RESEARCH ARTICLE

•

Shrub Seedling Establishment is Limited by Dispersal, Slow Growth, and Fire in Two Wet Pine Savannahs in Mississippi

Sarah E. Hinman[1]
J. Stephen Brewer
Steven W. Ashley
Department of Biology
University of Mississippi
University, Mississippi 38677-1848

•

Natural Areas Journal 28:37–43

ABSTRACT: Identifying the mechanisms that drive invasions of open habitats by woody species is critical for preserving diverse savannas. Trees can promote the establishment of bird-dispersed woody plant species in savannas by reducing dispersal limitation. Previous work in wet pine savannas has shown that densities of bird-dispersed shrubs are higher and species richness of herbaceous species, most of which are not bird-dispersed, is lower in areas near trees. To test the hypothesis that shrub seedling density in wet pine savannas was limited by dispersal and thus the availability of perches for seed-dispersing birds, seed traps and artificial perches were placed near and away from pines. To measure fire-induced mortality of trees and shrubs, *Pinus elliottii* juveniles and shrub seedlings that had emerged during a fire-free interval were quantified before and after fires. Trees provided perches for birds that dispersed shrubs, thereby reducing dispersal limitation of shrubs. Significantly more seeds of the shrubs, *Ilex glabra* and *I. vomitoria*, were encountered in seed traps at the bases of *P. elliottii* than in areas away from trees in two consecutive years. Seedlings of woody species with fleshy fruits occurred more frequently at the bases of artificial perches than away from perches, and the effect of the perches on seedling density was greater away from trees. Eight- and nine-year periods without fire were not long enough for the majority (>99%) of post-fire recruits of *P. elliottii* to grow large enough to survive growing-season fires. A small but greater fraction of shrub seedlings (10%) survived the fires. We argue that periodic fires are sufficient to preclude further invasion of wet pine savannas by *P. elliottii*, expansion of shrub thickets, and associated declines in plant diversity.

Index terms: dispersal limitation, fire interval, *Ilex glabra*, pine savanna, *Pinus elliottii*

INTRODUCTION

The longleaf pine ecosystem currently covers less than 1.2 million ha of the 37 million ha it historically occupied (Frost 1993; Landers et al. 1995). To restore and maintain the remaining areas, fires must occur at frequencies that will preserve species diversity and composition in the long term. One of the major threats to plant diversity in longleaf pine savannas is an increase in the abundance of woody species (Brockway and Lewis 1997; Glitzenstein et al. 2003). Although fire clearly plays an important role in limiting the size and density of woody species in longleaf pine savannas, dispersal limitation of seedling recruitment may also affect densities of woody plants. Because most woody plants of pine savannas (other than pines) tend to be animal dispersed, understanding how animal dispersal patterns interact with other factors known to have important effects on woody plant populations (i.e., fire, soil conditions) is crucial to elucidating controls on plant diversity in longleaf pine savannas.

Seed dispersal of woody species by birds can accelerate the rate of succession from open areas to woods (McAtee 1947; Werner and Harbeck 1982; McClanahan and Wolfe 1987; McClanahan and Wolfe 1993; Nepstad et al. 1996; Thornton et al. 1996; Brown and Archer 1999). Because birds are attracted to tall structures, trees often serve as perches and aid seed dispersal. Where forest recovery is the desired management goal, both artificial and natural perches have been erected in abandoned fields and pastures to increase seed deposition and expedite colonization by woody species (Debussche et al. 1982; Werner and Harbeck 1982; McDonnell and Stiles 1983; Guevara et al. 1986; McDonnell 1986; McClanahan and Wolfe 1987; Kollmann 1995). Where preservation of savannas is the desired management goal, the reduction of potential perches via the reduction of tree densities may help to reduce seed deposition and the rate of colonization of woody species.

Increases in tree density in savanna or grassland communities have previously been shown to facilitate establishment of additional woody plants (Debussche and Isenmann 1994; Joy and Young 2002). Such increases in the establishment of woody species can lead to losses or reduced cover of herbaceous plants in some systems (Archer 1990; Fowler and Batchelor 2005). Considering that large trees often increase seed rain of avian dispersed plants (Debussche et al. 1982; McDonnell and Stiles 1983; Schupp et al. 1989) and can change the local physical environment, trees have the potential to enhance dispersal of bird-dispersed shrubs and create a microhabitat that favors shrubs over herbaceous plants

---

[1] Corresponding author: hinmansarah@gmail.com

(Brewer 1998, 2002). A previous study showed increased species richness of woody species and lower herbaceous richness near (< 2 m) *Pinus elliotii* Engelm. trees in a wet pine savanna, resulting in a net decrease in species richness near trees (Brewer 1998). Seedling growth of one of the most common shrub species in this wet pine savanna, *Ilex glabra* (L.) Gray, was not greater near than away from trees, however. Together, these findings suggested that the main effect of trees on shrub establishment in wet pine savannas was to reduce dispersal limitation.

Before extensive logging and fire suppression in southern Mississippi, wet savannas were dominated by low-density stands of longleaf pine (*Pinus palustris* P. Mill.; Hilgard 1860); therefore, available perches for birds were limited. Slash pine (*Pinus elliottii*) occurred in the surrounding habitat, but was restricted by fire to wetter areas (Hilgard 1860; Harper 1914) because its seedlings and saplings were not as tolerant of fire as those of *P. palustris* (Monk 1968; Landers 1991). However, *P. elliottii* produces a large seed crop and has rapidly colonized logged and fire-protected areas formerly dominated by *P. palustris* (Harper 1914; Hebb and Clewell 1976; Landers 1991; Platt 1999). In addition, aside from the effects of fire suppression, many wet pine savannas have been converted to high-density pine plantations and are now targets for restoration (Brewer 2002). Therefore, if communities with high densities of natural or planted recruits of *P. elliottii* are protected from fire long enough to allow these recruits to grow large enough to survive the next fire (3-4.5 m tall or 10-12 yr. age; Chapman 1932; Garren 1943), they could provide persistent perches and promote the dispersal of shrubs into wet pine savannas. Once these shrub recruits grow large enough, they are extremely resistant to mortality by fire (Olson and Platt 1995; Drewa et al. 2002). In theory, increased densities of pines may indirectly increase shrub densities, but this hypothesis remains untested.

In this study, we tested two hypotheses: (1) a single period of eight/nine years without fire is not sufficient to increase *P. elliotii* density or shrub seedling density, and (2) slash pine densities can indirectly increase shrub recruitment by providing perches for avian dispersers of shrub seeds. The specific objectives of this research were to: (1) count seedlings of *P. elliottii* before and after a fire in 2004 after eight/nine years without fire, (2) determine if seed deposition of bird-dispersed shrubs was greater near trees, and (3) determine if artificial perches were more effective at increasing seedling densities of bird-dispersed shrubs in areas away from trees.

METHODS

Description of Bird Dispersed Shrub Species

Ilex glabra is an evergreen, rhizomatous shrub found in pine flatwoods and savannas throughout the southeastern United States and northward along the Atlantic coast into southeastern Canada. It flowers from May until June and produces a drupe from September to November. Dispersal via birds generally occurs from early winter to early summer, and is quickly followed by seedling emergence. While adult plants are quite tolerant of fire and will sprout back from rhizomes, they typically do not flower the first year following a fire (Brewer 2002). *Ilex vomitoria* Ait. is also a drupe-producing shrub that is commonly found in the mid and understory of pine savannas and forests. This evergreen ranges from Texas east to Virginia. *Ilex vomitoria* flowers in the spring (March to May), and produces fruit in late fall (October to November) that often persists through the winter. This species is tolerant of low intensity fires, but is normally top-killed (Halls 1977). Historic accounts of mesic and wet longleaf pine savannas in southern Mississippi suggest that *I. vomitoria* was not common in either mesic or wet pine savannas, presumably due to frequent fires (Hilgard 1860; Harper 1914).

Additional bird-dispersed species that were of interest included *Gaylussacia mosieri* Small, a berry producing, long-lived shrub, *Myrica cerifera* (L.) Small, a drupe-producing shrub common in pinelands, two berry-producing *Smilax* spp. (L.), and *Magnolia virginiana* (L.), a tree that is found in swamps and low areas and has an aggregate follicle. Nomenclature and authorities follow Radford et al. (1968).

Study Site

This study was conduced at two sites in Desoto National Forest in Stone County, Mississippi. The two sites (hereafter Sandy Creek and Wolf Branch), chosen by J.S. Brewer in 1996, occur within relatively open wet pine savannas. Poor drainage, low pH, and frequent fire result in a *Sarracenia* and grass-sedge dominated community (Brewer 1998). Historically, such wet pine savannas and surrounding flatwoods were described as park-like due to their open canopy, which was dominated by *P. palustris* (Hilgard 1860). *Pinus elliottii* invaded following logging and fire suppression in the 1900s (Harper 1914) and presently dominates the overstory, along with *P. palustris* at Wolf Branch and Sandy Creek (Brewer 1998). From the early 1980s to 1996, the two sites experienced a fire on average every three years, but were protected from fire between 1996 and 2004 (A. Albritton, forester, University of Mississippi, pers. comm.). Wolf Branch was burned in January of 1996, and Sandy Creek was burned in November of 1996; therefore, before both were burned in May 2004, they remained unburned for nine and eight years, respectively. Since the early 1980s, the staff of Desoto National Forest has burned most pine savannas in the vicinity of our sites on a three- to four-year rotation, usually between March and May (K. Coursey, park ranger, Desoto National Forest, pers. comm.). The prescribed burns conducted by the Desoto National Forest staff in 2004 occurred on 21 May 2004 (May is a peak month for lightning fires; Robbins and Myers 1992). Prescribed burning in May is being used more frequently by Desoto National Forest to control shrubs and stimulate flowering of herbaceous species (K. Coursey, pers. comm.). The fires on 21 May were within the U.S. Forest Service (USFS) prescription window. Relative humidity ranged from 48 to 62%, ambient temperature varied between 27° and 30°C, and flame lengths were between 0.9 and 1.1 m. The burns were complete, leaving no obvious unburned patches (K.

Coursey, pers. comm.).

Experimental Design

Seed deposition in traps near and away from trees

To determine if there was increased seed deposition below pine trees in wet pine savannas, seed rain (via fecal deposit or bird regurgitant) was measured for two years for two common shrub species, *I. glabra* and *I. vomitoria*. Beginning in 1998, 20 trees (dbh > 9 cm) were marked at each of the sites. Each tree had a pair of seed traps placed directly below (10 cm from trunk) and a pair placed more than 5 m away (and from other trees). Seed traps were circular, 0.75 m in diameter, and were constructed out of very fine mesh with a wire frame. Traps were placed > 10 cm above the ground to avoid seed predation, and vegetation below them was clipped. Seeds were counted and removed five times from January to April 1998 and four times from February to April 1999. Sampling dates occurred in the winter and early spring due to observed preference by birds for other food sources during the fall. Birds alter their eating habits from a water and sugar rich diet to one high in lipids (like the fruits of *I. glabra* and *I. vomitoria*) with the onset of winter (Short and Epps 1976; Herrera 1982).

After seeds of the two species were quantified, each pair of traps was pooled, and then these values were pooled across censuses for each year to obtain a cumulative sum of seeds captured in each pair of traps for the year. The effect of distance from the tree (i.e., near versus away) was analyzed for each species and for both sites in 1999 by examining differences in seed counts near versus away from trees using split-plot analysis of variance (ANOVA). Site was the main factor and distance from the tree was the split-plot factor. Values for both species were ln-transformed to reduce heteroscedacity. The prescribed fire in late 1996 at Sandy Creek prevented flower and fruit production at this site in 1997. There was, therefore, very little seed deposition at Sandy Creek in the winter of 1998, and as a result, chi-square tests of non-independent, paired samples (Steele and Torrie 1980) were used to analyze presence or absence of seeds in traps. A chi-square test of non-independent, paired samples was also used to analyze differences in seed deposition between 1998 and 1999 at Sandy Creek. A paired t-test was used to examine differences in seed number near and away from trees at Wolf Branch in 1998.

Effects of artificial perches on seedling densities near and away from trees

Artificial perch posts were used to determine if recruitment by shrubs was dispersal limited and if the magnitude of this limitation differed near and away from trees. The use of artificial perches reduces possible microhabitat conditions provided by trees that may aid seedling survival (e.g., raised elevation and soil moisture; Brewer 1998). We assumed that seedling densities near and away from perches at each of these microsites largely reflected differences in dispersal limitation and not microsite differences. We observed no obvious apparatus effects (e.g., increased sedimentation, predator attraction, etc.) associated with the perch posts. Furthermore, a small pilot study comparing emergent (1.5 m) and short (< 30 cm tall) posts revealed that short posts did not increase seedling emergence.

In 1999, 0.25-m^2 subplots were established to count seedling densities near and away from perches at 16 locations within each of two microhabitats (open areas away from trees, thickets near trees) at each of the two sites. Hence, at each site, each subplot belonged to one of the categories: (1) near perch posts, away from trees; (2) near perch posts, near trees; (3) away from perch posts, near trees; and (4) away from perch posts, away from trees. Perch posts consisted of PVC pipe and stood 1.5 m above the ground. The height of 1.5 m followed McDonnell's (1986) recommendation that as long as perches projected above the current vegetation matrix, they would be attractive to birds. The 16 pairs of subplots located in open areas were placed more than 5 m from the nearest tree. One subplot in each of these pairs was located more than 1 m from the associated perch post, whereas the other in each open-area pair was placed directly adjacent to the perch post. Subplots located near trees were placed directly at the tree's base. Subplots located near trees and perch posts were also located next to a perch post, and the other subplot in each pair was placed on the opposite side of the tree, away from the perch post. Seedlings (i.e., juveniles not derived from existing rhizomes) were identified and counted in each subplot in July 2001, December 2003, and after the prescribed fire in July 2004. Seedlings were easily distinguished from juveniles derived from rhizomes by virtue of their shape and size. All individuals identified as seedlings either contained cotyledons at the time of the census or had basal stem diameters of less than 2 mm and primary leaf lengths of less 5 mm (which were less than 1/3 of what we typically observed in newly emerged ramets from rhizomes). Data from 2001 and 2003 were log-transformed and analyzed separately using a split-plot ANOVA. Here, site and distance from tree were main factors and distance from the perch post was the split-plot factor. Because seedling mortality was high in 2004, the data were not normal and were not analyzed.

Mortality of Slash Pine Recruits

To determine if a period of eight or nine years was long enough for post-1996 recruits of *P. elliottii* to grow large enough to survive the 2004 fire, the number and height of surviving saplings was counted before and after the fire in 2004. Saplings were quantified within one large rectangular plot and within 16 subplots (0.25 m x 0.25 m) at each site. Subplots were also sampled in 1997. The areas of the large plots were 475 m^2 and 300 m^2 at Wolf Branch and Sandy Creek, respectively.

RESULTS

Seed Deposition Near and Away From Trees

In 1998, Wolf Branch seed deposition was significantly greater near trees than away from trees, for both *I. glabra* ($t_{19} = 16.81$, $p < 0.001$) and *I. vomitoria* ($t_{19} = 12.65$, $p < 0.001$, Figure 1). At Sandy Creek, the probability of seeds only being deposited below a tree was significantly greater than only being deposited away from a tree for both *I. glabra* ($\chi^2_1 = 6$, $p = 0.014$) and *I. vomitoria* ($\chi^2_1 = 8$, $p = 0.005$, Figure 1). In 1999, *I. glabra* seed deposition differed significantly between near and away from trees ($F_{1,38} = 104.94$, $p < 0.001$), as well as between sites ($F_{1,38} = 35.01$, $p < 0.001$, Figure 1). However, the interaction between distance from tree and site was not significant ($p = 0.089$). As for *I. vomitoria*, overall seed deposition was lower than for *I. glabra*, but still differed significantly ($F_{1,38} = 64.06$, $p < 0.001$, Figure 1) with distance from tree. Again, the interaction between site and distance from tree was not significant ($p = 0.585$), nor was the difference between sites ($p = 0.472$). The probability of more seeds being deposited both near and away from trees was significantly greater in 1999 than it was in 1998 (*I. glabra*, $\chi^2_1 = 400$, $p < 0.001$; *I. vomitoria*, $\chi^2_1 = 400$, $p < 0.001$) at Sandy Creek.

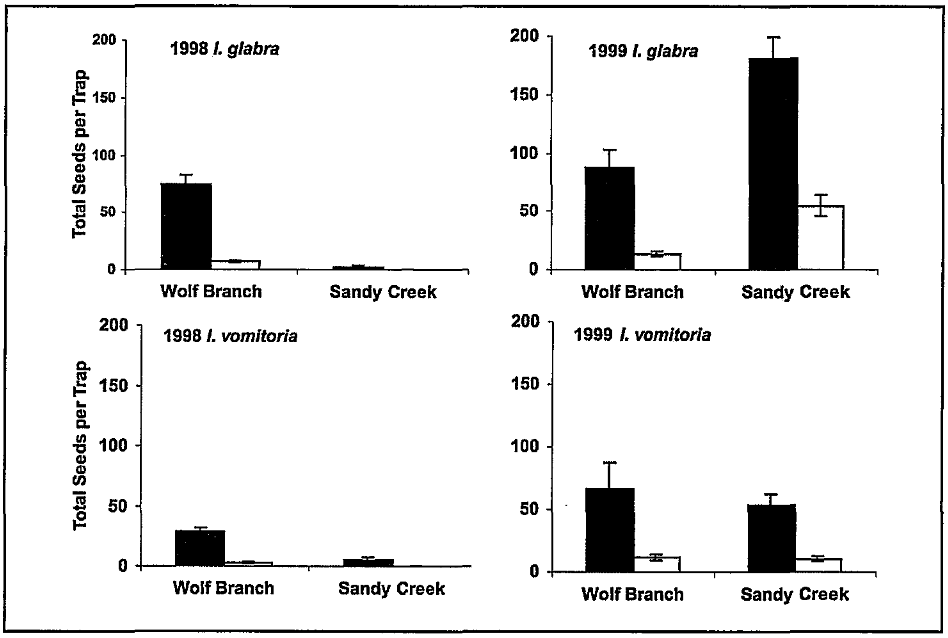

Figure 1. Mean seed counts in 1998 and 1999 for Ilex glabra and I. vomitoria for traps near pine trees (filled bars) and away from pine trees (open bars) at Wolf Branch (burned in January 1996) and Sandy Creek (burned in November 1996). Error bars are ± 1 standard error.

The Effects of Perch Posts on Seedling Density Near and Away From Trees

Perch posts increased seedling densities of several shrub species, including *Ilex glabra*, *I. vomitoria*, *Gaylussacia mosieri*, *Myrica cerifera*, *Magnolia virginiana*, and two *Smilax* spp. in open areas away from trees. In 2001, the number of seedlings near a perch post was significantly greater than the number away from a perch post ($F_{1,60} = 136.76$, $p < 0.001$, Figure 2). The effect of the perch posts on seedling density was greater, however, in areas from trees than near trees, resulting in a highly significant interaction between distance from tree and distance from perch post ($F_{1,60} = 126.33$, $p < 0.001$). This interaction was equally strong at both field sites, as indicated by the lack of a three-way interaction among site, distance from tree, and distance from perch post ($p = 0.882$).

Results in 2003 were similar to those in 2001, with a significant effect of the distance from perch post ($F_{1,60} = 60.16$, $p < 0.001$, Figure 2) and a significant interaction between distance from tree and distance from perch post at both sites ($F_{1,60} = 51.39$, $p < 0.001$). Following the 2004 fire, the number of surviving shrub seedlings was very much reduced in all four treatments (Figure 2). The total number of seedlings in 2001 was 1209, 1080 seedlings in 2003, but only 95 seedlings were present in 2004 (> 90 % mortality).

Mortality of Slash Pine Recruits

Densities of seedlings of post-1997 recruits of *Pinus elliottii* were highest for both the large plots and subplots at the end of the fire free period in 2004 (Table 1). In the large plots, only three individuals were alive in the post-fire 2004 census, thus indicating > 99% mortality for both sites, which we attributed to the prescribed fires. All recruits, both survivors and dead individuals, were less than 1.5 m tall.

DISCUSSION

The results of this study lead us to conclude that an increased density of trees (and thus perches) leads to a corresponding increase in the deposition of seeds of shrubs, vines, and bird-dispersed trees in wet pine savannas. Deposition of seeds of two common bird-dispersed shrubs, *I. glabra* and *I. vomitoria*, was much greater below trees than away from trees. Because perches increased seedling densities of these and other shrub species to a much greater extent in areas away from trees than near trees, we conclude that pines increase dispersal of shrubs by serving as bird perches. These results are consistent with Brewer's (1998) hypothesis that dispersal by birds increases both the abundance and richness of woody species near trees.

Our results indicate that seed production of shrubs was reduced by fire. The reduced seed deposition for the 1998 season at Sandy Creek (compared to 1999) confirms field observations that neither *Ilex* species flowers or produces fruit during the first flowering season following fire. *Gaylussacia* spp. and *Rubus* spp. are also pine savanna species that usually do not fruit following a fire (Garren 1943). The few *Ilex* seeds that were collected in the traps likely originated from the surrounding unburned forest. Therefore, most seed deposition at a given spot originates from shrubs in the immediate area. These findings are further supported by our observations of foraging American robins (*Turdus migratorius*),

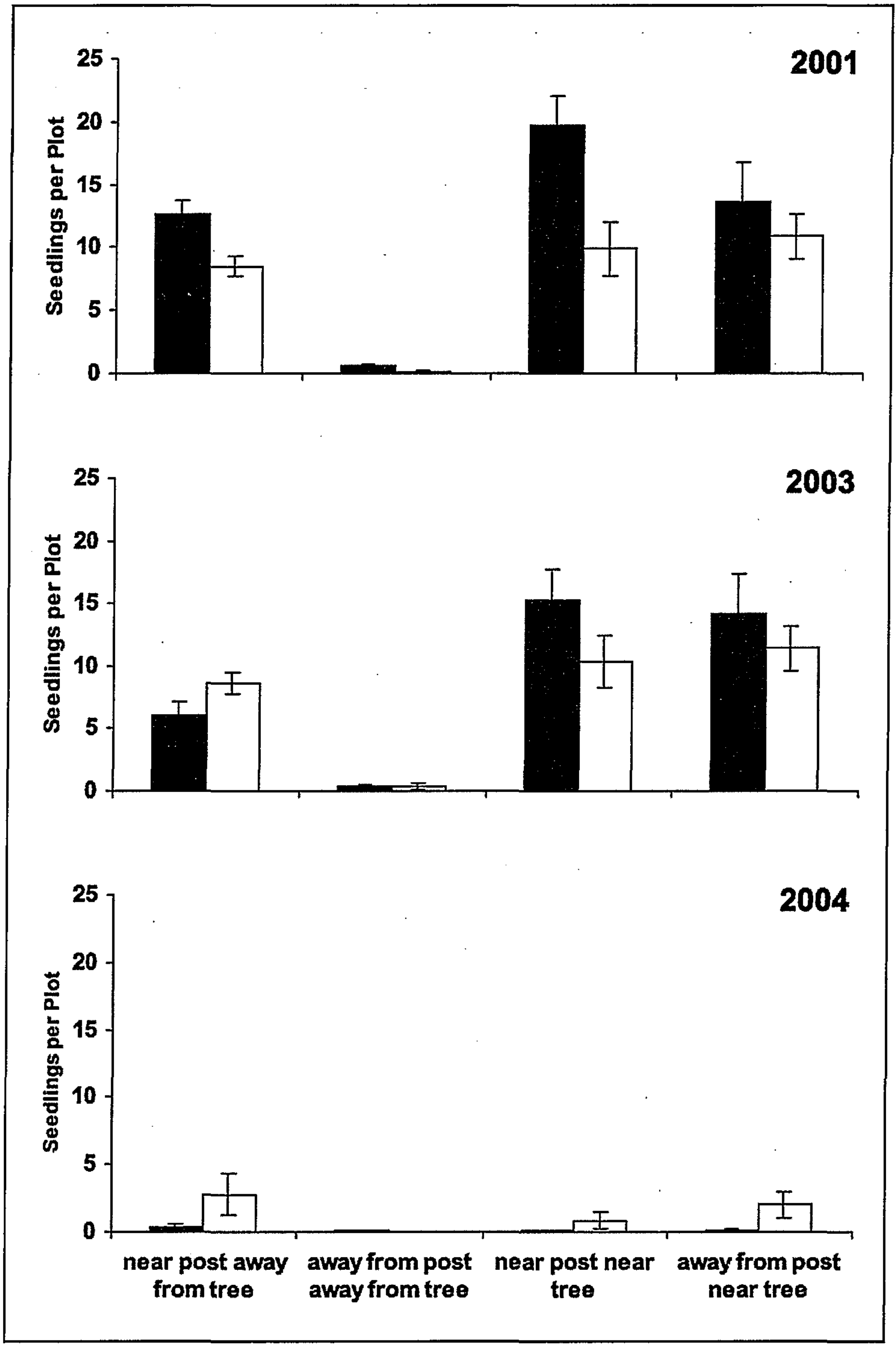

Figure 2. Mean shrub seedling counts for perch post and pine tree treatments for three years (2001, 2003 and 2004 post-fire) at Wolf Branch (filled bars) and Sandy Creek (open bars). Error bars are ± 1 standard error.

which primarily appeared to perch on nearby trees after removing fruits from *I. glabra* (J.S. Brewer, pers. observations).

The relevance of our results to mesic pine flatwoods communities, where shrub densities are high and not closely associated with the bases of trees, is not clear (Brewer 2002). The higher densities of pines typically observed in pine flatwoods could generate higher rates of seed deposition of bird-dispersed woody species (S.W. Ashley and J.S. Brewer, unpubl. data). What we do not know is whether or how seed deposition during prolonged fire-free intervals in the past contributed to the high stem densities of established adult shrubs and vines we typically see in pine flatwoods today. Most previous studies of limits on shrub density in longleaf pine savannas have focused primarily on the effects of fire (Olson and Platt 1995; Brockway and Lewis 1997; Drewa et al. 2002; Glitzenstein et al. 2003). Although these studies provide conflicting results regarding fire effects on ramet densities, all agree that repeated fires do not generally cause substantial mortality of adult shrub genets (Drewa et al. 2002). If fire suppression in the past was partly responsible for the high genet densities of shrubs we see today (due to increased seed deposition and seedling establishment), then repeated low-intensity burning (regardless of season or frequency) may do little to restore pre-suppression genet densities in pine flatwoods (Drewa et al. 2002).

Examination of longleaf pine flatwoods in southern Mississippi in the mid 1800s (pre-fire-suppression) provides some support for this hypothesis. Hilgard (1860) noted that *I. glabra* dominated the groundcover of mesic pine flatwoods communities in southern Mississippi. *Ilex glabra* is a rhizomatous shrub, and overall stem density might have been affected more by clonal growth than by seedling establishment in flatwoods (Brewer 2002). Although *I. vomitoria* is quite common and abundant in pine flatwoods in southern Mississippi today, Hilgard made no reference to *I. vomitoria* in these same communities in the mid 1800s. Unlike *I. glabra*, *I. vomitoria* is not a strongly rhizomatous shrub. Hence, the high stem densities of this shrub in pine flatwoods of southern Mississippi today may be highly correlated with genet densities and thus a legacy of increased tree densities following logging (Noel et al. 1998) and increased seed deposition and seedling establishment during prolonged periods of fire suppression in the past.

Nine years without fire was not sufficient to allow recruits of *P. elliottii* to grow large enough to become tolerant of the prescribed fires in the wet pine savannas studied here. Only three individuals of *P. elliottii* (out of 354) survived the 2004 fires. The slow

Table 1. Total numbers of *Pinus elliottii* seedlings and saplings surviving in large plots and subplots at both sites for three census dates.

Plot size and site	1997	2004 (pre-fire)	2004 (post-fire)
Subplots (0.25 m^2)			
Wolf Branch	5	8	0
Sandy Creek	0	7	1 *
Large Plots			
Wolf Branch (475 m^2)	–	271	2 *
Sandy Creek (300 m^2)	–	83	1 *

* surviving saplings were less than 1.5 m in height

growth of *P. elliottii* at our sites (all recruits were less 1.5 m tall) was likely caused by poor soil drainage (Streng and Harcombe 1982; Tiarks and Shoulders 1982). Therefore, the length of time necessary for a *P. elliottii* to grow large enough to survive a fire almost certainly depends on local edaphic conditions and hydrology, in addition to fuel loads and fire temperatures. The fires also apparently caused considerable mortality of shrub seedlings (> 90%). Ten percent survivorship of seedlings following growing-season fires, however, is not an insignificant level of recruitment for long-lived perennial shrubs. Hence, shrub seedling recruitment may be limited more by the establishment of trees (and thus dispersal) than by the ability of seedlings to survive fire. Nevertheless, all recruits (including some that were five years old) were less than 15 cm tall by the time of the 2004 fires, indicating very slow growth and thus low rates of recruitment of shrubs into adult size classes.

CONCLUSION

Identifying the mechanisms that drive invasions of open habitats by woody species is critical for effective restoration of diverse forests and preservation of diverse savannas. The results of this study agree with those of many tropical forest restoration studies, which show that trees facilitate invasion of open habitats by woody species (McDonnell and Stiles 1983; Guevara et al. 1986; McClanahan and Wolfe 1987). A desired goal of longleaf pine savanna conservation is to use fire to reduce recruitment of and dominance by woody species (Folkerts 1982; Means and Grow 1985; Noss 1988; Glitzenstein et al. 2003). Our results show that the effect of fire on maintaining biodiversity in wet pine savannas is more complex than simply "mowing down" established and resilient shrubs and reducing their competitive effect on herbaceous plants. By reducing both the supply and the deposition of seeds of shrubs in wet pine savannas, periodic fires may be crucial to reducing colonization and expansion of shrub populations in these highly diverse herbaceous plant communities. Knowledge of fire-tolerance thresholds for fire-sensitive tree species, especially in wet pine savannas, would improve our understanding of how variability in fire frequency interacts with dispersal limitation of shrubs to maintain the ecological integrity of wet pine savannas.

ACKNOWLEDGMENTS

Prescribed burns and access to field sites were possible thanks to the Desoto National Forest staff. The seed trap experiment was partially funded by the University of Mississippi Biology Department. This manuscript was improved vastly by the comments of Paul Drewa and three anonymous reviewers.

Sarah Hinman is a Research Technician for the Nantucket Conservation Foundation in Massachusetts. She holds an M.S. in Biology from the University of Mississippi. Her current work involves the management and conservation of plant communities on the island of Nantucket.

J. Stephen Brewer is an Associate Professor of Biology at the University of Mississippi. His research focuses on ecological restoration, fire ecology, and invasive species in ecosystems of the southeastern United States.

Steven W. Ashley is a graduate of the University of Georgia with a B.S. degree in Botany and a former graduate student at the University of Mississippi, now residing in Atlanta, Georgia.

LITERATURE CITED

Archer, S. 1990. Development and stability of grass/woody mosaics in subtropical savanna parkland, Texas, U.S.A. Journal of Biogeography 17:453-462.

Brewer, J.S. 1998. Patterns of plant species richness in a wet slash-pine (*Pinus elliottii*) savanna. Journal of the Torrey Botanical Society 125:216-224.

Brewer, J.S. 2002. Disturbances increase seedling emergence of an invasive native shrub in pitcher-plant bogs. Natural Areas Journal 22:4-10.

Brockway, D., and C.E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure, and productivity in a longleaf pine wiregrass ecosystem. Forest Ecology and Management 96:167-183.

Brown, J.F., and S. Archer. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. Ecology 80:2385-2396.

Chapman, H.H. 1932. Is the longleaf type a climax? Ecology 13:328-334.

Debussche, M., J. Escarré, and J. Lepart. 1982. Ornithochory and plant succession in Mediterranean abandoned orchards. Vegetatio 48:255-266.

Debussche M., and P. Isenmann. 1994. Bird-dispersed seed rain and seedling establishment in patch Mediterranean vegetation. Oikos 69:414-426.

Drewa, P.B., W.J. Platt, and E.B. Moser. 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology 83:755-767.

Folkerts, G.W. 1982. The Gulf Coast pitcher plant bogs. American Scientist 70:260-267.

Fowler, N.A. and M. Batchelor. 2005. Understanding the juniper juggernaut: patterns and mechanisms of shrub encroachment in central Texas. Abstract *in* Ecological Society of America meeting program, 7-12 August 2005, Montréal, Canada. Available online <http://abstracts.co.allenpress.com/pweb/esa2005/document/?ID=47925>.

Frost, C.C. 1993. Four centuries of changing landscape patterns in the Longleaf Pine ecosystem. Pp. 17-43 *in* S. Hermann, ed., The longleaf pine ecosystem; ecology, restoration and management. The Tall Timbers Fire Ecology Conference Proceedings, Tall Timbers Research Station. Tallahassee, Fla.

Garren, K.H. 1943. Effects of fire on vegetation of the southeastern United States. Botanical Review 9:617-654.

Glitzenstein, J.S., D.R. Streng, and 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.

Guevara, S., S.E. Purata, and E. Van der Maarel. 1986. The role of remnant forest trees in tropical secondary succession. Vegetatio 66:77-84.

Halls, L.K. 1977. Southern fruit-producing woody plants used by wildlife. General Technical Report SO-1, U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, La.

Harper, R.M. 1914. A superficial study of the pine-barren vegetation of Mississippi. Journal of the Torrey Botanical Society 103:1-9.

Hebb, E.A., and A.F. Clewell. 1976. A remnant stand of old-growth slash pine in the Florida panhandle. Bulletin of the Torrey Botanical Club 103:1-9.

Herrera, C.M. 1982. Defense of ripe fruit from pests: its significance in relation to plant-disperser interactions. American Naturalist 120:218-241.

Hilgard. 1860. A report on the geology and agriculture of the state of Mississippi. Mississippi State Geological Survey, Jackson.

Joy, D.A., and D.R. Young. 2002. Promotion of mid-successional seedling recruitment and establishment by *Juniperus virginiana* in a coastal environment. Plant Ecology 160:125-135.

Kollmann, J. 1995. Regeneration window for fleshy-fruited plants during scrub development on abandoned grassland. Ecoscience 2:213-222.

Landers, J.L. 1991. Disturbance influences on pine traits in the southeastern United States. Pp. 61-98 *in* S.H. Herman, ed., High intensity fire in wildlands, management challenges and options. Proceedings of the 17th Tall Timbers Fire Ecology conference, Tall Timbers Research Station, Tallahassee, Fla.

Landers, J. L., D.H. Van Lear, and W.D. Boyer. 1995. The longleaf pine forests of the southeast: requiem or renaissance? Journal of Forestry 93:39-44.

McAtee, W.L. 1947. Distribution of seeds by birds. American Midland Naturalist 38:214-223.

McClanahan, T.R., and R.W. Wolfe. 1987. Dispersal of ornithochorous seeds from forest edges in central Florida. Vegetatio 71:107-112.

McClanahan, T.R., and R.W. Wolfe. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conservation Biology 7:279-288.

McDonnell, M.J. 1986. Old filed vegetation height and the dispersal pattern of bird-disseminated woody plants. Bulletin of the Torrey Botanical Club 113:6-11.

McDonnell, M.J., and E.W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. Oecologia 53:109-116.

Means, D.B., and G. Grow. 1985. The endangered longleaf pine community. ENFO Report 85:1-12.

Monk, C.D. 1968. Successional and environmental relationships of the forest vegetation of North Central Florida. American Midland Naturalist 79:441-457.

Nepstad, D.C., C. Uhl, C.A. Pereira, and J.M. Cardosa da Silva. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76:25-39.

Noel, J.M., W.J. Platt, and E.B. Moser. 1998. Structural characteristics of old- and second-growth stands of longleaf pine (*Pinus palustris*) in the Gulf Coast region of the U.S.A. Conservation Biology 12:533-548.

Noss, R.F. 1988. The longleaf pine landscape of the Southeast: almost gone and almost forgotten. Endangered Species Update 5:1-8.

Olson, M.S., and W.J. Platt. 1995. Effects of habitat and growing season fires on resprouting of shrubs in longleaf pine savannas. Vegetatio 119:101-118.

Platt, W.J. 1999. Southeastern pine savannas. Pp. 23-51 *in* R.C. Anderson, J.S. Fralish, and J.M. Baskin, eds., Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cambridge University Press, Cambridge, U.K.

Radford, A.E., H.F. Ahles, and C.R. Bell. 1968. Manual of the Vascular Flora of the Carolinas. University of North Carolina Press, Chapel Hill.

Robbins, L.E., and R.L. Myers. 1992. Seasonal effects of prescribed burning in Florida: a review. Miscellaneous Publication 8, Tall Timbers Research Station, Tallahassee, Fla.

Schupp, E.W., H.F. Howe, C.F. Augspurger, and D. Levey. 1989. Arrival and survival in tropical tree-fall gaps. Ecology 70:562-564.

Short, H.L., and E.A. Epps. 1976. Nutrient quality and digestibility of seeds and fruits from southern forests. Journal of Wildlife Management 40:238-289.

Steele, R.G.D., and J.H. Torrie. 1980. Principles and Procedures of Statistics: a biometric approach, 2nd ed. McGrall-Hill, New York.

Streng, D.R., and P.A. Harcombe. 1982. Why don't east Texas savannas grow up to forest? The American Midland Naturalist 108:278-294.

Thorton, I.W.B., S.G. Compton, and C.N. Wilson. 1996. The role of animals in the colonization of the Krakatau Islands by fig trees (*Ficus* species). Journal of Biogeography 23:577-592.

Tiarks, A.E., and E. Shoulders. 1982. Effects of shallow water tables on height, growth, and phosphorus uptake by loblolly and slash pines. Research Note SO-285, U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, La.

Werner, P.A., and A.L. Harbeck. 1982. The pattern of tree seedling establishment relative to staghorn sumac cover in Michigan old fields. American Midland Naturalist 108:124-132.