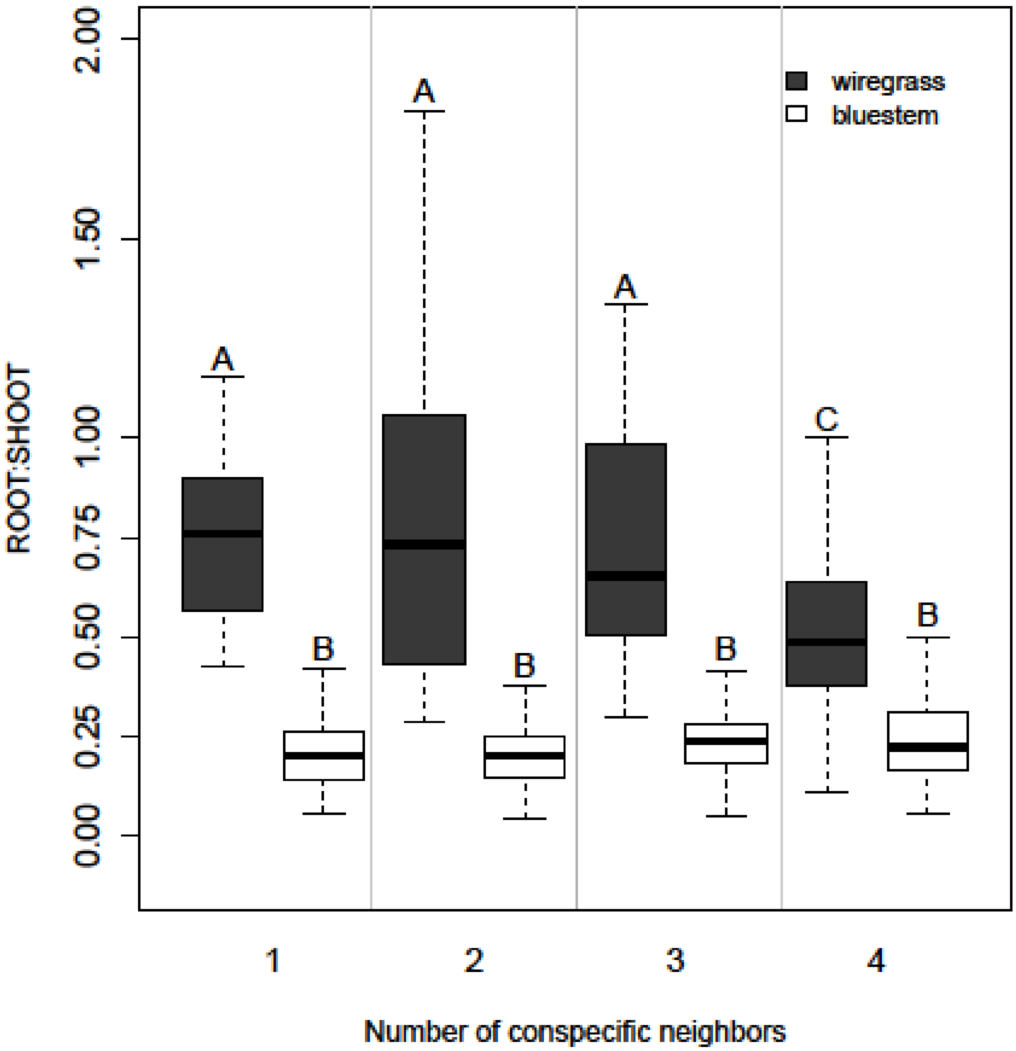

Figure 4. Root:shoot ratio of wiregrass and little bluestem in response to different numbers of heterospecific and conspecific neighbors in pots in the greenhouse. Number of conspecific neighbors was complementary to the number of heterospecific neighbors, with all pots containing four study individuals. Error bars represent 1 SE. Letters indicate significant differences in the response of each species at $P < 0.05$ based on pairwise Tukey post-hoc tests.

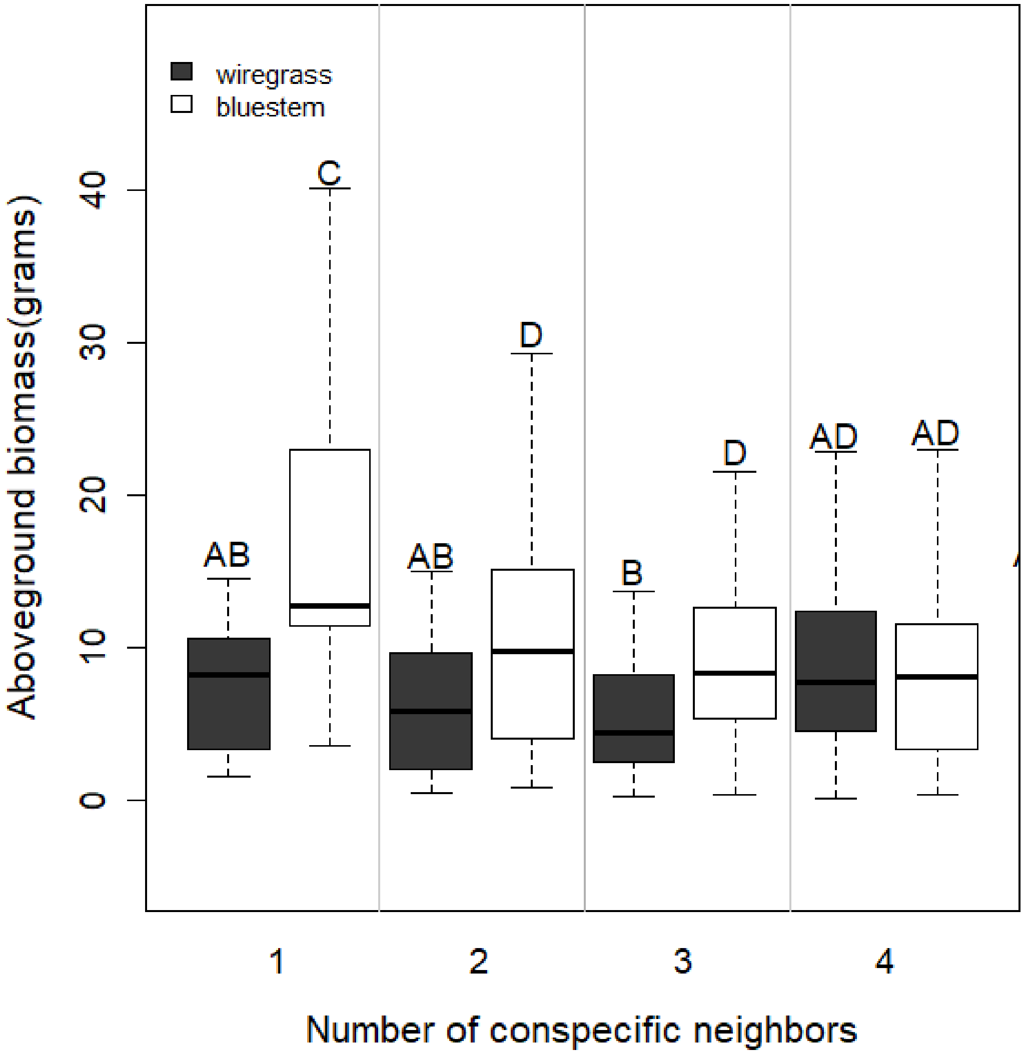

Figure 5. Aboveground biomass produced by wiregrass and little bluestem in response to different numbers of heterospecific and conspecific neighbors in pots in the greenhouse. Number of conspecific neighbors was complementary to the number of heterospecific neighbors, with all pots containing four study individuals. Error bars represent 1 SE. Letters indicate significant differences in the response of each species at $P < 0.05$ based on pairwise Tukey post-hoc tests.

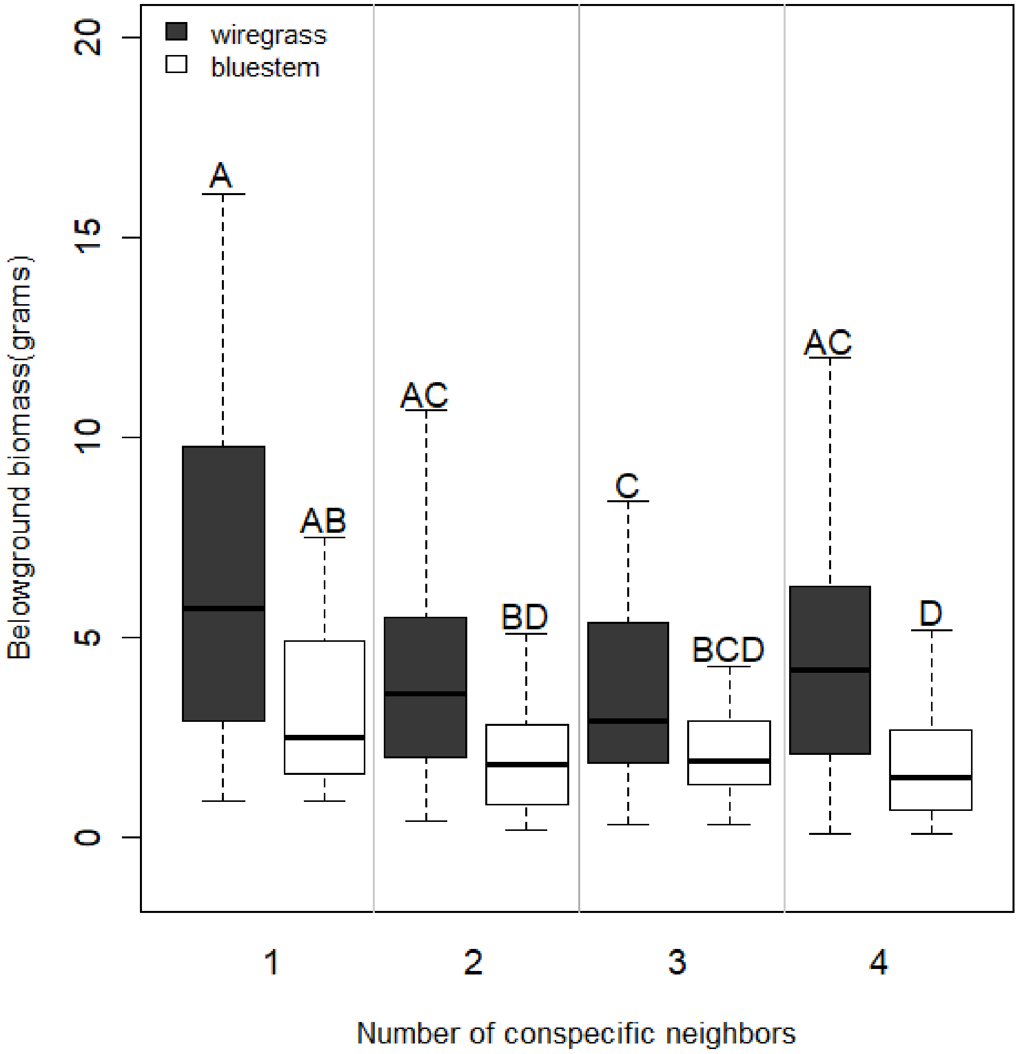

Figure 6. Belowground biomass produced by wiregrass and little bluestem in response to different numbers of heterospecific and conspecific neighbors in pots in the greenhouse. Number of conspecific neighbors was complementary to the number of heterospecific neighbors, with all pots containing four study individuals. Error bars represent 1 SE. Letters indicate significant differences in comparisons between groups at *P* < 0.05 based on pairwise Tukey post-hoc tests.

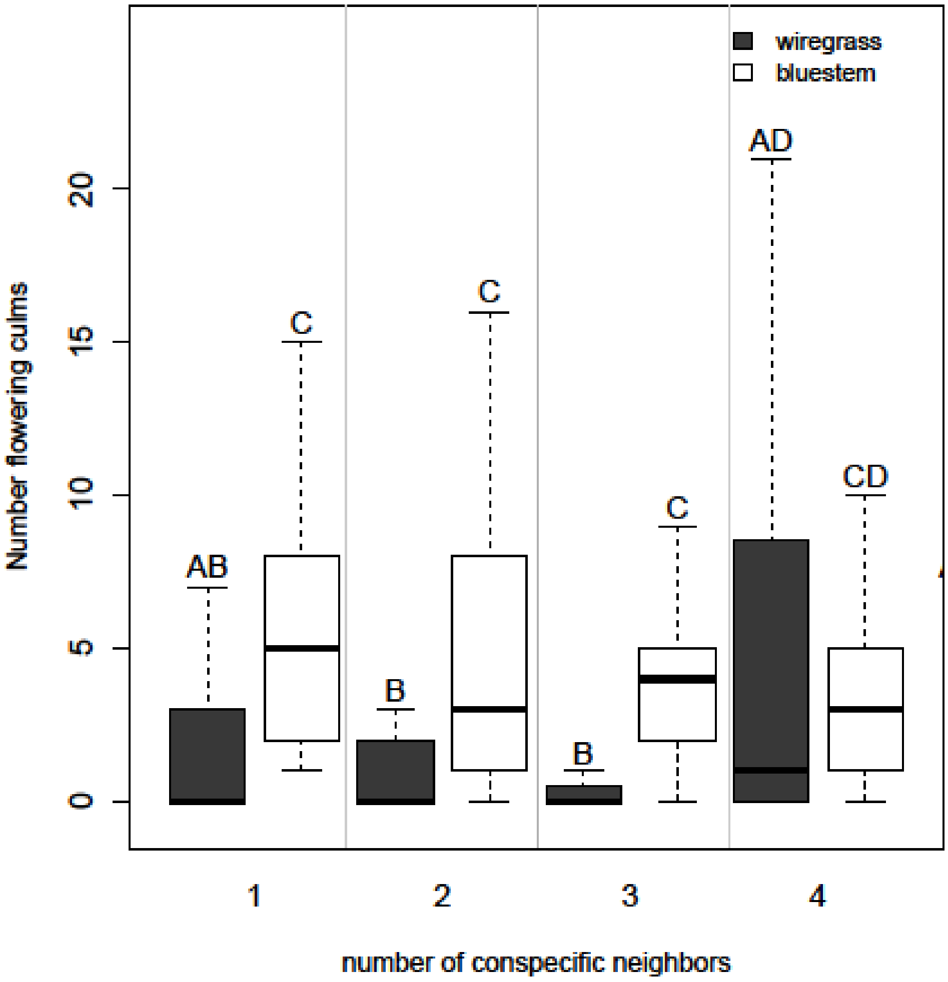

Figure 7. Number of flowering culms produced by wiregrass and little bluestem in response to different numbers of heterospecific and conspecific neighbors in pots in the greenhouse. Number of conspecific neighbors was complementary to the number of heterospecific neighbors, with all pots containing four study individuals. Error bars represent 1 SE. Letters indicate significant differences in comparisons between groups at *P* < 0.05 based on pairwise Tukey post-hoc tests.

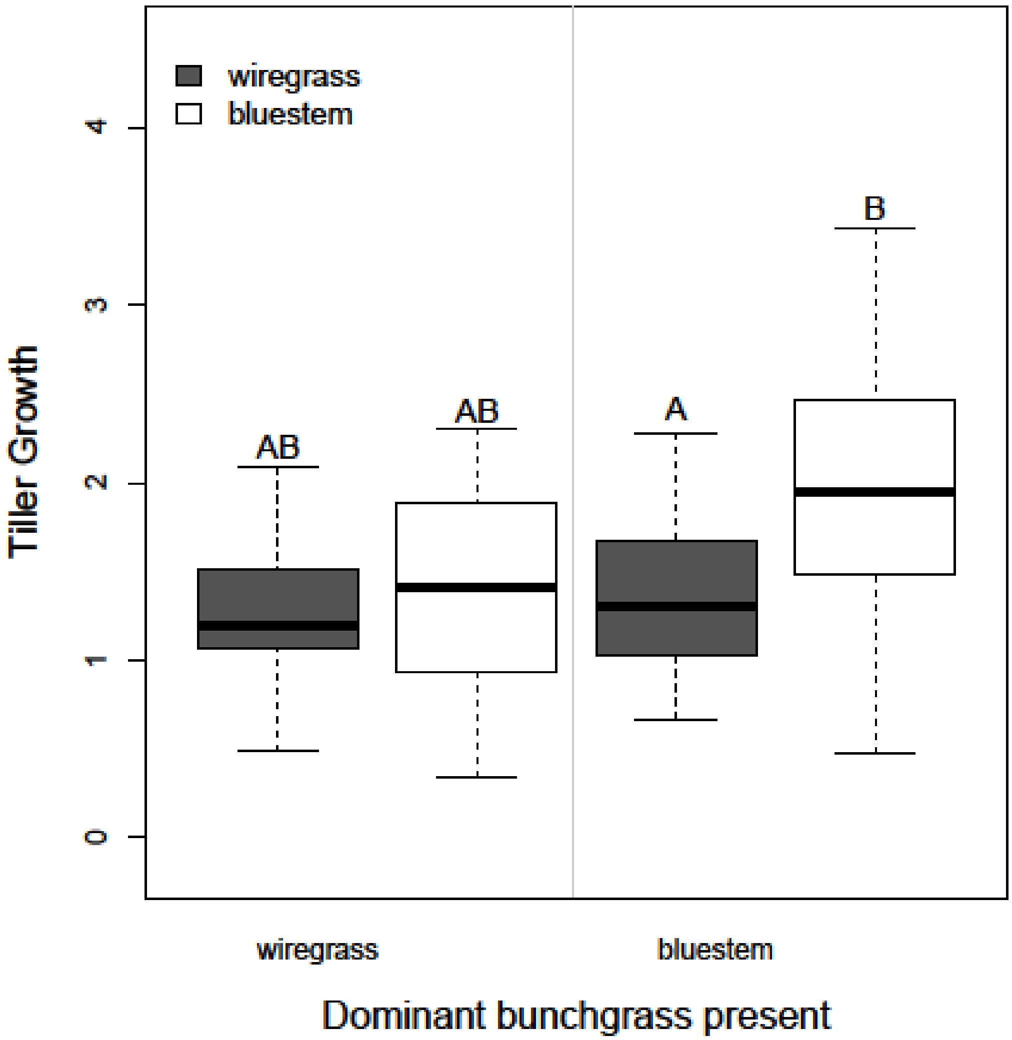

Figure 8. Mean tiller growth of wiregrass and bluestem tussocks transplanted into destinations dominated by one or the other species at Eglin Air Force Base. White boxes are bluestem tussocks; gray boxes are wiregrass individuals. Wiregrass- and bluestem-dominated destinations are indicated on the X-axis. Error bars represent 1 SE. Letters indicate significant differences in comparisons between groups at $P < 0.05$ based on pairwise Tukey post-hoc tests.

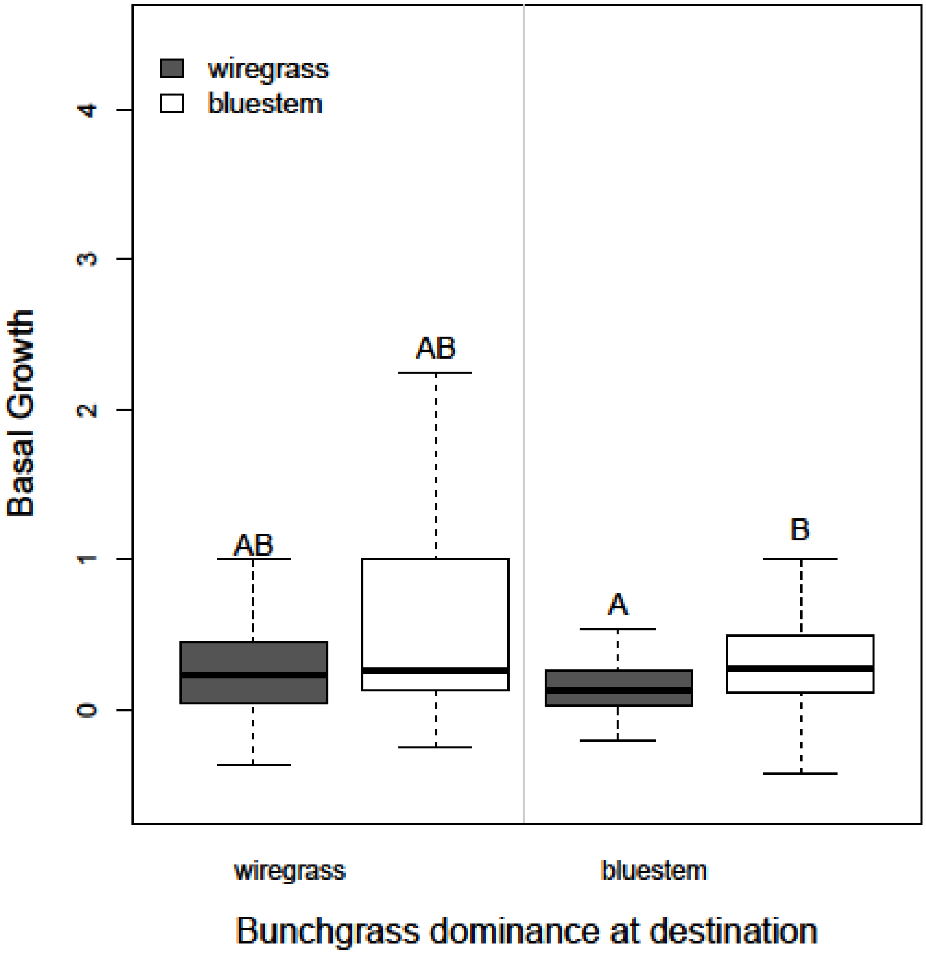

Figure 9. Mean change in basal diameter of wiregrass and bluestem tussocks transplanted into destinations dominated by one or the other species. White boxes are bluestem tussocks; gray boxes are wiregrass individuals. Wiregrass- and bluestem-dominated destinations are indicated on the X-axis. Error bars represent 1 SE. Letters indicate significant differences in comparisons between groups at $P < 0.05$ based on pairwise Tukey post-hoc tests.

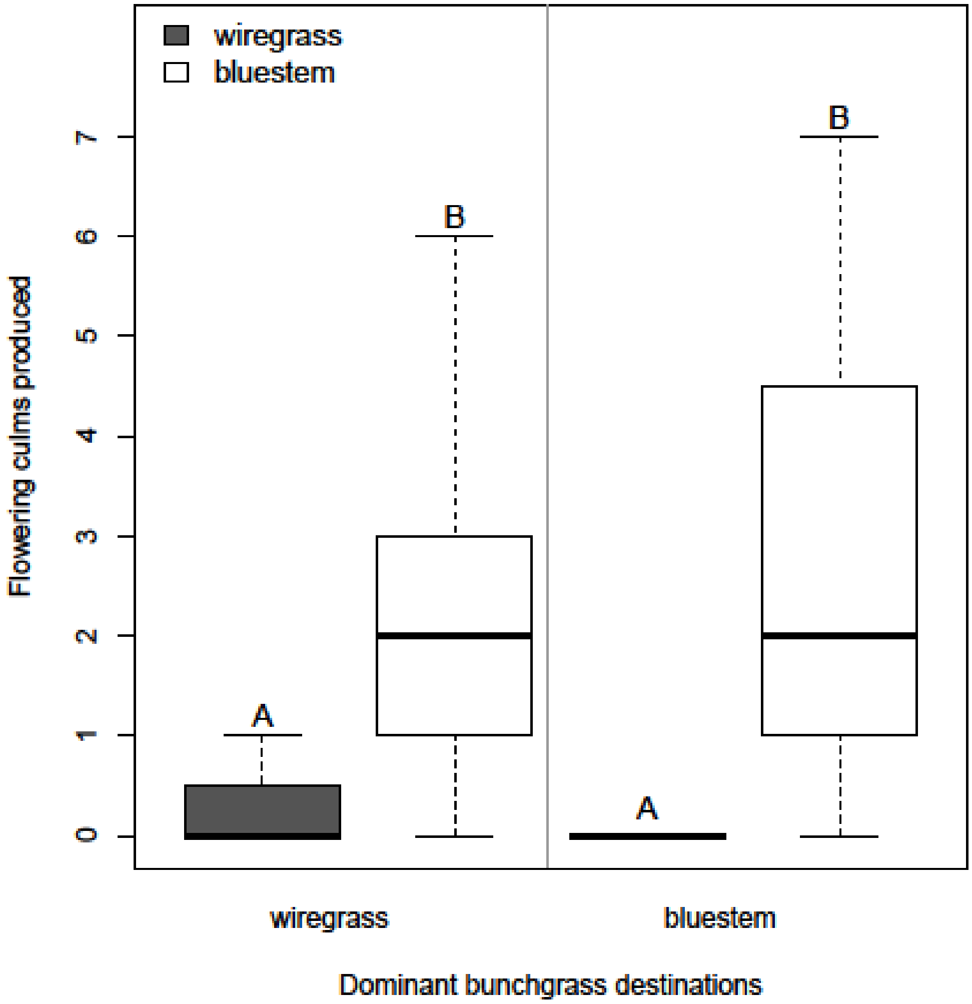

Figure 10. Mean number of flowering culms produced throughout the study by wiregrass and bluestem tussocks transplanted into destinations dominated by one or the other species. White boxes are bluestem tussocks; gray boxes are wiregrass. Wiregrass- and bluestem-dominated destinations are indicated on the X-axis. Error bars represent 1 SE. Letters indicate significant differences in comparisons between groups at $P < 0.05$ based on pairwise Tukey post-hoc tests.

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