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

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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 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.


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...
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 Toul-Tangi 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-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 functional 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...


**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.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th><em>P</em></th>
<th>MS</th>
<th><em>F</em></th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>1</td>
<td>17,451.5</td>
<td>16.0</td>
<td>&lt; 0.001</td>
<td>52.9</td>
<td>4.2</td>
<td>0.047</td>
</tr>
<tr>
<td>Removal</td>
<td>1</td>
<td>6592.1</td>
<td>6.1</td>
<td>0.019</td>
<td>0.0</td>
<td>0.0</td>
<td>0.965</td>
</tr>
<tr>
<td>Site × removal</td>
<td>1</td>
<td>888.3</td>
<td>0.8</td>
<td>0.372</td>
<td>4.9</td>
<td>0.4</td>
<td>0.535</td>
</tr>
<tr>
<td>Error among treatments</td>
<td>36</td>
<td>1088.6</td>
<td>12.5</td>
<td>0.095</td>
<td>12.5</td>
<td>0.095</td>
<td>0.535</td>
</tr>
<tr>
<td>Sample date</td>
<td>3</td>
<td>13,231.2</td>
<td>24.1</td>
<td>&lt; 0.001</td>
<td>234.5</td>
<td>82.8</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Sample date × site</td>
<td>3</td>
<td>10,721.0</td>
<td>19.6</td>
<td>&lt; 0.001</td>
<td>7.3</td>
<td>2.6</td>
<td>0.066</td>
</tr>
<tr>
<td>Sample date × removal</td>
<td>3</td>
<td>1194.7</td>
<td>22.2</td>
<td>0.095</td>
<td>1.2</td>
<td>0.4</td>
<td>0.725</td>
</tr>
<tr>
<td>Sample date × site × removal</td>
<td>3</td>
<td>499.6</td>
<td>0.9</td>
<td>0.438</td>
<td>7.5</td>
<td>2.6</td>
<td>0.060</td>
</tr>
<tr>
<td>Error within treatments</td>
<td>108</td>
<td>548.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**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.

<table>
<thead>
<tr>
<th>Sample date</th>
<th>Species cover</th>
<th>Functional groups</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample date</td>
<td>Moist site</td>
<td>Dry site</td>
<td>Moist site</td>
<td>Dry site</td>
<td></td>
</tr>
<tr>
<td>2001 Aug</td>
<td>0.436</td>
<td>0.365</td>
<td>0.2</td>
<td>0.248</td>
<td></td>
</tr>
<tr>
<td>2001 Sep–Oct</td>
<td>0.408</td>
<td>0.114</td>
<td>0.228</td>
<td>0.129</td>
<td></td>
</tr>
<tr>
<td>2002 Apr</td>
<td>0.061</td>
<td>0.403</td>
<td>0.327</td>
<td>0.108</td>
<td></td>
</tr>
<tr>
<td>2002 Aug</td>
<td>0.272</td>
<td>0.502</td>
<td>0.313</td>
<td>0.33</td>
<td></td>
</tr>
</tbody>
</table>

*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 m² moist versus 9.2 m² 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 *Dichanthelium laxiflorum* was more abundant (*P* = 0.054) in the removal (6.2%) than the control (1.4%) plots, while *Dichanthelium scabriusculum* was less abundant in removal plots (1.4% versus 10.1%, *P* = 0.029), as was Morella cerifera (1.4% versus 19.9%, *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; Muntean & Platt, 1999).

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 may 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 to temperate florals (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.

Acknowledgements

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Literature cited


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 ± SD (n = 10).

<table>
<thead>
<tr>
<th>Species</th>
<th>Functional group</th>
<th>Moist Site 2001</th>
<th>Moist Site 2002</th>
<th>Dry Site 2001</th>
<th>Dry Site 2002</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>August</td>
<td>Sep–Oct</td>
<td>April</td>
<td>August</td>
</tr>
<tr>
<td>Andropogon gerardii</td>
<td>perennial tussock</td>
<td>4.9 ± 9.4</td>
<td>5.2 ± 9.3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Andropogon virginicus</td>
<td>perennial tussock</td>
<td>8.4 ± 14.5</td>
<td>16.2 ± 24.8</td>
<td>29.5 ± 27.8</td>
<td>4.8 ± 5.8</td>
</tr>
<tr>
<td>Aster spp.</td>
<td>perennial tussock</td>
<td>3.9 ± 5.9</td>
<td>5.9 ± 7.9</td>
<td>0.1 ± 0.3</td>
<td>1.9 ± 1.3</td>
</tr>
<tr>
<td>Dichanthelium aciculare</td>
<td>perennial tussock</td>
<td>0</td>
<td>4.5 ± 7.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dichanthelium laxiflorum</td>
<td>perennial tussock</td>
<td>0.8 ± 0.9</td>
<td>1.2 ± 1.5</td>
<td>1.4 ± 1.8</td>
<td>2.3 ± 2.3</td>
</tr>
<tr>
<td>Dichanthelium scabriusculum</td>
<td>perennial tussock</td>
<td>4.8 ± 8.1</td>
<td>11.4 ± 18.4</td>
<td>10.1 ± 11.1</td>
<td>2.9 ± 3.3</td>
</tr>
<tr>
<td>Dichanthelium sphaerocarpon</td>
<td>perennial tussock</td>
<td>0</td>
<td>0</td>
<td>0.2 ± 0.6</td>
<td>0.2 ± 0.6</td>
</tr>
<tr>
<td>Diodia virginiana</td>
<td>perennial forb</td>
<td>7.6 ± 7.7</td>
<td>9.5 ± 12.0</td>
<td>2.8 ± 6.1</td>
<td>2.0 ± 1.3</td>
</tr>
<tr>
<td>Eupatorium leucolepis</td>
<td>perennial forb</td>
<td>7.2 ± 12.2</td>
<td>7.1 ± 9.6</td>
<td>3.6 ± 6.1</td>
<td>2.3 ± 2.8</td>
</tr>
<tr>
<td>Hibiscus aculeatus</td>
<td>deciduous shrub</td>
<td>8.2 ± 12.8</td>
<td>1.8 ± 1.9</td>
<td>1.3 ± 2.0</td>
<td>1.5 ± 2.4</td>
</tr>
<tr>
<td>Ilex glabra</td>
<td>evergreen shrub</td>
<td>6.0 ± 19.0</td>
<td>6.0 ± 19.0</td>
<td>6.0 ± 19.0</td>
<td>2.6 ± 7.9</td>
</tr>
<tr>
<td>Morella cerifera</td>
<td>evergreen shrub</td>
<td>4.9 ± 12.4</td>
<td>7.5 ± 9.4</td>
<td>11.9 ± 18.5</td>
<td>5.8 ± 8.0</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>deciduous tree</td>
<td>6.0 ± 19.0</td>
<td>5.0 ± 15.8</td>
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<td>2.0 ± 6.3</td>
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<td>Panicum anceps</td>
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<td>4.5 ± 9.3</td>
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<td>3.8 ± 6.1</td>
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<td>3.7 ± 6.6</td>
<td>14.4 ± 19.0</td>
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<td>1.5 ± 4.7</td>
<td>7.2 ± 16.3</td>
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