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Notes and Discussion Piece

Wiregrass (Aristida beyrichiana) May Limit Woody Plant Encroachment in Longleaf Pine (Pinus palustris) Ecosystems

Abstract.—Wiregrass (*Aristida beyrichiana*) is a dominant groundcover species that facilitates fire in southeastern U.S.A. pine savannas, thereby limiting woody plant cover and maintaining a herbaceous dominated understory. In December 1993 two of us planted a plot of wiregrass (*Aristida beyrichiana*) in the midst of fire-maintained little bluestem (*Schizachyrium scoparium)* longleaf pine (*Pinus palustris*) savanna in the outer Coastal Plain of South Carolina. The plot and the surrounding area burned three times in the following 20 y. Vegetation sampling carried out in late summer 2013 indicated wiregrass dominated the plot and the majority of little bluestem had disappeared. The wiregrass plot was comparatively open and grass dominated, whereas the surrounding formerly bluestem dominated stand had filled in with loblolly pine (*Pinus taeda*) saplings as well as hardwood trees and shrubs. In addition wiregrass had reproduced and established away from the original planted area, most noticeably within a soil-disturbed plow line. A subsequent prescribed fire in spring 2014 burned with higher intensity within the wiregrass plot than in the surrounding area. Our observations suggest suppression of woody plant encroachment by dense wiregrass in pine savannas even during long fire free periods, which should reduce the likelihood of transition to hardwood dominated ecosystems.

Introduction

Fire-maintained longleaf pine (*Pinus palustris*) ecosystems were once widespread throughout the southeastern United States, extending from southeastern Virginia to eastern Texas and from northeast Alabama and northwest Georgia to the Florida peninsula (Noss *et al.*, 2014), an area of ca. 90 million acres (Landers *et al.*, 1995). Longleaf pine was the prevalent canopy tree on ca. 74 million acres (Frost, 1993) but mature hardwoods (*e.g.*, *Quercus* and *Carya spp.*) were part of the canopy mosaic on some sites (Harcombe *et al.*, 1993; Hiers *et al.*, 2014). Dominant matrix grasses in these open pinelands included various species of *Andropogon*, *Aristida*, *Sporobolus*, *Muhlenbergia*, *Schizachyrium*, *Ctenium*, and *Panicum* (Peet, 2006). An abundance of fine fuels (grasses, pine needles, hardwood litter) in the herbaceous ground cover sustained a frequent fire regime that maintained low understory and midstory tree densities and a diverse herbaceous ground cover in these systems (Glitzenstein *et al.*, 2003; Van Lear *et al.*, 2005; Slocum *et al.*, 2010; Stambaugh *et al.*, 2011). In the absence of fire, pine savannas, and woodlands can shift to closed canopy forest (Lemon, 1949; Beckage *et al.*, 2009, 2011). Widespread logging, agricultural conversion, and fire exclusion have severely reduced the distribution of minimally disturbed longleaf pine savannas and woodlands (Frost, 1993; Van Lear *et al.*, 2005; Noss *et al.*, 2014).

Pyrogenic grasses are important ground cover fuels in longleaf ecosystems. Flammable grasses promote fires that depress woody plant encroachment, stimulate nitrogen-fixing legumes, and encourage an herbaceous understory (Platt, 1999; Beckage *et al.*, 2011). Wiregrass (*Aristida stricta*, *A. beyrichiana*)[1] is a prevalent ground cover species across a large portion of longleaf pine's range (Noss, 1989; Landers *et al.*, 1995) and an important driver of the high frequency fire regime (1–3 y; Frost, 1993; Huffman, 2006; Stambaugh *et al.*, 2011) that helps maintain open pine savannas and woodlands. Long term studies of this species and its role in ecosystem dynamics are lacking. In this study we present a comparison of vegetation composition and wiregrass reproduction resulting from an unintended experiment of planted wiregrass plots and surrounding vegetation 20 y post-planting.

Note added after acceptance: Dr. L. K. Kirkman of Jones Ecological Research Center informed us of an ongoing experiment at the Jones Center examining the role of wiregrass in controlling invasion by woody plants. Thus there are now two independent observations of this outcome.

[1] Two species are recognized by some authors (Peet, 1993; Weakley, 2015): *A. stricta* in North Carolina and northern South Carolina, and *A. beyrichiana* south of the "wiregrass gap" in central South Carolina (Peet, 1993). Other authors have found support for a single taxon, *A. stricta* (Kesler *et al.*, 2003).

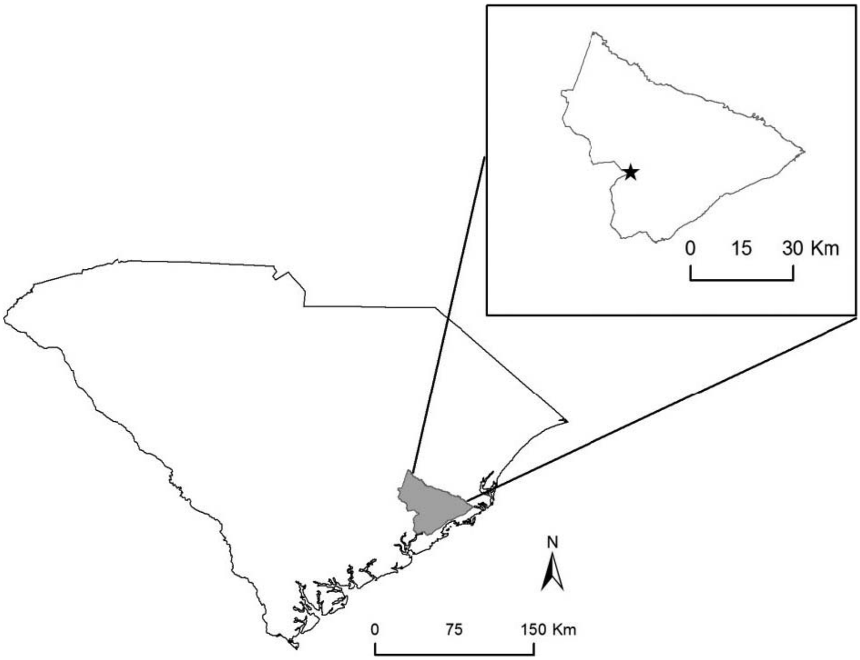

FIG. 1.—Location of Francis Marion National Forest (FMNF) in central coastal South Carolina. Inset: Location of FMNF Seed Orchard within FMNF

METHODS

Site description.—In December 1993 JSG and DRS planted three 3 m × 15 m plots of southern wiregrass into the northwest corner of Francis Marion National Forest Seed Orchard (33°07′32″N, 79°47′02″W; Fig. 1 inset). Francis Marion National Forest (FMNF), in Berkeley and Charleston counties, South Carolina (Fig. 1), is located within the range of longleaf pine (Platt, 1999; Peet, 2006) in a section presently characterized by low density of wiregrass sometimes referred to as the wiregrass gap (Peet, 1993) The planting site, a natural fire-maintained longleaf pine stand, had been prescription-burned the previous February and had a history of regular fire at that time. At the time of planting, groundcover was dominated by little bluestem with characteristic forbs of mesic/moist longleaf pinelands of central South Carolina Outer Coastal Plain (Peet, 2006). Soils are Ultisols of the Lenoir and Duplin series (USDA Web Soil Survey data; <websoilsurvey.nrcs.usda.gov>). Plots were placed side by side oriented roughly N-S but separated by approximately 3 m (*see* red boxes in Fig. 2). Plugs (*i.e.,* container-grown tubelings) were planted with hand trowels on approximately 30 cm spacing (*i.e.,* approximately 10 plugs per m^2). Seed for the plugs was obtained from the Webb Wildlife Center in Hampton County, owned and managed by the South Carolina Department of Natural Resources. Seeds were collected from mesic sites with Goldsboro soils. Plugs were approximately 10 cm × 3 cm, grown at Santee Experiment Station in FMNF in standard plug trays for pine seedling production. Plug age was approximately 10 mo at the time of planting. By 2013 the wiregrass plot had remained fairly open with a relatively dense wiregrass groundcover, while the surrounding area had transitioned to closed mixed pine-hardwood canopy.

The site was burned infrequently (four times) after the wiregrass planting: a prescribed fire in late winter 1997; an escaped prescribed fire in February 2000, during which a control line was plowed through the eastern edge of the wiregrass planting; a prescribed burn in April 2010; and following the majority of our sampling for this study, a second prescribed fire in April 2014. We observed the wiregrass flowering in October 2014.

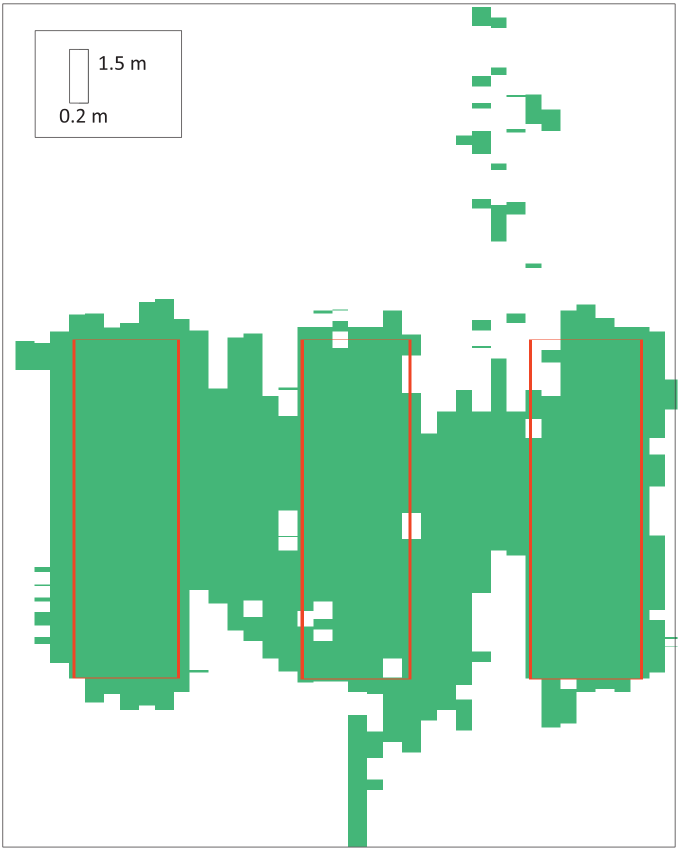

FIG. 2.—Map of wiregrass (*Aristida beyrichiana*) cover in the wiregrass plot, oriented N-S. This figure shows the extent of wiregrass spread outside the original planted area. The length of the image represents 80 ft (24.4 m), and the width represents 64 ft (19.5 m). Boxes (shown as red for online version) indicate the original 10 × 3 m plantings, which are 3 m apart

DATA COLLECTION

Plot delineation.—To compare vegetation in the planted site with adjacent unplanted sites, three 10 × 15 m plots were established in late summer 2013. The wiregrass plot (WG) was in the center of the tract and encompassed the three original 10 × 3 m wiregrass plantings. To avoid a north-south gradient of increasing soil moisture, the other two plots were established to the west and the east of the WG plot with a 5 m buffer between plots. The west plot (P) was characterized by a relatively high density of young loblolly pine (*Pinus taeda*), while the unplanted plot to the east (U) was characterized by a high density of shrubs, primarily gallberry holly (*Ilex glabra*). A north-south fireline had been plowed between the center and eastern original wiregrass plantings within the WG plot to control an escaped fire in 2000.

Data on canopy closure and herbaceous and woody cover were collected in August 2013. Wiregrass was mapped and woody stems were counted and measured in February 2014. We estimated scorch height on trees in November 2014 (after the prescribed fire in spring 2014). Taxonomy follows Weakley (2015).

Canopy closure.—A spherical densiometer with 24 cells was used to measure percent canopy closure. Standing in the center of a plot, we took 24 readings in each of the four cardinal directions. The readings for each direction were averaged, and then the four directional means were averaged to obtain an estimate for the plot as a whole.

Cover class.—Within each of the three plots (WG, U, P) a cover class for each vascular plant species was estimated using intervals as defined in Carolina Vegetation Survey (Peet *et al.*, 1998: 0–0.25 = 1; 0.25–1% = 2; 1–2% = 3; 2–5% = 4; 5–10% = 5; 10–25% = 6; 25–50% = 7; 50–75% = 8; 75–95% = 9; 95–100% = 10). Cover class assignment was based on vertical downward projection, disregarding overlapping foliage. Species not rooted in the plot were included. Each woody species received a score for overall cover as well as for cover in each of four strata: (1) herbaceous layer (<0.5 m), (2) shrub layer (0.5 m to <2 m), (3) midstory layer (2 m to <10 m), and (4) overstory layer (>10 m). We also calculated an index consisting of the sum of the individual species covers (henceforth referred to as "sum of cover") separately for herbaceous and woody cover in each plot. Herbaceous plants were restricted to the herb layer: Therefore, there was only a single herb cover index for each plot. Cover scores were back-transformed to the class interval mean before summing. The sum of cover is greater than overall cover because the latter does not take into account species with overlapping cover (for example, if species A has 37.5% cover and species B has 17.5% cover, and A completely overlaps B, sum of cover would be 37.5 + 17.5 = 55 whereas total cover would be 37.5). Herbaceous and woody species richness were defined in the standard manner as the number of herbaceous and woody species in each plot.

Woody stem data.—Woody plant stems were counted per species, and the diameter of each stem was measured at breast height (1.37 m). If a plant had multiple stems the largest stem was measured.

Scorch height.—The height of maximum crown scorch following the 2014 fire was measured using a clinometer and trigonometry (www.tiem.utk.edu/~gross/bioed/bealsmodules/triangle.html; Waring and Schlesinger, 1985). We calculated the vertical distance from eye level to height of scorch and then added the height of the observer.

Wiregrass mapping.—Wiregrass was mapped onto a grid of transect lines. We established a baseline across the southern end of the WG plot extending 2 m beyond the plot corners in each direction to encompass the furthest extent of wiregrass. We then established S-N perpendicular transects to either side of the baseline with the length of each transect determined by the furthest distance of wiregrass. Sections of each S-N transect intersected by wiregrass were then recorded. ArcGIS 10.1 (ESRI 2011, Redlands, California) was used to create a digital representation of the grid and each cell in the digital grid was populated based on the presence/absence of wiregrass.

RESULTS

Measures related to woody cover were lowest in the wiregrass plot. Canopy cover (mean ± SD: WG, 54 ± 0.17; P, 84 ± 0.04; U, 78 ± 0.11), sum of overall woody cover, and woody stem counts were much lower in the wiregrass plot than in the other two plots (Tables 1 and 2). The wiregrass plot was also essentially lacking in midstory. However, the surrounding area was characterized by dense midstory (Table 1) dominated by *P. taeda* and *Liquidambar styraciflua*, two tree species that readily invade savannas during periods of reduced fire (Glitzenstein *et al.*, 2003, 2012; Clewell, 2014).

Sum of herbaceous cover was highest in the wiregrass plot, although species richness values were similar among plots (Table 3). The large majority (21/34 = 61.8%) of herbs in the wiregrass plot were present at trace levels, suggesting competitive suppression by wiregrass. *Schizachyrium scoparium*, the original dominant grass in the pre-1993 fire maintained savanna (Glitzenstein and Streng, pers. obs.), had disappeared from P and U and occurred at only trace levels in the wiregrass plot.

The map of wiregrass showed wiregrass not only dominated the original planted area but had also spread away from the original plantings (Fig. 2). In addition to filling in space between plantings, wiregrass also established in disturbed soil associated with the 2000 fire suppression line (Fig. 3). Wiregrass plants in this plow line occurred up to 10 m distant from the original plantings. Although it is possible that some of these plants may have been uprooted and moved by the plow itself, wiregrass flowered abundantly in the fall/winter after the fire and newly germinated seedlings were abundant in the line the following growing season (Glitzenstein, pers. obs.).

After the majority of our data were collected, the wiregrass plot and surroundings were burned in a prescribed fire during Apr. 2014. Maximum height of scorch after this fire was 12.7 m in WG, 6.4 m in P, and 5.6 m in U.

TABLE 1.—Percent cover for dominant woody species in each of the three plots: WG (wiregrass; *Aristida beyrichiana*) and plots to the east (U) and west (P). Percentages were obtained by back-transforming to the cover class midpoint. Overall cover is listed along with cover for herbaceous, shrub, midstory and canopy strata. A cover index derived from the sum of the individual species covers is the final entry for each plot

Plot	Species	Overall	Herb	Shrub	Midstory	Overstory
U	*Pinus taeda*	62.5	0	0	62.5	3.5
	Liquidambar styraciflua	62.5	3.5	7.5	37.5	0
	Quercus stellata	17.5	0	0	17.5	0
	Quercus nigra	17.5	0	3.5	17.5	0
	Ilex glabra	17.5	3.5	17.5	3.5	0
	Other	14.6	13.1	1.5	0	0
	Sum of Covers	192.1	20.1	30	138.5	3.5
P	*Pinus taeda*	85	0.1	0	85	0
	Liquidambar styraciflua	62.5	7.5	37.5	7.5	0
	Quercus stellata	17.5	0	0	17.5	0
	Arundinaria tecta	17.5	3.5	17.5	0	0
	Other	32	6.5	17.5	3.5	7.5
	Sum of covers	214.5	17.6	72.5	113.5	7.5
WG	*Pinus palustris*	37.5	0	0	0	37.5
	Liquidambar styraciflua	37.5	7.5	37.5	0.5	0
	Quercus marilandica	17.5	0.5	0	3.5	17.5
	Quercus nigra	17.5	3.5	17.5	0	0
	Other	5.6	3	3	0	0
	Sum of covers	152.1	22.5	77.5	15.1	55

DISCUSSION

When the wiregrass plot (WG) was planted in 1993, the plot and vicinity were in open fire-maintained savanna (Glitzenstein and Streng, pers. obs.). Although the surrounding area, including adjacent plots P and U, transitioned to closed forest, the wiregrass plot itself remained more open and herbaceous. The

TABLE 2.—Numbers of woody stems and average diameter-at-breast-height (in parentheses, cm) in the planted plot of wiregrass (*Aristida beyrichiana*, WG) and plots to the east (U) and the west (P) in the central South Carolina Coastal Plain

Species	U	P	WG
Ilex glabra	108 (0.4)		
Liquidambar styraciflua	59 (1.4)	90 (1.0)	18 (1.2)
Morellaa cerifera	5 (1.7)		
Pinus echinata	2 (16.6)		
Pinus palustris	2 (29.3)		
Pinus taeda	16 (12.4)	63 (8.4)	2 (7.2)
Quercus marilandica	1 (9.2)	2 (13.2)	
Quercus nigra	6 (3.6)	2 (3.3)	9 (1.0)
Quercus stellata	5 (8.4)	11 (6.1)	1 (7.2)
Quercus velutina/pagoda	8 (1.2)		
Rhus copallinum	2 (0.7)	3 (0.8)	
Vaccinium fuscatum	2 (0.4)	1 (0.2)	
Total	206	175	37

TABLE 3.—Percent cover for dominant herbaceous species in each of the three plots: WG (wiregrass; *Aristida beyrichiana*) and plots to the east (U) and west (P). Percentages were obtained by back-transforming to the cover class midpoint. A cover index derived from the sum of the individual species covers is the final entry for each plot. Data for WG excluding wiregrass are in parentheses

Species	U	WG	P
Aristida beyrichiana	0	85	0
Pteridium aquilinum	37.5	37.5	0
Coleataenia anceps ssp. rhizomata	7.5	1.5	7.5
Tephrosia hispidula	0.5	3.5	0.5
Baptisia tinctoria	3.5	0.1	0.1
Other	10.7	6.5	3.6
Sum of covers	59.7	134.1 (49.1)	11.7
Herbaceous richness	29	34 (33)	31

wiregrass plot did have appreciable woody cover in the herbaceous and shrub layers, indicating that woody plants had begun to establish but perhaps more recently than in the adjacent plots without wiregrass. In addition to the influence of wiregrass on fire behavior (Fill *et al.*, 2016), our results suggest another potential keystone property of wiregrass, that of low invasibility especially during fire-free

FIG. 3.—Wiregrass (*Aristida beyrichiana*) seedlings in the plowline

periods. Davis *et al.* (2005) defined invasibility as the tendency to resist establishment by propagules of other species. For example Hill *et al.* (1995) studied invasibility in rights-of-way in New York, U.S.A. Their studies showed certain shrub and herbaceous species and communities were much less invasible by tree seedlings. Hill *et al.* (1995) found among the most resistant of the herbaceous cover types was one dominated by little bluestem, which in mid-Atlantic and southern New England, U.S.A., is a dominant matrix grass of fire-maintained oak-hickory woodlands.

Wiregrass appears to be even more resistant to invasion than little bluestem. Wiregrass has a cespitose growth form with arching foliage that densely covers the ground within several years after fire. In contrast most bluestem grasses (*Schizachyrium* and *Andropogon* spp) tend to be columnar, potentially leaving more open space for woody seedlings to establish. Because wiregrass is more resistant to woody plant encroachment this predominant herbaceous fuel is more likely to persist even during longer intervals between fires. Therefore fires when they do occur will burn with higher intensity, further decreasing woody plants.

Despite the regime of infrequent fire, the planted wiregrass not only survived and grew into large clumps but also reproduced. There have been few observations of natural wiregrass seedling recruitment in field populations and it has been suggested that this accounts in part for the inability of wiregrass to recover after episodes of anthropogenic soil disturbance (Clewell, 1989). The likely explanation is that wiregrass tends not to flower or fruit except after growing season fires and most fires are conducted in the dormant season (Robbins and Myers, 1992; Streng *et al.*, 1993; Fill *et al.*, 2012). Our observations can be added to those of van Eerden (1997) and Mulligan *et al.* (2002) indicating wiregrass seedlings do become established after growing season fires. Furthermore, we showed wiregrass can recruit into disturbed soils if viable seed are produced. However, after the Apr. 2014 prescribed fire, flowering culm, and seed production were limited and of 100 seeds collected none germinated in the lab (Glitzenstein, pers. obs.). Although other less plausible explanations can be suggested, it seems likely that low culm and seed production as well as low seed viability reflected highly stressed plants due to encroaching shrub and canopy competition. Clewell (1989) observed wiregrass can tolerate 2–4 decades of fire exclusion depending on site conditions and our results would appear to fall within that range.

We acknowledge our unintended experiment represents only a very preliminary exploration of wiregrass invasibility and limitation of woody cover. We did not plant the wiregrass plot intending to investigate invasibility, the "treatment" was neither randomized nor replicated, and some confounding factors may have been responsible. The study was carried out in the wiregrass gap region of central South Carolina (Fig. 1; Peet, 1993); therefore, it might be argued our results are not relevant to areas dominated by wiregrass. However, several naturally occurring patches of wiregrass exist in Francis Marion NF, the closest approximately 5.5 km distant from the planting area (Glitzenstein, pers. obs.). Superficial soil disturbance treatments associated with forestry as well as a history of agriculture are well known to reduce or eliminate wiregrass (Swindel, 1982). Wiregrass may have been more abundant historically in FMNF and vicinity.

Despite these caveats, we believe our observations are still noteworthy in suggesting a possible hitherto undetected mechanism for persistence of grass dominated pine savannas. Differences between the wiregrass plot and the adjacent plots were rather striking with no obvious explanation other than the history of planting wiregrass. Future experiments could focus more precisely on postulated differences in invasibility among grass species and attempt to elucidate possible mechanisms. This could include experiments focusing on the relationship between planting density and invasibility and interactions with fire.

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