

How important is competition in a species-rich grassland? A two-year removal experiment in a pine savanna¹

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Abstract: Although we know that competition sometimes controls the composition of plant communities, we still do not understand its significance in communities having high species richness. We removed an abundant and apparently dominant grass (*Andropogon virginicus*) in species-rich pine grassland in southeastern Louisiana and evaluated the effects on species richness and composition. At 2 sites, moist and dry, we located twenty 1- × 1-m plots with 10 randomly assigned control plots and 10 treatment plots, in which herbicide was applied to individual shoots of *A. virginicus* over 2 y. Plant cover, species richness, and species composition were recorded 4 times over this period. Repeated measures analyses of variance and Mantel tests were used to evaluate differences between control and removal plots. Although there were more than 90 species of vascular plants that might have responded to the removal of *A. virginicus*, no significant effect on cover, species richness, species composition, or functional group composition was found. Competition apparently played a minor role in determining the composition of this subtropical grassland. The general model of competition in temperate grasslands, which assumes a few species of grasses dominate the community through competition and other species survive in the interstices, does not seem to apply. Infertile soils may reduce rates of competitive exclusion and establishment, minimize interactions between grasses and forbs, or produce a fundamentally different kind of competition that is inherently slower and more symmetrical than in most experimental situations.

Keywords: *Andropogon virginicus*, competition, grasslands, longleaf pine savannas, removal experiments, species richness.

Résumé : Bien que nous sachions que la compétition contrôle parfois la composition des communautés de plantes, nous ne comprenons pas son rôle dans les communautés possédant une grande richesse en espèces. Nous avons retiré une graminée abondante et apparemment dominante (*Andropogon virginicus*) d'une savane de pins riche en espèces du sud-est de la Louisiane et évalué les effets sur la richesse et la composition en espèces. Dans 2 sites, un humide et un sec, nous avons installé 20 parcelles de 1 × 1 m dont 10 ont été sélectionnées au hasard pour servir de contrôle et le traitement a été appliqué aux 10 autres. Le traitement consistait à appliquer un herbicide aux pousses individuelles de *A. virginicus* sur une période de 2 ans. Le recouvrement ainsi que la richesse et la composition en espèces ont été mesurés 4 fois durant cette période. Des analyses de variance à mesures répétées et des tests de Mantel ont été utilisés pour évaluer les différences entre les parcelles contrôles et celles traitées. Bien que plus de 90 espèces de plantes vasculaires auraient pu répondre au retrait de *A. virginicus*, aucun effet significatif n'a été observé sur le recouvrement, la richesse ou la composition en espèces ou la composition des groupes fonctionnels. La compétition semble avoir joué un rôle mineur dans la détermination de la composition de cette prairie subtropicale. Le modèle général de compétition des prairies tempérées dans lequel quelques espèces de graminées dominent la communauté par la compétition et les autres espèces survivent dans les interstices ne semble pas s'appliquer ici. Les sols infertiles pourraient diminuer les taux d'exclusion compétitive et d'établissement, minimiser les interactions entre les graminées et les dicotylédones herbacées et ainsi établir un type de compétition complètement différent, plus lent et plus symétrique que dans la plupart des situations expérimentales.

Mots-clés : *Andropogon virginicus*, compétition, expériences de retrait, prairies, richesse en espèces, savanes de pin des marais.

Nomenclature: USDA, NRCS, 2006.

Introduction

Plant communities can be strongly structured or weakly structured by species interactions (Keddy, 2001), and the ubiquity of competition suggests that interactions can play key roles. Species tend to be organized in competitive hierarchies by means of asymmetric competition for

light, a phenomenon now well explored with experiments (Goldsmith, 1978; Grace & Wetzel, 1981; Wilson & Keddy, 1986), null models (Shipley, 1993; Shipley & Keddy, 1994), and theoretical models (Givnish, 1982; Tilman, 1982). The role of competition is of particular interest in communities containing large numbers of species (Grime, 1979; Huston, 1979; Grubb, 1986; Grace, 1999; Keddy, 2001), but there is a serious conceptual and practical problem—as the number of species in a community increases, the number of possible pair-wise interactions increases factorially (Rigler, 1982). It therefore rapidly becomes difficult to assess the role of

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pair-wise interactions in structuring more diverse communities. Yet if we restrict competition experiments to only low-diversity communities, we will bias our research to an unknown degree and fail to obtain experimental results from an entire class of vegetation types with high theoretical and conservation significance.

One way to probe the intensity of species interactions and the (unseen) structure of diverse plant communities is to remove one abundant species and then measure how many other species respond to its removal (Keddy, 2001). Such removal experiments are a standard technique in field studies of competition (Goldberg & Barton, 1992; Keddy, 2001). They do have limitations. First, without extensive monitoring of resources and secondary effects on the associated biota, it is usually not possible to provide a mechanistic interpretation for any changes that occur (Tilman, 1987; Connell, 1990). There is always the risk too that experimental effects such as decaying belowground organs or disrupted mycorrhizal networks might underlie observed changes (Grime, 2001; Wardle, 2002). At the same time, removal experiments can be regarded as just one of the multiple tools used to explore natural communities (Keddy, 2001) and at the very least as a first essential stage of research—one to be followed, if necessary, by much larger experiments that eliminate alternative hypotheses. Indeed, one can argue that the preliminary search for general patterns must precede mechanistic studies (Keddy, 2005).

In order to eventually understand the effects of competition in a full range of natural communities, we need to select locations for experiments with care, searching deliberately for useful extremes already present in nature. Locations for experiments might be chosen for intense physical constraints, with examples including deserts (Fonteyn & Mahall, 1978) or salt marshes (Bertness, 1991). Other experimental locations might be chosen for strong natural gradients, with examples including soil depth in alvars (Belcher, Keddy & Twolan-Strutt, 1995), water depth in wetlands (Grace & Wetzel, 1981), and fertility on shorelines (Wilson & Keddy, 1986). Other experimental locations might be chosen for their high plant diversity, with examples including chalk grasslands (Grime, 1979), fynbos shrublands (Richards, Cowling & Stock, 1997), coastal prairies (Jutila & Grace, 2002), and the system used in this study, coastal plain savannas (Walker & Peet, 1983). Grasses and sedges tend to dominate these coastal plain savannas. Our objective in this study was to remove one abundant grass species, *A. virginicus*, and test for the effects of this removal on the remaining herbaceous flora. The main questions were (1) is there an overall competitive effect of *A. virginicus* on other herbaceous plants and (2) which species or functional groups are most affected?

Methods

STUDY SITE

Pine savannas are naturally occurring fire-prone, nutrient-poor ecosystems (Platt, 1999; Glitzenstein, Streng & Wade, 2003) that once covered over 228 500 km² across the southeastern coastal plain of the United States (Frost, 1993). Natural fire frequency is at least once per decade

(Platt, 1999), although managers often burn at shorter intervals of 1 to 3 y (Walker & Peet, 1983; Kirkman *et al.*, 2001; Glitzenstein, Streng & Wade, 2003). Our experiment was conducted in a remnant longleaf pine savanna in southeastern Louisiana (Girl Scouts of America's Camp Whispering Pines; 30° 41' N, 90° 28' W). It is considered to be one of the better-restored examples of eastern upland longleaf pine (*Pinus palustris*) forest (also known as sandhill pine forest), which is typical of hilly uplands in the central and eastern subregions of southeastern Louisiana (Faulkner, 2004). Our study sites were on the eastern edge of the property, east of Highway 1054 (Roth, 2003), where *P. palustris* was the only overstory species (having a canopy closure of less than 25 percent) and a diverse herbaceous flora was dominated by Poaceae and Asteraceae. The rolling terrain naturally creates a moisture gradient with 2 extremes, ridges and valleys, which we designated dry and moist sites, respectively. Although both had scattered *P. palustris* trees and an understory dominated by grasses, particularly *A. virginicus*, there were differences in composition (Appendix I). Valleys had higher densities of shrub shoots (*e.g.*, *Ilex glabra*, *Morella cerifera*), while ridges had more *Schizachyrium tenerum*.

The soil was a poorly drained silty loam termed Toulantangi soil (McDaniel, 1990), and slopes within the study sites were less than 1%. At Amite, 5 km to the northwest, mean annual temperature is 19.0 °C (January: 9.4 °C; July: 27.3 °C), and mean annual precipitation is 166.9 cm, based on 1971–2000 climate normals (SRCC, 2004a,b). The experiment began 3 weeks after the site was burned in April 2001, during a prolonged drought. In the preceding year, precipitation had been 47.7 cm below normal. The drought provided a further reason for comparing a moist valley with a drier ridge, but in 2001 the drought ended. Precipitation surged to 21.5 cm above normal in 2001, largely as a result of over 50 cm of rain associated with tropical storm Allison from June 4 to 12, which flooded the valley for several days in more than 10 cm of running water, and produced pools of standing water in depressions on the ridge. Precipitation remained 22.5 cm above normal in the following year, 2002 (LOSC, 2000–2002). Selective logging, fire, and replanting have been used as management tools over the past decades, and since 1994 controlled burns have been applied every 1 to 2 y (W. Platt, pers. comm.).

PLANT SPECIES

Approximately 200 species are present in this savanna (Girl Scouts of America, unpubl. data), including several rare species (*Agalinis aphylla*, *Helianthus mollis*, *Rhynchospora compressa*). Over the course of the study period, 91 species of vascular plants in 31 families were found within 50 m of study plots, the largest families being the Poaceae (29 species), Asteraceae (12 species), and Cyperaceae (8 species). Perennial tussock grasses were the most common species at the site, especially *A. virginicus*, *Dichanthelium* spp., *Panicum* spp., *Paspalum* spp., and *S. tenerum*.

Andropogon virginicus was selected for removal because it was the most abundant species at the study site and was also prevalent at other savanna habitats in the region. Although it has highly variable traits such as

the size and shape of the inflorescence and presence and type of pubescence, it is treated as a single species in both of the standard sources for identification for Louisiana grasses, Allen (1992) and Hitchcock (1950). Hitchcock suggests that it is closely related to *Andropogon glomeratus*. Only 2 varieties of *A. virginicus* are recognized, and only var. *virginicus* occurs west of Florida (USDA, NRCS, 2006).

EXPERIMENTAL DESIGN

All aboveground herbaceous biomass, smaller woody plants, and litter had been removed from both the moist site and dry site (100 m to the north) by a recent prescribed burn. At each site 20 1- × 1-m plots were arranged in a 4 × 5 rectangle with 1-m-wide buffers between them. On 23–25 April, when the area was still smouldering (Roth, 2003), the glyphosate herbicide Rodeo® (diluted to 15 mg·l⁻¹) was applied to *A. virginicus* shoots in half of the plots at each site, selected at random, using cotton-tipped swabs; follow-up treatments were applied on 5 June at the moist site and 10 June at the dry site. Throughout the remainder of the experiment, occasional new shoots of *A. virginicus* in the removal plots were treated with herbicide (this was a press rather than a pulse experiment; Bender, Case & Gilpin, 1984). Dead *A. virginicus* was not subsequently removed, but since plants were treated with herbicide as young shoots, they did not form substantial litter. The buffer strips were not treated in any way, which may have produced some edge effects. In order to provide a non-destructive surrogate for biomass, percent cover of each species in the community was assessed by eye with 2 experienced observers. Cover was recorded for each plot over 2 y, in August and late September/early October 2001 and April and August 2002.

ANALYSIS

Repeated measures analyses of variance were used to compare plant cover sum and species richness between removal and control plots at both sites over the 4 sampling periods, using SYSTAT (SPSS, 1998). Mantel tests were then used to test for differences in species composition between removal and control plots at different sites and sampling dates, using PC-ORD (McCune & Mefford, 1999). For the Mantel tests, *A. virginicus* was first excluded and then a distance matrix based on percent cover was calculated using the Kulczynski coefficient between all control and removal plots for each sampling date and site. This coefficient was chosen because it is a robust measure of compositional dissimilarity that gives equal weight to rare and frequent species (Faith, Minchin & Belbin, 1987). A second model distance matrix was constructed with values of 0 for “within group” distances within either control or removal plots and values of 1 for “between group” distances between control and removal plots (Legendre & Legendre, 1998). Differences between each distance matrix and the model matrix were then tested using Mantel tests and 5000 random runs.

These plant communities not only had high diversity of functional groups, but also many species within functional groups. To examine the possibility that the response to removal was dispersed among several species within a func-

tional group, we repeated Mantel tests on the cover of functional groups (Du Rietz, 1931; Raunkiaer, 1934). Species were assigned to 1 of 13 functional groups (Boutin & Keddy, 1993; Weiher *et al.*, 1999) according to published life history information: (1) carnivorous plants, (2) hemiparasites, (3) legumes, (4) deciduous rosettes, (5) evergreen rosettes, (6) perennial tussocks, (7) perennial forbs, (8) annuals/biennials, (9) vines, (10) evergreen shrubs, (11) evergreen trees, (12) deciduous shrubs, and (13) deciduous trees.

To further explore some of the differences in assemblages observed in the Mantel tests, 2 sample permutation tests based on 10 000 random shuffles were conducted to determine which species had significant differences in cover between removal and control plots (Resampling Stats, 2001). Significance for all tests was assessed at $P \leq 0.05$.

Results

TOTAL PLANT COVER

Plant cover varied in space and time in the study area. *Andropogon virginicus* was the principal dominant in control plots at both sites, except in late September 2001 when *Paspalum floridanum* had slightly more cover in the moist site and in August 2002 when *Schizachyrium tenerum* became more dominant at the dry site (Appendix I). Mean sum of plant cover was higher in the moist site (73.7%) than the dry site (52.9%; Figure 1; Table I). Plant cover varied strongly between sampling periods at both sites (Table I) and was highest in September/October 2001, when it exceeded 125% in control plots at the moist site and 83% at the dry site (Figure 1). Plant cover in August 2001 was over twice that in August 2002 in the moist site but not in the dry site (Figure 1; Table I, significant date × site interaction).

Plant cover was significantly lower ($P = 0.019$) in the removal plots (56.9%) than in the control plots (69.7%), which reflects, in part, the continual removal of

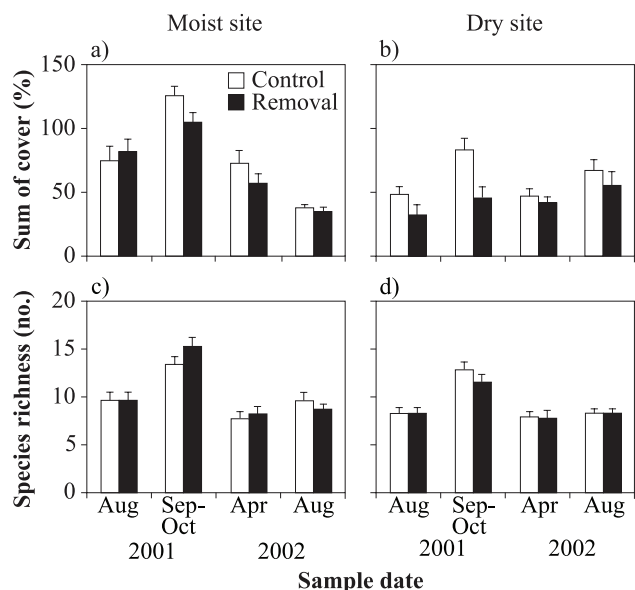


FIGURE 1. Mean sum of plant cover and species richness (+ SD) in the moist and dry sites over the course of the experiment, with and without the removal of *A. virginicus*.

TABLE I. Repeated measures ANOVA of the effects of the removal of *A. virginicus* on plant cover sum and species richness at both sampling sites and across sampling dates. For species richness only, Huynh–Feldt adjusted *P* values are shown for within treatment effects.

Source of variation	df	MS	Cover sum		Species richness		
			<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Site	1	17,451.5	16.0	< 0.001	52.9	4.2	0.047
Removal	1	6592.1	6.1	0.019	0.0	0.0	0.965
Site × removal	1	888.3	0.8	0.372	4.9	0.4	0.535
Error among treatments	36	1088.6			12.5		
Sample date	3	13,232.1	24.1	< 0.001	234.5	82.8	< 0.001
Sample date × site	3	10,721.0	19.6	< 0.001	7.3	2.6	0.066
Sample date × removal	3	1194.7	2.2	0.095	1.2	0.4	0.725
Sample date × site × removal	3	499.6	0.9	0.438	7.5	2.6	0.060
Error within treatments	108	548.2			2.8		

A. virginicus over the study period, and there were no interactions (Table I).

SPECIES RICHNESS

More species were encountered in the dry site (72 dry *versus* 58 moist) over the course of the study, but mean species richness was higher in plots in the moist site (10.4 m⁻² moist *versus* 9.2 m⁻² dry; Figure 1). Species richness varied across sampling periods (Table I) and was highest in September/October 2001 (Figure 1). The removal of *A. virginicus*, however, did not have any effect on species richness at either site (Table I).

COMMUNITY COMPOSITION

Mantel tests showed that species composition was not significantly different between control and removal plots (Table II), although it was close to being significantly different in April 2002 at the moist site (*P* = 0.061). At this site and sampling date, permutation tests show that *Dichantheium laxiflorum* was more abundant (*P* = 0.054) in the removal (6.2%) than the control (1.4%) plots, while *Dichantheium scabriusculum* was less abundant in removal plots (1.4% *versus* 10.1%, *P* = 0.029), as was *Morella cerifera* (1.4% *versus* 11.9%, *P* = 0.021). Relatively low *P* values (0.054, 0.029, and lower) would fade to insignificance with Bonferroni correction. Functional group composition was not significantly different between control and removal plots (Table II).

Discussion

We expected to detect competitive release in at least some species with the removal of *A. virginicus* since it had up to 30% mean cover (Appendix I) and there was a wide array of species and functional types to respond. The absence of any measurable effect on species composition supports the null hypothesis that competition from *A. virginicus* was not significant in structuring the community over the course of the study. However, several caveats must be considered in the interpretation of these results.

(1) The time required for canopy biomass to accumulate and competition to exert an influence after a fire may be more than 2 y owing to delays in germination and the production of new shoots in these nutrient-poor systems. In other studies of grasslands, however, results were found within time periods ranging from a few months to 2 growing seasons (Allen & Forman, 1976;

TABLE II. *P* values of Mantel tests for differences between control and removal plots based on species cover and functional group cover at both sites for all sampling dates. *Andropogon virginicus* was excluded from the data matrices prior to running the tests.

Sample date	Species cover		Functional groups	
	Moist site	Dry site	Moist site	Dry site
2001 Aug	0.436	0.365	0.2	0.248
2001 Sep–Oct	0.408	0.114	0.228	0.129
2002 Apr	0.061	0.403	0.327	0.108
2002 Aug	0.272	0.502	0.313	0.33

Gurevitch & Unnasch, 1989; Inchausti, 1995; Köchy & Wilson, 2000). The natural (and restored) fire regime in coastal plain savannas frequently allows for only 2 y of re-growth between fires.

- (2) Fluctuation in abiotic conditions may have changed competitive interactions. Water was probably a main limiting resource prior to beginning the experiment, but during the first summer, a heavy rain caused standing water in the moist site. However, fluctuations in hydrology are a standard characteristic of pine savannas along the Gulf coastal plain (Peet & Allard, 1993; Platt, 1999).
- (3) The large number of species in the savanna may have limited our ability to detect competitive release. In the extreme case, if a different species responded in each removal plot, one would have a reduced probability of detecting a significant response, even with Mantel tests.
- (4) The large number of life history types in savannas may allow greater partitioning of resources, reducing the intensity of interspecific competition. For example, carnivorous plants and legumes have access to different sources of nitrogen, and ancient soils may allow subtle belowground niche differentiation. Yet this must be balanced against Harper's (1977) reminder that all plants are limited by relatively few resources, reducing the possibilities for resource partitioning.

Having considered 4 possible caveats above, we suggest it is likely that species interactions in pine savannas are indeed weaker than in other grasslands. There are several plausible reasons why this might be so. All require us to think rather carefully about what removal experiments actually measure and the different kinds of competition that exist in plant communities (Keddy, 2001). It is well known that aboveground interactions involving competition for light are inherently asymmetric, allowing a few species to

exert dominance over the others (Shipley & Keddy, 1994). In pine savannas, regular burning of the aboveground biomass, combined with slow recovery rates owing to low soil fertility, may minimize interactions among plant canopies. Instead, belowground competition may predominate. Belowground interactions may be inherently more symmetric (Weiner, 1990; Keddy, 2001), and if this is the case, then no single species may be able to rapidly dominate a site as a result of competitive release.

In conclusion, the general model of temperate grasslands by Grime (1980), largely corroborated by more recent work (Grubb, 1986; Gurevitch & Unnasch, 1989; Carson & Pickett, 1990; Shipley & Keddy, 1994), assumes that a few species of grasses dominate communities through competition and that other species must then survive in the interstices. Our failure to detect competition in pine savannas suggests that these savannas are different from less speciose temperate grasslands. Our current working hypothesis includes 4 possible modifications (hypotheses) for refinement of the simpler model of grass dominance. First, low soil fertility and recurring fire are likely to reduce the canopy effects of grasses in comparison to temperate grasslands. Second, low rates of establishment from seed may complicate the design of experiments in these habitats. Seed and seedling ecology is currently poorly understood (Glitzenstein *et al.*, 2001) in comparison with temperate floras (Grime *et al.*, 1981). Third, whatever the habitat, the larger number of species may reduce the probability that any single species will respond significantly in a removal experiment. Fourth, low aboveground competition may force more interactions belowground; additionally, these may be inherently slower and more symmetric. We conclude that future work will have to include press experiments that remove more than one species, run for more than 2 y, separate competition into above- and belowground components, and measure asymmetry of belowground interactions.

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Literature cited

- Allen, C. M., 1992. Grasses of Louisiana. Cajun Prairie Habitat Preservation Society, Eunice, Louisiana.
- Allen, E. B. & R. T. T. Forman, 1976. Plant species removal and old-field community structure and stability. *Ecology*, 57: 1233–1243.
- Belcher, J. W., P. A. Keddy & L. Twolan-Strutt, 1995. Root and shoot competition intensity along a soil depth gradient. *Journal of Ecology*, 83: 673–682.
- Bender, E. A., T. J. Case & M. E. Gilpin, 1984. Perturbation experiments in community ecology: Theory and practice. *Ecology*, 65: 1–13.
- Bertness, M. D., 1991. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology*, 72: 125–137.
- Boutin, C. & P. A. Keddy, 1993. A functional classification of wetland plants. *Journal of Vegetation Science*, 4: 591–600.
- Carson, W. P. & S. T. A. Pickett, 1990. Role of resources and disturbance in the organization of an old field plant community. *Ecology*, 71: 226–238.
- Connell, J. H., 1990. Apparent versus “real” competition in plants. Pages 9–26 in J. B. Grace & D. Tilman (eds.). *Perspectives on Plant Competition*. Academic Press, San Diego, California.
- Du Rietz, G. E., 1931. Life-forms of terrestrial flowering plants. *Acta Phytogeographica Suecica*, 3: 1–95.
- Faith, D. P., P. R. Minchin & L. Belbin, 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, 69: 57–68.
- Faulkner, P. (ed.), 2004. *The Natural Communities of Louisiana*. Louisiana Natural Heritage Program, Louisiana Department of Wildlife and Fisheries, Baton Rouge, Louisiana.
- Fonteyn, P. J. & B. E. Mahall, 1978. Competition among desert perennials. *Nature*, 275: 544–545.
- Frost, C. C., 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pages 17–43 in S. M. Hermann (ed.). *The Longleaf Pine Ecosystem: Ecology, Restoration and Management*. Tall Timbers Research, Tallahassee, Florida.
- Givnish, T. J., 1982. On the adaptive significance of leaf height in forest herbs. *American Naturalist*, 120: 353–381.
- Glitzenstein, J. S., D. R. Streng & D. D. Wade, 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. *Natural Areas Journal*, 23: 22–37.
- Glitzenstein, J. S., D. R. Streng, D. D. Wade & J. Brubaker, 2001. Starting new populations of longleaf pine ground-layer plants in the outer coastal plain of South Carolina, USA. *Natural Areas Journal*, 21: 89–110.
- Goldberg, D. E. & A. M. Barton, 1992. Patterns and consequences of interspecific competition in natural communities: A review of field experiments with plants. *American Naturalist*, 139: 771–801.
- Goldsmith, F. B., 1978. Interaction (competition) studies as a step towards the synthesis of sea-cliff vegetation. *Journal of Ecology*, 66: 921–931.
- Grace, J. B., 1999. The factors controlling species density in herbaceous plant communities: An assessment. *Perspectives in Plant Ecology, Evolution and Systematics*, 2: 1–28.
- Grace, J. B. & R. G. Wetzel, 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): Experimental field studies. *American Naturalist*, 118: 463–474.
- Grime, J. P., 1979. *Plant Strategies and Vegetation Processes*. John Wiley and Sons, Chichester.
- Grime, J. P., 1980. An ecological approach to management. Pages 13–55 in I. H. Rorison & R. Hunt (eds.). *Amenity Grassland: An Ecological Perspective*. John Wiley and Sons, Chichester.
- Grime, J. P., 2001. *Plant Strategies, Vegetation Processes and Ecosystem Properties*. John Wiley and Sons, Chichester.
- Grime, J. P., G. Mason, A. V. Curtis, J. Rodman, S. R. Band, M. A. G. Mowforth, A. M. Neal & S. Shaw, 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology*, 69: 1017–1059.
- Grubb, P. J., 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. Pages 207–225 in J. Diamond & T. J. Case (eds.). *Community Ecology*. Harper and Row, New York, New York.
- Gurevitch, J. & R. S. Unnasch, 1989. Experimental removal of a dominant species at two levels of soil fertility. *Canadian Journal of Botany*, 67: 3470–3477.
- Harper, J. L., 1977. *Population Biology of Plants*. Academic Press, London.

- Hitchcock, A. S., 1950. *Manual of the Grasses of the United States*. US Government Printing Office, Washington, DC.
- Huston, M., 1979. A general hypothesis of species diversity. *American Naturalist*, 113: 81–101.
- Inchausti, P., 1995. Competition between perennial grasses in a neotropical savanna: The effects of fire and of hydric-nutritional stress. *Journal of Ecology*, 83: 231–243.
- Jutila, H. M. & J. B. Grace, 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: A test of the competitive release hypothesis. *Journal of Ecology*, 90: 291–302.
- Keddy, P. A., 2001. *Competition*. 2nd Edition. Kluwer, Dordrecht.
- Keddy, P. A., 2005. Putting the plants back into plant ecology: Six pragmatic models for understanding and conserving plant diversity. *Annals of Botany*, 95: 1–13.
- Kirkman, L. K., R. J. Mitchell, R. C. Helton & M. D. Drew, 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany*, 88: 2119–2128.
- Köchy, M. & S. D. Wilson, 2000. Competitive effects of shrubs and grasses in prairies. *Oikos*, 91: 385–395.
- Legendre, P. & L. Legendre, 1998. *Numerical Ecology*. 2nd Edition. Elsevier, Amsterdam.
- LOSC, 2000–2002. *Louisiana Monthly Climate Review*. Louisiana Office of State Climatology, Baton Rouge, Louisiana.
- McCune, B. & M. J. Mefford, 1999. *PC-ORD Multivariate Analysis of Ecological Data*, Version 4.25. MjM Software, Gleneden Beach, Oregon.
- McDaniel, D., 1990. *Soil Survey of Tangipahoa Parish, Louisiana*. US Department of Agriculture, Soil Conservation Service, Washington, DC.
- Peet, R. K. & D. J. Allard, 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: A preliminary classification. Pages 45–81 *in* S. M. Hermann (ed.). *The Longleaf Pine Ecosystem: Ecology, Restoration and Management*. Tall Timbers Research Station, Tallahassee, Florida.
- Platt, W. J., 1999. Southeastern pine savannas. Pages 23–51 *in* R. C. Anderson, J. S. Fralish & J. M. Baskin (eds.). *Savannas, Barrens and Rock Outcrop Communities of North America*. Cambridge University Press, Cambridge.
- Raunkiaer, C., 1934. *The Life Forms of Plants and Statistical Plant Geography*. Clarendon Press, Oxford.
- Resampling Stats, 2001. *Resampling Stats for Excel 2.0*. Resampling Stats, Arlington, Virginia.
- Richards, M. B., R. M. Cowling & W. D. Stock, 1997. Soil factors and competition as determinants of the distribution of six fynbos Proteaceae. *Oikos*, 79: 394–406.
- Rigler, F. H., 1982. Recognition of the possible: An advantage of empiricism in ecology. *Canadian Journal of Fisheries and Aquatic Sciences*, 39: 1323–1331.
- Roth, A.-M. F., 2003. *Plant Species Diversity and Experimental Removal Studies in Longleaf Pine Savannas in the St. Tammany and Tangipahoa Parishes, Louisiana*. M.Sc. thesis, Southeastern Louisiana University, Hammond, Louisiana.
- Shipley, B., 1993. A null model for competitive hierarchies in competition matrices. *Ecology*, 74: 1693–1699.
- Shipley, B. & P. A. Keddy, 1994. Evaluating the evidence for competitive hierarchies in plant communities. *Oikos*, 69: 340–345.
- SPSS, 1998. *Systat*, Version 8.0. SPSS Inc., Chicago, Illinois.
- SRCC, 2004a. Normal Daily Average Temperature. Southern Regional Climate Center, Baton Rouge, Louisiana. [Online] URL: <http://www.srcc.lsu.edu/southernClimate/atlas/images/LAtavg.html> (November 2004).
- SRCC, 2004b. Normal Monthly Precipitation. Southern Regional Climate Center, Baton Rouge, Louisiana. [Online] URL: <http://www.srcc.lsu.edu/southernClimate/atlas/images/LAprcp.html> (November 2004).
- Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.
- Tilman, D., 1987. The importance of the mechanisms of interspecific competition. *American Naturalist*, 129: 769–74.
- USDA, NRCS, 2006. *The PLANTS Database*. National Plant Data Center, Baton Rouge, Louisiana. [Online] URL: <http://plants.usda.gov>
- Walker, J. & R. K. Peet, 1983. Composition and species diversity of pine–wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio*, 55: 163–179.
- Wardle, D. A., 2002. *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton, New Jersey.
- Weiher, E., A. van der Werf, K. Thompson, M. Roderick, E. Garnier & O. Eriksson, 1999. Challenging *Theophrastus*: A common core list of plant traits for functional ecology. *Journal of Vegetation Science*, 10: 609–620.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Trends in Ecology and Evolution*, 5: 360–364.
- Wilson, S. D. & P. A. Keddy, 1986. Measuring diffuse competition along an environmental gradient: Results from a shoreline plant community. *American Naturalist*, 127: 862–869.

APPENDIX I. Dominant species in the control plots at Camp Whispering Pines, Louisiana. These species had at least 3% mean cover across control plots during one sampling period. Values are mean percent cover \pm SD ($n = 10$).

Species	Functional group	Moist Site				Dry Site			
		2001		2002		2001		2002	
		August	Sep–Oct	April	August	August	Sep–Oct	April	August
<i>Andropogon gerardii</i>	perennial tussock	4.9 \pm 9.4	5.2 \pm 9.3	0	0	0	0	0	0
<i>Andropogon virginicus</i>	perennial tussock	8.4 \pm 14.5	16.2 \pm 24.8	29.5 \pm 27.8	4.8 \pm 5.8	10.7 \pm 11.2	29.7 \pm 20.3	14.4 \pm 14.9	5.7 \pm 7.3
<i>Aster</i> spp.	perennial forb	3.9 \pm 5.9	5.9 \pm 7.9	0.1 \pm 0.3	1.9 \pm 1.3	0	0	0	0
<i>Dichanthelium aciculare</i>	perennial tussock	0	4.5 \pm 7.2	0	0	0	0.5 \pm 1.6	0.2 \pm 0.6	0
<i>Dichanthelium laxiflorum</i>	perennial tussock	0.8 \pm 0.9	1.2 \pm 1.5	1.4 \pm 1.8	2.3 \pm 2.3	3.8 \pm 3.9	2.8 \pm 3.6	3.2 \pm 2.4	2.0 \pm 3.1
<i>Dichanthelium scabriusculum</i>	perennial tussock	4.8 \pm 8.1	11.4 \pm 18.4	10.1 \pm 11.1	2.9 \pm 3.3	0	0	0	0
<i>Dichanthelium sphaerocarpon</i>	perennial tussock	0	0	0	0	0.2 \pm 0.6	0.2 \pm 0.6	15.8 \pm 5.5	1.2 \pm 0.9
<i>Diodia virginiana</i>	perennial forb	7.6 \pm 7.7	9.5 \pm 12.0	2.8 \pm 6.1	2.0 \pm 1.3	0	0	0	0
<i>Eupatorium leucolepis</i>	perennial forb	7.2 \pm 12.2	7.1 \pm 9.6	3.6 \pm 6.1	2.3 \pm 2.8	0	0	0	0
<i>Hibiscus aculeatus</i>	deciduous shrub	8.2 \pm 12.8	1.8 \pm 1.9	1.3 \pm 2.0	1.5 \pm 2.4	6.0 \pm 19.0	5.0 \pm 15.8	0.2 \pm 0.4	0.4 \pm 1.3
<i>Ilex glabra</i>	evergreen shrub	6.0 \pm 19.0	6.0 \pm 19.0	6.0 \pm 19.0	2.6 \pm 7.9	0.4 \pm 0.7	1.1 \pm 2.1	0.5 \pm 1.6	0.7 \pm 1.6
<i>Morella cerifera</i>	evergreen shrub	4.9 \pm 12.4	7.5 \pm 9.4	11.9 \pm 18.5	5.8 \pm 8.0	0	0.5 \pm 1.6	0.1 \pm 0.3	0.1 \pm 0.3
<i>Nyssa sylvatica</i>	deciduous tree	6.0 \pm 19.0	5.0 \pm 15.8	0	2.0 \pm 6.3	0	0	0	0
<i>Panicum anceps</i>	perennial tussock	0	4.5 \pm 9.3	0	0	3.8 \pm 6.1	3.8 \pm 6.1	0	0.7 \pm 1.2
<i>Panicum rigidulum</i>	perennial tussock	0	0	0	0	0	3.0 \pm 6.7	0	0
<i>Panicum verrucosum</i>	perennial tussock	1.5 \pm 4.7	7.2 \pm 16.3	0	0	0	0	0	0
<i>Paspalum floridanum</i>	perennial tussock	3.5 \pm 6.7	19.5 \pm 28.3	0	4.6 \pm 3.7	0	0.8 \pm 1.6	0	1.0 \pm 2.5
<i>Paspalum setaceum</i>	perennial tussock	0	0	0	0	0.2 \pm 0.4	3.0 \pm 4.2	0	0.6 \pm 1.3
<i>Schizachyrium tenerum</i>	perennial tussock	0	0.1 \pm 0.3	0	0	3.7 \pm 6.6	14.4 \pm 19	4.7 \pm 6.3	43.7 \pm 35.1