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RESEARCH ARTICLE

Restoring Perennial Warm-Season Grasses as a Means of Reversing Mesophication of Oak Woodlands in Northern Mississippi

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Abstract

Fire suppression has removed an important ecological force previously responsible for shaping many plant communities throughout the world. Upland areas of north-central Mississippi that have been protected from fire are now closed-canopy forests including species known to be uncommon as bearing/witness trees in upland portions of the landscape (historically off-site species) and sparse ground cover vegetation. Anecdotal evidence suggests that warm-season grasses were prevalent in the understory of these communities, which could have provided more consistent fuel. We corroborate the historic presence of these grasses by looking at their natural co-occurrence with oak regeneration (a requisite of self-replacing stands of oaks found historically). Restoration of these communities has typically focused on burning and off-site tree thinning. Utilizing a restoration experiment implementing these treatments, we found significantly reduced understory leaf litter in treatment areas. To test which variables associated with restoration treatments were most important for the survival of these grasses, we measured the effect of leaf litter removal and its interaction with environmental conditions on the survival of transplanted shoots. Survival of little bluestem increased with decreasing canopy density and decreasing leaf litter. Leaf-litter removal did not increase survival, nor did it interact with either pre-treatment leaf litter depth or canopy density. These results show that little bluestem benefits from conditions expected historically: increased light and possibly fire.

Key words: ***Andropogon virginicus*, fire, leaf litter, *Schizachyrium scoparium*, thinning.**

Introduction

Among the many factors that have and continue to contribute to landscape changes worldwide, the alteration of fire regimes has had consequences for plant community structure in many ecosystems (Bowles & McBride 1998; Brewer 2001; Bond et al. 2005; Nowacki & Abrams 2008). Specifically for the upland landscape of the Midwest and interior South of the United States, fire-maintained woodlands and savannas were an important component of the landscape historically (Anderson & Bowles 1999; Fralish et al. 1999; Heikens 1999; Brewer 2001; Surrette et al. 2008). In the 20th century, fire suppression enabled fire-sensitive, shade-tolerant hardwoods to colonize previously fire-maintained oak woodlands (Hart et al. 2008; Nowacki & Abrams 2008), a pattern of vegetation change repeated in fire-adapted ecosystems worldwide (Parsons & DeBenedetti 1979; Costello et al. 2000). These fire-sensitive species produced a more closed canopy than the historically open, sparse canopies of oak woodlands (Bowles & McBride 1998), leading to widespread oak regeneration failure, losses of ground cover plant diversity, and reduced flammability (Abrams 1992; Bowles & McBride 1998), a process described as mesophication (Nowacki & Abrams 2008).

Although it would seem that the logical approach to reversing mesophication of oak woodlands following fire suppression would simply be to reintroduce fire, there are at least three obstacles to reversing mesophication via fire alone. First, reintroduction of fire alone has not proven sufficient to restore natural regeneration of oaks in forests of the lower Midwest or interior South of the United States (Arthur et al. 1998; Franklin et al. 2003; Hutchinson et al. 2005*a*; Albrecht & McCarthy 2006). With decades of fire suppression, many fire-sensitive tree species have reached size classes that are not affected by low-intensity ground burns (Franklin et al. 2003). Second, although repeated burning alone can increase ground cover plant diversity in previously fire-suppressed oak forests (Hutchinson et al. 2005*b*), open woodlands support greater plant diversity than do closed woodlands (Taft 2009), and fire itself may not shift ground cover species composition to that indicative of open woodlands (Hutchinson et al. 2005*b*). Some combination of persistent canopy openings and repeated

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burning appears to be necessary to promote oak regeneration and favor a diverse ground cover dominated by open woodland vegetation (Brose et al. 1999; Iverson et al. 2008; Brewer & Menzel 2009; Taft 2009). Third, even the combination of canopy tree thinning and repeated burning may not be sufficient to rapidly recover certain elements of open woodland ground cover vegetation, most notably, warm-season grasses. Many of these species are shade-intolerant, do not regenerate rapidly from seed, and do not produce a persistent seed bank (Rabinowitz 1981; Leck & Leck 1998). Hence, warm-season grasses, in particular, are likely to be lost relatively rapidly with fire suppression (Bowles & McBride 1998) but are not likely to recover rapidly following restoration of open canopies and repeated fire.

In north Mississippi, there is anecdotal evidence that warm-season grasses (e.g. *Schizachyrium scoparium* [little bluestem] and *Andropogon* spp.) were possibly a significant component of the ground cover vegetation in some upland oak-dominated woodlands in the early 1800s (Nutt [1805] in Jennings [1947]). *Andropogon virginicus* (broomsedge) and little bluestem have important effects on wildlife habitat quality and fire regimes. They provide cover, nesting sites, and seed as food for small mammals, disturbance-dependent songbirds, and game birds (including quail; Martin et al. 1951; Askins 1995; Masters et al. 1998; Brawn 2006). Restoring a more flammable grassy understory could be important for allowing a complete and spreading burn resulting in greater topkill of mesophytic saplings, thereby constituting a crucial aspect of restoration in this fire-dependent ecosystem currently suffering from mesophication (Platt et al. 1991; Brose & Van Lear 1998; Brewer & Rogers 2006). With very little understory growth in these forests, deciduous leaf litter (hereafter, litter) currently provides the bulk of surface fuels available for burning, limiting the timing and effectiveness of prescribed fire (Brewer & Rogers 2006).

Currently, warm-season grasses are largely absent from the interiors of fire-suppressed remnants of these communities. Inferences about their abundance in the past could be informed by current assessments of environmental conditions that favor both warm-season grasses and natural regeneration of tree species known to dominate the historic landscape. Preliminary observations indicated that one or both species of grasses currently is abundant in areas where oak sapling densities are high (e.g. forest edges, and large, relatively old canopy gaps). Given that oak saplings, and thus natural oak regeneration, were common in the early 1800s in north Mississippi (Surrette et al. 2008), it would follow that the environmental conditions that favored oak regeneration (e.g. fire, open tree canopies) likely also favor the establishment of these grasses. Testing this hypothesis requires quantification of natural patterns of co-occurrence of warm-season grasses and oak regeneration. In addition, transplant experiments with warm-season grasses are necessary to determine whether the current absence or low frequency of grasses in the understory of the interior of fire-suppressed forests are due to low light levels, high leaf litter amounts, and/or a lag in colonization of suitable sites with recently opened tree canopies.

In this study, we used a restoration experiment initiated at Strawberry Plains Audubon Center (north-central Mississippi, U.S.A.) in 2004 to test several hypotheses: (1) warm-season grasses and oak saplings co-occur in areas with open canopies, at persistent forest edges, and with low litter amounts; (2) burning and thinning treatment areas are associated with more open canopies and lower litter amounts than control areas; and (3) litter removal increases the success of transplanted grasses and this effect is greatest in areas with relatively high pre-treatment litter amounts and low canopy density (i.e. areas that were thinned but not recently burned).

Methods

Restoration Treatments

The restoration experiment utilized to address our hypotheses was initiated in 2004 at Strawberry Plains Audubon Center, a 1,000-ha sanctuary in Holly Springs, Mississippi. The experiment consisted of two sites, several kilometers apart, each containing control and treatment areas (site 1:34°49′60″N, 89°28′32″W; site 2:34°49′52″N, 89°27′17″W). Although both sites occurred with a mixture of Providence silt loam and Cahaba sandy loam, Providence silt loam predominated at site 1, whereas Cahaba sandy loam predominated at site 2.

As part of the existing restoration experiment, treatments and controls were assigned to approximately 70×75−m areas at site 1 and to 30×30−m areas at site 2. Fire-sensitive tree species known to be locally absent historically (e.g. *Liquidambar styraciflua* [sweetgum], *Ulmus alata* [winged elm], *Nyssa sylvatica* [blackgum]; Brewer 2001) were thinned in the treatment areas beginning in 2004 at site 1 and 2007 at site 2. Prescribed fires were attempted within the treatment area at site 1 in late September 2004, early October 2006 (Brewer & Menzel 2009), and at sites 1 and 2 in early July 2008. Due to the mesophication and lack of understory vegetation at the site discussed in the Introduction section, the treatments were not always successfully employed across the entire treatment area. To specifically address hypothesis 1, 10×30−m areas were marked off where burning was most uniformly applied within which our sampling plots were established. These sampling plots were then used in the analyses for all the hypotheses. Within the treatment area at site 1, three 10×30−m areas were established, one adjacent and parallel to the edge that had burned in all 3 years (burned and thinned edge), one within a natural tree-fall gap in the forest interior that existed before the experiment and had burned once in 2006 (burned and thinned interior gap), and one within the interior that had not been burned (thinned only). Within the control area at site 1, we established one 10×30−m area at the forest edge (control edge) and one in the interior (control interior). The forest edge at site 1 is adjacent to a power-line clearing running perpendicular to the slope maintained by mowing. At site 2, both the treated and control areas were oriented along the forest edge, adjacent to a non-forested ridge. Until around 2000, this ridge was maintained as pastureland and is now a mowed path (C. Pope 2009, Strawberry Plains Audubon Center, personal communication). We established a single 10 × 30−m area at site 2 for each of the burned and thinned and control edge.

Sampling

To test all the hypotheses, 1.5 × 1.5−m sampling plots were established to record as much of the environmental variability as possible. The location of the plots within each 10 × 30−m area was randomly stratified, and the number of plots established increased in proportion to observed ground cover plant diversity. At site 1, there were 9 plots within the control edge, 8 in the control interior, 9 in the thinned only, 12 in the burned and thinned edge, and 11 in the burned and thinned interior gap. At site 2, the burned and thinned and control areas each contained 13 plots. This gave a total of 75 plots. Soil samples were taken from each plot for texture analysis. A spherical concave densiometer was used to obtain canopy density for each plot. The percent cover and depth of leaf litter within each plot were estimated. To address the hypothesis that broomsedge and little bluestem naturally co-occurred with oaks where environmental conditions also favored oak regeneration, we recorded the presence or absence of broomsedge and little bluestem and the presence of oak saplings (>1 m tall and <10 cm dbh) in or within 1 m of the border of each plot.

Transplant and Litter Removal Experiment

We used transplants to determine whether the current absence or low frequency of grasses in the understory of the interior of fire-suppressed forests was due to low light levels, high leaf litter amounts, and/or a lag in colonization of suitable sites created at more interior plots where restoration treatments were being preformed (hypothesis 3). Litter removal by hand over areas that were thinned and burned as well as areas that were not was intended to tease out the potential interactions between canopy density (light availability) and litter depth. To measure the effect of litter removal and its interaction with environmental conditions (e.g. canopy openness, litter depth before removal) on survival, we transplanted one shoot (ramet) of each grass species into each half of plots in fall 2008, then randomly assigned a litter removal treatment to one or the other half. No transplanted shoot was located within 0.5 m of another. A total of 300 grass shoots were transplanted into the 75 plots, although a few unforeseen anthropogenic disturbances (i.e. damage of the control area and the burned-thinned edge area at site 1 by road construction and power-line clearing expansion in the early spring 2009) reduced this to 240 grasses within 60 plots. The shoots were obtained from bunches harvested close to the sites. Each shoot was picked at random from clumps, clipped and weighed without soil prior to planting to ensure the transplants were as similar as possible (approximately 2 g wet weight). The litter removal treatment was initially administered in late fall 2008 and repeated in early spring 2009. Grasses were harvested in fall 2009. Success was assessed through survival determined by the presence of green leaves.

Data Analysis

Because restoration treatments must be implemented at large spatial scales, adequate replication is difficult to achieve. Hence, detailed measurements of environmental variables within and among the sites and treatment/control areas were used in combination with multivariate methods to associate differences in these variables between plots to address our hypotheses. We used discriminate analysis (DA) to determine which conditions favored the natural co-occurrence of grasses and oak saplings (hypothesis 1). Environmental variables used in the analyses included canopy density, litter depth, litter percent cover, silt-to-sand ratio, and distance to the nearest persistent forest edge. The groups were defined as follows: plots that contained broomsedge only, plots that contained oak saplings only, plots that contained both broomsedge and oak sapling, and plots that contained neither. A second DA considered little bluestem in place of broomsedge. Both DAs included all 75 plots. These analyses revealed (1) the extent to which the environmental conditions that favored oak sapling recruitment also favored warm-season grasses and (2) whether plots associated with relatively recent decreases in canopy density (i.e. thinned areas within forest interiors) were as likely to contain grasses and oak saplings as plots associated with canopy openings that have been maintained for long time periods (i.e. persistent forest edges).

To address the second hypothesis, we used DA to quantify the effects of restoration treatments on environmental variables, which allowed us to determine which variables were most important in discriminating between treatments. We considered two groups or categories produced by the treatments: plots within the control areas and plots within a treatment area, last burned 1 July 2008. This DA of the treatment versus control groups quantified the impact of the treatments on variables suspected to influence establishment and growth of the grasses. To ensure that plot differences were related primarily to the treatments and not to differences between sites, we performed a DA of environmental variation categorizing plots according to site (excluding those plots within the forest interior at site 1). We then assessed whether the environmental variables that distinguished the treatments differed from those that distinguished the sites.

To address the third hypothesis, we examined the effect of litter removal and its interactions with environmental conditions on transplant survival using multiple logistic regression for each grass species. To account for the nonindependence of survival responses to litter removal, we considered two survival response categories: plots in which transplants survived following litter removal but not without it and plots in which the reverse was true (see Steel and Torrie 1980; chi-square of nonindependent observations). A significantly positive intercept in the logistic regression indicated a significantly positive main effect of litter removal on transplant survival. A significantly positive parameter estimate of litter amounts (prior to litter removal) indicated an interaction, wherein the positive effect of litter removal increased with increasing pre-removal litter amounts. A significantly negative parameter estimate of canopy density indicated an interaction, wherein the positive effect of litter removal decreased with increasing canopy density.

The relationship between survival of the transplants and all the measured environmental variables was analyzed using multiple ordinal regression for each grass species. Because there was no main effect of the litter removal treatment in the logistic regression analyses (see Results section), each plot was ranked according to the number of surviving transplants for each species (0, 1, or 2), irrespective of litter removal. If litter removal had no effect on survival, then we predicted that survival would be negatively associated with canopy density and would have no association with pre-removal litter amounts. Furthermore, if high survival near forest edges was simply a function of canopy density, then we predicted that a multiple ordinal regression that included canopy density would reveal no association between survival and distance from the edge.

The silt-to-sand ratio was determined from soil texture analysis and the equation: ln(silt) − ln(sand). The canopy density was transformed by taking the arcsine of the square root of the proportion of obscured sky to normalize the residuals in the regression and DAs. The distance to the nearest edge was transformed using a fourth root function. Litter depth and percent cover were strongly correlated ($r^2 = 0.7323$). To avoid multicollinearity, the first principal component of a principal components analysis (PCA) of the two variables was used. Hereafter, this first principle component of litter depth and percent cover will be referred to as litter amount or simply litter.

Results

Co-Occurrence of Warm-Season Grasses and Oak Saplings

The first hypothesis that warm-season grasses and oak saplings would co-occur in areas with open canopies, at persistent forest edges, and with low litter (one effect of fire) was partially supported by DA. With respect to broomsedge, as predicted, canopy density and distance to nearest edge significantly contributed to the first axis; however, silt-to-sand ratio also significantly contributed to the differences between groups on this axis (indicating site differences in the occurrence of broomsedge and saplings; Fig. 1). Plots that contained oak saplings or both oak saplings and broomsedge overlapped greatly and were significantly different from plots that contained neither. Plots that contained neither oak saplings nor broomsedge tended to have greater canopy density, higher silt-to-sand ratio, and were farther from the nearest edge than groups containing oak saplings and broomsedge; however, the group containing broomsedge (without saplings) was intermediate between these. Hence, light was the most important factor limiting the occurrence of oak saplings with broomsedge, but these plants were also less common in plots with higher silt-to-sand ratios and thus were less common at site 1 than at site 2. The second axis explained much less of the variation between groups, with none of the groups being significantly different on this axis.

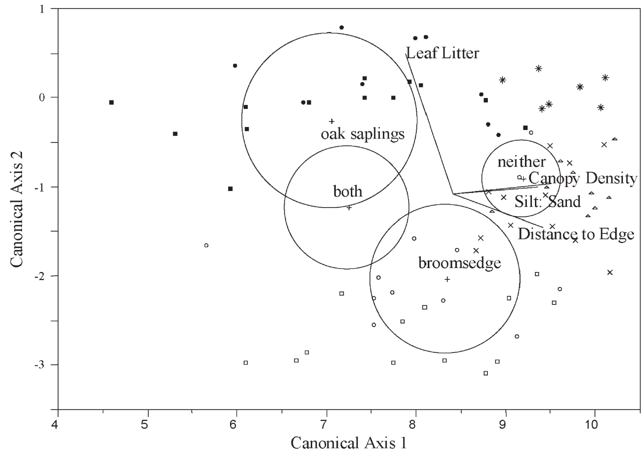

Figure 1. Discriminant analysis using 75 plots containing broomsedge, an oak sapling, both or neither as the groups. Partial correlation coefficients and their associated p-values for the first axis are canopy density (2008), 0.495, $p < 0.0001$; silt: sand, 0.469, $p < 0.0001$; litter, −0.144, $p = 0.2166$; and distance to nearest edge, 0.561, $p < 0.0001$. Partial correlation coefficients and their associated p-values for the second axis are canopy density, −0.200, $p = 0.0849$; silt: sand, −0.249, $p = 0.0313$; litter, 0.911, $p < 0.0001$; and distance to nearest edge, 0.052, $p = 0.6567$. Wilks' Lambda $p < 0.0001$, 34/75 misclassified. Plot locations in canonical space are marked with symbols corresponding to the treatment area where the plots are located. For site 1: burned and thinned edge, ○; burned and thinned interior gap, ×; thinned only, △; control edge, ●; control interior, ∗. For site 2: burned and thinned, □; control, ■.

The DA for little bluestem produced results similar to those of the previous analysis. The key difference was that plots containing oak saplings, little bluestem, or both overlapped greatly and were all significantly different from plots that contained neither little bluestem nor oaks (Fig. 2). Plots that contained neither oak saplings nor little bluestem tended to have a greater canopy density, a higher silt-to-sand ratio, lower litter amounts, and were farther from the nearest edge than the other three groups.

Effects of Restoration Treatments on Environmental Variables

Litter amount was the most important discriminator of treated and control plots, whereas canopy density was much less important (Fig. 3). The groups differed significantly (95% confidence limit ellipses do not overlap), and the plots that were thinned and recently burned had less litter than the control plots.

In contrast to the results of the DA of treatment effects, the DA of site differences revealed silt-to-sand ratio and canopy density as the most important variables distinguishing the sites (Fig. 4). Site 1 plots had greater silt-to-sand ratio and higher canopy density than site 2.

Responses of Transplants

Contrary to our predictions, litter removal had no effect on transplant survival nor did it interact with any of the measured environmental variables to influence transplant survival

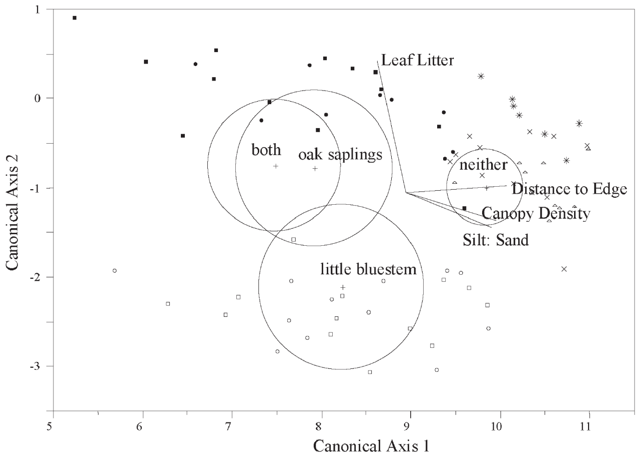

Figure 2. Discriminant analysis using 75 plots that contained little bluestem, an oak sapling, both or neither as the groups. Partial correlation coefficients and their associated p-values for the first axis are canopy density (2008), 0.576, $p < 0.0001$; silt: sand, 0.489, $p < 0.0001$; litter, −0.266, $p = 0.021$; and distance to nearest edge, 0.469, $p < 0.0001$. Partial correlation coefficients and their associated p-values for the second axis are canopy density, 0.069, $p = 0.5440$; silt: sand, 0.042, $p = 0.7222$; litter, 0.954, $p < 0.0001$; and distance to nearest edge, −0.231, $p = 0.046$. Wilks' Lambda $p < 0.0001$, 28/75 misclassified. Plot locations in canonical space are marked with symbols corresponding to the treatment area where the plots are located. For site 1: burned and thinned edge, ○; burned and thinned interior gap, ×; thinned only, △; control edge, ●; control interior, ∗. For site 2: burned and thinned, □; control, ■.

(Tables 1 & 2). None of the parameter estimates in the multiple logistic regression, including the intercept, were significant for either species (Tables 1 & 2).

Consistent with our predictions, we found that the survival of transplants of little bluestem decreased with increasing canopy density (Table 3). Survival also showed a modest but significant increase farther from the nearest edge (once canopy density was accounted for; Table 3). Survival of little bluestem transplants decreased with increasing pre-removal litter amounts (Table 3). Survival did not differ between sites, indicating that any environmental differences between

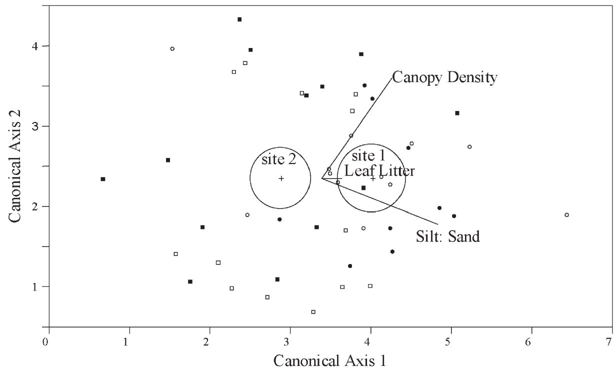

Figure 4. Discriminant analysis using the location of the 47 plots (either site 1 or site 2) as the groups. Partial correlation coefficients and their associated p-values for the first axis are canopy density (2008), 0.502, $p = 0.0003$; silt: sand, 0.911, $p < 0.0001$; and litter, 0.141, $p = 0.3445$. Axis 2 represents the first principal component axis of residual variation not accounted for by the discriminant analysis. Wilks' Lambda $p = 0.006$, 13/47 misclassified. Plot locations in canonical space are marked with symbols corresponding to the treatment area where the plots are located. For site 1: burned and thinned edge, ○; control edge, ●. For site 2: burned and thinned, □; control, ■.

Table 1. Logistic regression for little bluestem transplant survival.

Term	*Estimate*	*Chi-square*	*Prob > ChiSq*
Intercept	−0.846	0.01	0.918
Canopy density*	1.034	0.04	0.843
Silt: sand	−7.410	3.59	0.058
Leaf litter	3.760	3.01	0.083
Distance to edge	0.402	0.02	0.900
Site (site 1)	0.693	0.17	0.680

Whole-model test found Prob > ChiSq = 0.035; 27 plots were used for this analysis.
* Based on average of 2008 and 2009 growing season measurements.

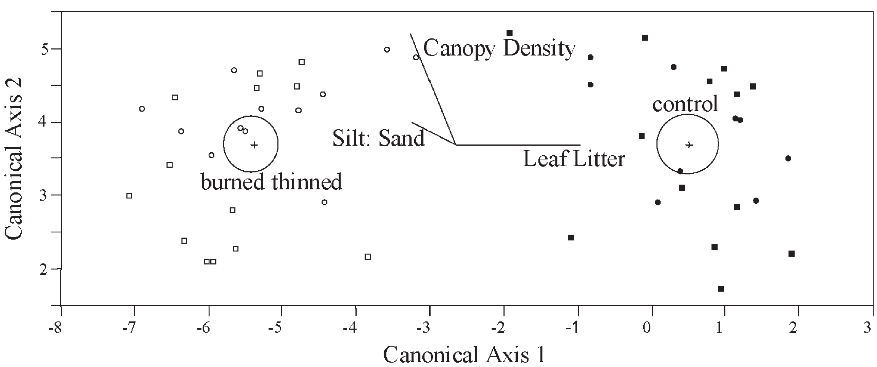

Figure 3. Discriminant analysis using plots within the control areas ("control" in figure), and plots within treatment areas that were recently burned ("burned, thinned" in figure) as the groups (47 plots total). Partial correlation coefficients and their associated p-values for the first axis are canopy density (2008), −0.127, $p = 0.3960$; silt: sand, −0.128, $p = 0.3910$; and litter, 0.977, $p < 0.0001$. Axis 2 represents the first principal component axis of residual variation not accounted for by the discriminant analysis. Wilks' Lambda p, 0/47 misclassified. Plot locations in canonical space are marked with symbols corresponding to the treatment area where the plots are located. For site 1: burned and thinned edge, ○; control edge, ●. For site 2: burned and thinned, □; control, ■.

Table 2. Logistic regression for broomsedge transplant survival.

Term	*Estimate*	*Chi-square*	*Prob > ChiSq*
Intercept	−52.104	2.5	0.114
Canopy density*	5.984	1.16	0.282
Silt: sand	8.606	1.54	0.215
Leaf litter	0.423	0.06	0.800
Distance to edge	17.459	2.11	0.146
Site (site 1)	−7.054	2.52	0.113

Whole-model test found Prob > ChiSq = 0.003; 27 plots were used for this analysis.
* Based on average of 2008 and 2009 growing season measurements.

Table 3. Ordinal regression for little bluestem transplant survival.

Term	*Estimate*	*Chi-square*	*Prob > ChiSq*
Canopy density*	−3.295	6.52	0.012
Silt: sand	0.468	0.67	0.412
Leaf litter	−0.778	10.88	0.001
Distance to edge	1.872	4.25	0.039
Site (site 1)	−0.090	0.06	0.808

Whole-model test found Prob > ChiSq = 0.0002; 27 plots were used for this analysis.
* Based on average of 2008 and 2009 growing season measurements.

Table 4. Ordinal regression for broomsedge transplant survival.

Term	*Estimate*	*Chi-square*	*Prob > ChiSq*
Canopy density*	−0.398	0.11	0.745
Silt: sand	−0.278	0.25	0.614
Leaf litter	−0.102	0.23	0.634
Distance to edge	−0.847	0.88	0.349
Site (site 1)	−0.152	0.25	0.614

Whole model test found Prob > ChiSq = 0.502; 27 plots were used for this analysis.
* Based on average of 2008 and 2009 growing season measurements.

sites that could have had an effect on survival (e.g. canopy density) or that were not highly correlated with canopy density were accounted for in the model (Table 3). In contrast to little bluestem, broomsedge transplant survival was not significantly related to any of the measured environmental variables (Table 4).

Discussion

Our results support the hypothesis that warm-season grasses occur where environmental conditions also favor the natural regeneration of oaks. Such patterns of co-occurrence corroborate historical anecdotal evidence that these grasses were a component of the understory of self-replacing woodlands dominated by fire-tolerant oaks in upland areas now dominated by closed-canopy hardwood forests. Currently in north Mississippi, conditions favoring oak regeneration and warm-season grasses are most likely to be found near persistent forest edges, since very little upland landscape in north Mississippi is subject to restoration. This method of associating the presence of species proposed to be present historically to conditions or species known to be present could potentially be used to strengthen anecdotal evidence in other ecosystems lacking quantitative understory data.

Successful restoration of any ecosystem depends on establishing the environmental conditions that favor desired target species. Although frequent burning and thinning at Strawberry Plains appear to have reduced litter amounts, the treatments so far have not dramatically decreased canopy density. Much of the observed variation in canopy density was related to differences present before implementation of the treatments. The thinning treatments were initially only implemented for species that were known to be uncommon as bearing/witness trees in upland portions of the landscape. However, the current densities of upland oaks and hickories not initially targeted for thinning exceed historical densities of these trees, as inferred from public land surveys (Brewer 2001). Therefore, a significant reduction in the proportion of sky obscured by canopy will require partial thinning of upland oaks and hickories. Such modifications to the thinning treatments are now underway at Strawberry Plains. These findings highlight the universal importance of quantifying restoration treatment effects on the target environmental conditions.

Litter removal did not appear to have a direct effect on transplant survival for either species, nor did it interact with canopy density (as expected) or any other variable to affect transplant survival. Despite the nonsignificant effects of litter removal or its interaction with canopy density on little bluestem, increased transplant survival of this species was nonetheless associated with lower pre-treatment litter amounts and more open canopies. This apparent discrepancy of finding no significant effect of litter removal yet pre-treatment litter amounts significantly affecting little bluestem survival may be explained by litter measurements capturing an aspect of leaf area index of the canopy not quantified by canopy density (proportion of sky obscured by canopy). Canopy density and litter depth together could have accounted for light interception by both the overstory and midstory. This suggests that thinning of the midstory (irrespective of the overstory) could increase light availability and success of little bluestem. The results also agree with Taft's (2009) argument that the density of trees greater than 5 cm dbh may provide a better indication of suitable environmental conditions for woodland species than canopy density.

An important caveat to the conclusion that the negative relationship between little bluestem survival and litter amounts resulted from a negative effect of canopy cover is that transplants might have benefited from fire. Repeated fires might have reduced litter amounts and increased survival of little bluestem, but the beneficial effect of fire on transplant survival might not have resulted from fire-mediated reductions in litter. Furthermore, for little bluestem to be successful in the long term, these upland forests will require thinning as well as burning to maintain the opened canopies.

The increased survival of little bluestem transplants under open canopies (including recent gaps in the forest interior) suggests that the positive natural association of little bluestem with forest edges (but not with recent gaps) is largely the result of high light levels at forest edges and a lag in colonization of recently thinned forest interiors. Neither grass species produces a persistent seed bank (Rabinowitz 1981; Leck & Leck 1998), so the reintroduction of these grasses will likely be necessary to expedite reestablishment. Once the light environment was accounted for, transplant survival was slightly greater away from edges. These findings suggest that little bluestem will survive better within forest interiors than at edges, provided the forest canopy is open enough to permit adequate light to reach to the forest floor.

In contrast to little bluestem, no environmental variables predicted survival of transplants of broomsedge. Although we currently lack an adequate explanation for these results, it is possible that transplants of broomsedge required a combination of soil disturbance and canopy openings for success. Broomsedge colonizes disturbed areas more readily than does little bluestem (Restrepo & Vitousek 2001; Brewer et al. in press). In our transplant experiment, we attempted to minimize the amount of soil disturbance near transplants. For restoration on large tracts of relatively undisturbed forest, little bluestem may prove to be a better transplant candidate.

As treatments implementing fire for restoration of oak forests increase throughout the eastern United States, we must consider not only how the in situ vegetation responds to restoration treatments but also how these treatments will affect attempts to reintroduce species displaced by fire suppression. It is possible that vegetation and ecosystem responses to fire may depend on the presence and abundance of species displaced by prolonged fire suppression. For example, forb responses to fire may depend on the abundance of warm-season grasses before the fire. Similarly, ecosystem properties such as fire intensity, nutrient responses to fire, and carbon storage likely depend on the abundance of warm-season grasses in the ground cover. If warm-season grasses are potentially an important component of this ecosystem, then current assumptions about which prescribed burning regimes are optimal for restoration may need to be reevaluated. A ground cover with a significant presence of warm-season grasses could enable land managers to safely expand the prescribed burning window to include growing season fires. Such an expansion could expedite restoration and provide managers with greater flexibility to respond effectively to constraints imposed by climate change, population growth, and the human–wildland interface.

Implications for Practice

- Closed-canopy upland forests resulting from decades of fire suppression in northern Mississippi will require reduction of overstory on-site species (e.g. oaks) in addition to midstory off-site species to approach historic tree densities and canopy cover.
- When evaluating the success of restoration treatments following prolonged fire suppression, practitioners should consider responses of both remnant species suppressed by shade and shade-intolerant species completely displaced by fire suppression, the latter of which are easily overlooked when reference sites are lacking.
- One shade-intolerant ground cover species that is frequently missing from fire-suppressed oak woodlands, *Schizachyrium scoparium*, does not rapidly recolonize sites following overstory thinning, which means that reintroduction will likely be critical to recovering populations of this important species.
- Although burning may directly benefit transplants of *S. scoparium* and will be necessary to maintain more open canopies for their continued success, the positive effects of burning are not simply the result of litter removal and thus will not be mimicked by raking or other mechanical fire-surrogate methods.

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