The perpetual forest: Using undesirable species to bridge restoration

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The perpetual forest: using undesirable species to bridge restoration

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Summary

1. Conversion of established forests of undesirable species composition or structure to a multi-age, native forest community is a common restoration goal. However, for some ecosystems, the complexity of multiple disturbances and biotic factors requires unique approaches to advance community development. We use the longleaf pine (*Pinus palustris* Miller) ecosystem as a model of such a restoration paradigm with an approach that utilizes the undesirable species as a functional or structural bridge to foster ecological processes.
2. In the conversion of adult slash pine (*Pinus elliottii* Engelm.) plantations to the biologically diverse longleaf pine forests that once dominated the south-eastern US Coastal Plain, we examine techniques for restoring and maintaining critical structural and functional components. Through partial and variable retention of the undesirable slash pine canopy, establishment of longleaf pine seedlings is facilitated, while maintaining fuels essential for prescribed fire, a necessary management practice for longleaf pine. Furthermore, we project that with subsequent fires, fine fuels and species richness will be encouraged in the ground cover, and with future slash canopy harvest, established longleaf pine seedlings will be released.
3. In this study, we present a statistical approach that examines the compositional movement of vegetation in restoration sites over time relative to the reference conditions that are also changing through time.
4. *Synthesis and applications*. Restoration efforts that remove undesirable species initially may actually hinder rather than facilitate restoration. Restoration of fire-maintained ecosystems in which the production of adequate fuels is an important consideration may require the retention of a portion of the existing canopy to provide fuels during the restoration process, even if the canopy is comprised of less preferred species. Individual species often provide similar structural features and influences on function within an ecosystem; thus, systems other than longleaf pine may also benefit from retention of the undesirable species through the restoration process. We conclude that a gradual approach to restoration may be advantageous when legacies of past management have altered complex ecological dynamics and promoted development along a successional pathway strongly differing from that of the reference conditions.

Key-words: canopy conversion, canopy gaps, canopy retention, longleaf pine, reference sites, restoration, species functional redundancy, species richness

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Introduction

Many restoration strategies begin with a direct, intensive course of action such as the re-establishment of historic abiotic or biotic factors. This often includes the promotion of natural disturbance regimes, amelioration of degraded substrate conditions or the removal of

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undesirable species followed by the introduction of desired species. Such strategies have been advanced by theories of successional processes and community assembly (Young *et al*. 2001; Suding *et al*. 2004), and have been effective in restoring communities in many cases (Luken 1990; Mitsch & Wilson 1996). However, conversion of established forests of undesirable species composition or structure to a multi-age, native forest community may benefit from a more gradual approach that utilizes the undesirable species as a functional or structural bridge to foster ecological processes. Even though an established stand may consist of undesirable species, such as non-natives or industrial timber plantings, the structural and functional attributes that have accrued over decades may be more similar to those of the targeted restored conditions than attributes of a clear-cut forest planted with seedlings of the desirable species.

Conventional techniques for forest stand conversion include harvesting a substantial portion of canopy trees to achieve a desirable density or age structure based on reference conditions (Aronson *et al*. 1993; Covington *et al*. 1997; Fulé, Covington & Moore 1997; Taylor 2004) or the complete removal of an undesired canopy species and replacement planting with the desired species (Frelich & Puettman 1999). However, in some cases the reassemblage of conditions that promote biologically diverse and sustainable forests is fostered by natural regeneration processes that may be coupled with disturbance regimes (Covington *et al*. 1997; Allen *et al*. 2002; Lindenmayer & Franklin 2002; Palik, Mitchell & Hiers 2002; Schulte *et al*. 2006). For example, in fire-dependent communities the production of adequate fuel is an important consideration (Waldrop, White & Jones 1992; Swetnam, Allen & Betancourt 1999; Covington *et al*. 2001; Provencher *et al*. 2001; Mitchell *et al*. 2006) that may require retaining a portion of the existing canopy to provide fuel during the restoration process, even if the canopy is comprised of less preferred species.

A relevant example of such a restoration paradigm in which an undesirable species is beneficial in the restoration process is in the conversion of plantations of adult slash pine, *Pinus elliottii* Engelm. to the biologically diverse longleaf pine, *P. palustris* Miller forests that once dominated the south-eastern US Coastal Plain (approximately 36 million ha) (Noss 1989). This species-rich and fire-dependent ecosystem is currently the focus of significant ecological restoration efforts throughout the region, but is of global concern with respect to sustaining biodiversity (Mitchell *et al*. 2006). In longleaf pine stands, the grass-dominated ground cover and the pine needle litter play a crucial role in providing fuel and carrying fire (Clewell 1989; Noss 1989). The replacement of natural stands of longleaf pines with short-rotation plantations of more densely planted slash pine or loblolly pine, *P. taeda* L. requires that sites are protected from fire, because these species are vulnerable to fire during the first decade of development (Dixon *et al*. 1984). Deliberate fire suppression to permit seedling establishment increases the growth and dominance of shrub and midstorey hardwoods and reduces grasses and forbs dramatically (Lemon 1949), thereby negatively impacting the abundance of fine fuel and ground cover diversity. Thus, the initial conditions for restoration to longleaf pine forests often include an abundance of woody plants in the understorey as a legacy of past management that must be considered in the conversion strategy.

The prevailing technique for converting commercially planted stands of slash or loblolly pines to longleaf pine forests on former longleaf pine sites is to remove canopy trees completely and plant longleaf seedlings (Jack, Mitchell & Pecot 2006). However, loss of the overstorey pine canopy results in release of hardwoods in the ground cover or midstorey, which then compete with the planted pine seedlings (McGuire *et al*. 2001). To counter these conditions, chemical or mechanical site preparation to remove woody plants is often used to release longleaf pine seedlings (Johnson & Gjerstad 2006), but this technique can impact conservation and restoration goals negatively through reduced ground cover recovery, as well as increased operational costs. Moreover, in addition to the increased abundance of woody species, the absence of pine needles and the decline in grass fuels diminishes the effectiveness of subsequent fire management. Consequently, the successive fire regimes necessary for longer-term forest processes to unfold are hindered by inadequate fine fuels. This is an important consideration for restoration goals focusing on conservation of the diverse ground cover of the longleaf pine forest, because floral diversity of these systems is maximized by fire return intervals of 1–3 years (Kirkman *et al*. 2001; Glitzenstein, Streng & Wade 2003).

Development of management options that conserve biodiversity for forests in general, and in longleaf pine ecosystems specifically, have been constrained by a lack of information on the interactive effects of multiple disturbances such as canopy disturbance and fire. We present such an approach using an adaptive management process in which we examine techniques for restoring and maintaining the structural and functional components that facilitate establishment of longleaf pine seedlings, wiregrass *Aristida stricta* Michx. (a dominant ground cover species that is especially pyrogenic) and a rich assemblage of other ground cover species. In this work, we examine how canopy species and structure affect light conditions, and then how modification of the canopy and hardwood midstorey affect restoration trajectories. Specifically, we: (1) provide an estimate of variation in light across a range of slash pine canopy retention treatments and contrast light environments across comparable retention gradients in longleaf pine forests; and (2) describe how canopy and midstorey hardwood restoration treatments influence ground cover species and pine seedling establishment.

Methods

STUDY AREA

The study area is located on Ichauway, a 115-km^2 privately owned property of the Joseph W. Jones Ecological Research Center, in Baker County, Georgia, USA (31°13′ N, 84°29′ W). Ichauway is situated in the Lower Coastal Plain and Flatwoods (LCPF) Province (McNab & Avers 1994). The study is part of an ongoing restoration project to convert a planted slash pine stand to a multi-aged, longleaf pine forest with a diverse native ground cover. The 142-ha slash pine plantation was established in 1939. Although the previous land-use history of the tract is not well-documented, available aerial photography (1938, black and white, USDA 371–21) show it to be in agricultural production prior to conversion to a forest plantation. Stand management included timber thinning between 1953 and 1957 (aerial photos, 1953, black and white, USDA 2 M-108; 1957, black and white, USDA 5T-18), thinning again between 1962 and 1968 (aerial photos, 1962, black and white, IDD-122, ASCS 3–63 DC, 1968 black and white, IKK-147, ASCS 1–69 DC) and prescription burns approximately every 5–8 years (L. Neel personal communication). Prior to initiation of the study, the canopy was widely spaced with an average basal area of 16 m^2 ha^{-1} and tree density of 123 stems ha^{-1}. Due to infrequent fire, pre-treatment conditions consisted of a dense hardwood midstorey composed of *Quercus nigra* L., *Quercus virginiana* Mill., *Sassafras albidum* (Nutt.) Nees., and *Diospyros virginiana* L. and an inconspicuous or nearly absent ground cover (Fig. 1). Following the initial restoration burn, numerous grass and forb species were present, although wiregrass was absent. The absence of this dominant perennial bunchgrass is indicative of previous agricultural land-use because of its characteristic decline with excessive soil disturbance and fire exclusion (Clewell 1989).

EXPERIMENTAL DESIGN

The experimental design has been described previously in Kirkman *et al*. (2004). We selected 12 reference sites to represent the benchmark restoration goal for the study area. These sites were selected based on the presence of vegetation associated characteristically with frequently burned longleaf pine–wiregrass ecosystems and with similar landscape position and soil type to that of the study area (Goebel *et al*. 2001). Wiregrass is considered a keystone species due to its regional dominance and its importance as a fuel source for proliferating surface fire in many longleaf pine ecosystems; thus, it was an important criterion for selection of reference sites. It is also indicative of sites with a history of very little to no soil disturbance. The reference sites have been burned on a 2–4-year return interval for the past seven decades to promote bobwhite quail, *Colinus virginianus* habitat. They are characterized by a canopy of widely spaced longleaf pine and ground cover dominated by wiregrass with numerous perennial forbs and other grasses as interstitial species (Goebel *et al*. 2001). These reference sites have been shown to exhibit both high species richness (> 20 species m^{-2}) and presence of endemic species that characterize the diverse ground cover of frequently burned longleaf pine sites (Kirkman *et al*. 2004).

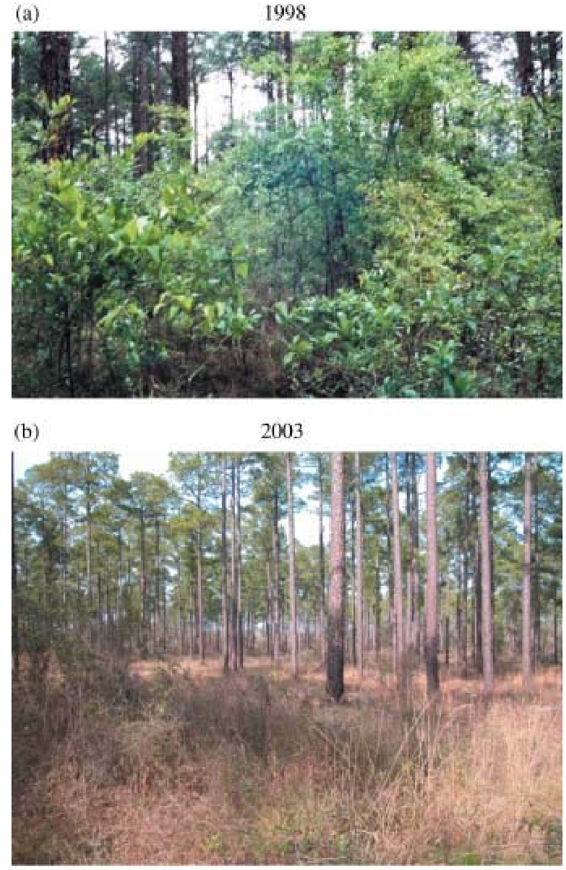

Fig. 1. Stand conditions of the same restoration plot before and after treatments: (a) in 1998, dominated by hardwoods in the understorey; (b) in 2003, following overstorey thinning and annual prescribed burning.

To examine the effects of overstorey and midstorey manipulations on successional trajectories, we used an experimental design in which overstorey canopy thinning treatments were nested within midstorey woody vegetation management. In March 1998, we established 18 100 × 100 m (1-ha) plots within the slash pine plantation. All plots were prescribed burned prior to initiation of the experiment between May and July 1998. Then, we assigned six plots randomly to each one of the following vegetation management treatments: herbicide, mowing or control (fire only). Subsequently, prescribed fire was used in all plots. Within each of the midstorey management treatment plots, we established three subplots, and assigned each to one of the following overstorey thinning treatments: high, medium or low basal area retention.

The herbicide treatment consisted of applying VELPAR (hexazinone) tablets at a rate of 3·0 kg ha^{-1} in May 1999 in a 5 × 5 m grid pattern over the entire plot to

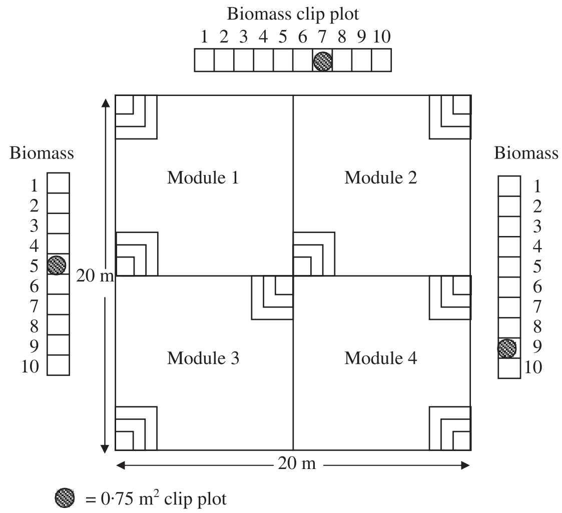

Fig. 2. Species richness was sampled in plots composed of four modules with subplots nested in two corners per module (0·1 m^2, 1 m^2 and 10 m^2 levels). Biomass of woody and herbaceous ground cover vegetation was sampled in randomly selected subplots located outside of each main vegetation sampling plot.

target midstorey hardwoods. The mowing treatment was conducted in November 1998 using a Brown Tree Cutter (Brown Manufacturing Corp., Ozark, AL, USA). In October 1999, we girdled (cut through the bark to the cambial layer) all large hardwoods in the mowing treatment with a chainsaw, and applied glyphosate to the cut surfaces. The overstorey was thinned in January 1999 using single-tree selection. Through variable retention of the basal area, we created three classes of canopy gaps (< 5 m^2 ha^{-1}, 5–9 m^2 ha^{-1} and > 9 m^2 ha^{-1}), designated as low, medium and high basal area subplots, respectively, within each of the 1-ha woody vegetation management treatment plots. Within each subplot, we established the following vegetation sampling plots: (a) 20×20 m species–area plot and (b) three 1×10 m biomass clip plots (Fig. 2).

Canopy gaps resulting from the overstorey thinning treatments were used to accommodate the establishment and growth of longleaf pine seedlings. Containerized longleaf pine seedlings were planted in the gaps after the initial burning and thinning of the stand at variable densities ranging from 450 to 1000 trees ha^{-1}. These rates corresponded to regeneration densities in natural stands (R. J. Mitchell, unpublished data). To re-establish wiregrass in the groundcover within the 400 m^2 species–area plots, we hand-dispersed seed in February 1999 (rate = approximately 260 g seed + bulk per plot). We obtained wiregrass seed by harvesting it from naturally occurring sites on Ichauway during the previous autumn.

VEGETATION SAMPLING

Species richness, understorey hardwood density and herbaceous ground cover biomass were assessed twice during the study: once prior to treatment installation in summer 1998 and again in summer 2003, 5 years post-treatment. We sampled vegetation composition (species richness) in the 20×20 m species–area plot using a nested quadrat sampling design adapted from Peet *et al.* (1998) (Fig. 2). Each subplot was divided into four 10×10 m modules. Within each module, we sampled vegetation in nested quadrats of 0·1 m^2, 1 m^2 and 10 m^2 from each of two corners and then in the 100 m^2 area, for a total of eight nested quadrats in each 20×20 m species–area plot. Species present in each module were identified and recorded.

In 1998 and 2003 we counted all woody stems within each 1×10 m biomass clip plot and assigned each stem to a height category of < 1 m, 1–2 m or > 2 m. We then randomly chose a 0·75 m^2 area (0·96 m diameter) in which all above-ground understorey/ground cover biomass was clipped and separated into forbs, grasses or woody plants. The samples were dried at 70 °C to a constant mass and weighed. Planted longleaf pine seedlings were assessed for survivorship 2 years post-planting.

LIGHT AVAILABILITY

We obtained hemispherical photographs in the centre of each subplot of the study area in summer 2003 using a Nikon Coolpix 5000 with a Nikon FC-E8 fisheye lens. To compare differences in light availability between longleaf pine canopies and slash pine canopies, we also obtained photographs from 54 sample locations in a 70–90-year-old, naturally regenerated longleaf pine forest of another study presented elsewhere (Battaglia *et al.* 2003; Palik *et al.* 2003). We acquired images in both forests during uniform sky conditions when the wind was minimal. In each location, the camera was installed on an aluminium, self-levelling mount at a height of 1·5 m above the ground and orientated due north. We also measured overstorey basal area using a one-factor wedge prism. The digital images were analysed using WinSCANOPY version 2004a (Régent Instruments, Quebec, QC, Canada), and gap fraction (as a measure of canopy openness) was calculated.

STATISTICAL ANALYSES

We aggregated ground cover species data within the hierarchical sampling structure to construct presence–absence data for specified plot sizes for both sampling dates. Species–area relationships were constructed for each 400 m^2 sampling plot by averaging the number of species for each plot size within the nested sampling structure. We examined species richness at multiple scales because of the importance of species packing (large number of species per unit area) as a restoration process over time in this species-rich ecosystem (Kirkman *et al.* 2004). Presence–absence data of the 1 m^2 plots were subjected to non-metric multidimensional scaling using 1 minus the Jaccard index. Dimensions resulting from the non-metric multidimensional scaling were treated as response variables in a multivariate response, general linear mixed-models analysis

(Wright 1998; Schabenberger & Pierce 2002) to accommodate the correlations induced by the hierarchical sampling scheme and for repeated sampling through time. Random effects of cluster observations made on the same woody vegetation treatments and on the same basal area treatments were included in the models. In addition, the multivariate analysis of variance (MANOVA) analysis was obtained using a multivariate structure for the residuals along with a no-intercept model with dummy variable coding for the multivariate dimensions (Wright 1998). We constructed multivariate contrasts to test simple effects within significant interactions. For verification of treatment effect on the directional change of restoration plots, we calculated Jaccard distances as an average distance of each restoration plot to all reference plots between 1998 and 2003. Positive values indicate movement toward the reference plots and negative values indicate movement away.

For species–area data, a first-order ante-dependence covariance structure (Macchiavelli & Arnold 1994) was imposed on the residuals to accommodate the hierarchical sampling structure including the accumulation of species with area sampled, and the concomitant inflation of variance as a function of area sampled. We used the Kenward–Roger (Kenward & Roger 1997) adjustment to the denominator degrees of freedom to improve estimation of all mixed-model test statistic P-values. All analyses were performed using SAS with mixed-models fit using PROC MIXED (SAS online documentation: http://support.sas.com/onlinedoc/913/docMainpage.jsp). The mixed-models approach was used because it is an iterative method that allows testing of both fixed effects and covariance components (Littell *et al*. 1996).

For the understorey hardwood stem density, ground cover biomass and light availability components of this study, we used a mixed-models analysis of variance. Stem density and biomass data were natural log-transformed to meet normality assumptions. We calculated mean hardwood density (by height class) and biomass (herbaceous, i.e. grasses and forbs and woody plants separately) by overstorey treatment. Significant treatment differences within and among variables were tested using a repeated-measures, mixed-models analysis. Specific contrasts were performed when statistical differences were detected.

We examined overstorey species differences (slash vs. longleaf pine) in the relationship between overstorey basal area and gap fraction using linear regression. We also examined the relationship between survivorship of planted longleaf pine seedlings and canopy light conditions with a linear regression.

Results

SPECIES RICHNESS AND COMPOSITION

Although a high floristic overlap occurred between restoration and reference sites, species richness of pine restoration plots was less than reference plots ($P < 0{\cdot}05$) at all sampling unit sizes (Fig. 3), both prior to (1998) and post-treatment (2003), with maximum difference in species at the 1 m^2 sampling unit size ($P < 0{\cdot}0001$; $P = 0{\cdot}0020$, respectively). No strong differences in species richness occurred in response to hardwood management treatments (mowing, herbicide or control) or overstorey basal area retention treatments (high, medium or low basal area) ($P = 0{\cdot}0948$, $F = 2{\cdot}41$). Because the entire fire-suppressed stand was burned prior to the application of experimental treatments, it is likely that the initial introduction of fire had a large impact on hardwood reduction and ground cover response that obscured response to the experimental treatments (Fig. 1).

Greater dissimilarity in species composition occurred between reference plots and restoration plots than within plot types based on presence–absence of species occurrence in ordination space. Non-metric multidimensional scaling ordination of species composition in 1998 and 2003 resulted in a four-dimensional solution, attained after 18 iterations (MDS badness-of-fit = 0·166). Dimension 1 accounted for 42% of the total variation and dimension 2 accounted for 21% of the variation in the data (Fig. 4). The ordination indicated a greater change in species composition (a larger number of species disappeared or were added) in restoration sites than reference sites between 1998 and 2003. Although species composition differences between restoration sites and reference plots occurred in both years (multivariate mixed models analysis; $P < 0{\cdot}0001$), these differences were greater in 1998 ($F = 73{\cdot}64$) than in 2003 ($F = 32{\cdot}43$), suggesting that restoration and reference sites became more alike over time. Similar results were obtained when the presence of wiregrass was excluded from the analyses, even though this species was introduced to all restoration plots (Table 1).

A positive change in average Jaccard distance (average distance of each restoration plot to all reference plots between 1998 and 2003) for 95% of the

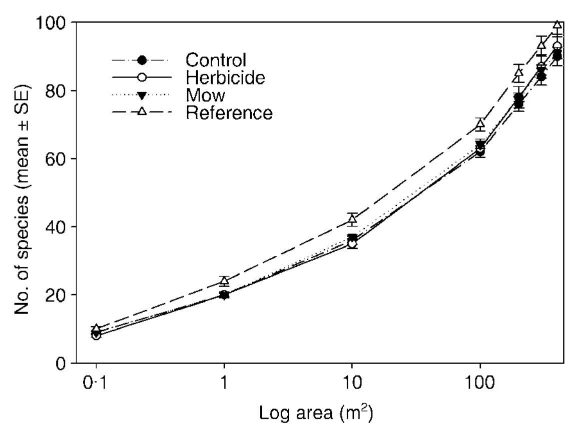

Fig. 3. Species–area relationship for reference and restoration plots in 2003 illustrates that species richness of reference plots is different ($P < 0{\cdot}05$) from restoration plots (herbicide, mow, control) at all sampling unit sizes.

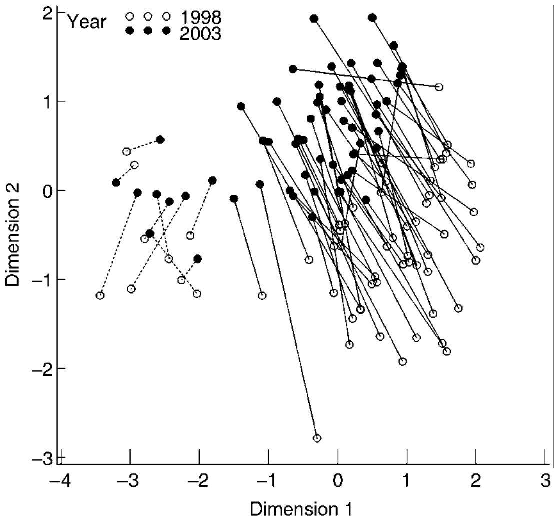

Fig. 4. Non-metric multidimensional scaling analysis of 1998 and 2003 presence–absence of occurrence data. Reference plots are represented by dashed lines (---) and slash pine restoration sites are represented by solid lines (—).

Table 1. Mixed models analysis test of fixed effects of mean species richness with wiregrass included and excluded in the analysis. Treatments include control (fire only), herbicide and mowing. Year includes 1998 (pretreatment) and 2003 (post-treatment). Asterisks denote significance at $\alpha = 0{\cdot}05$

	Tests of fixed effects			
	n.d.f.	d.d.f.	*F*	*P*
Wiregrass				
Treatment	12	37·2	26·11	< 0·0001*
Year	4	37·7	70·99	< 0·0001*
Treatment × year	12	70·6	3·21	0·0010*
No wiregrass				
Treatment	12	27	32·01	< 0·0001*
Year	4	21·8	63·96	< 0·0001*
Treatment × year	12	2·15	2·15	0·0332*

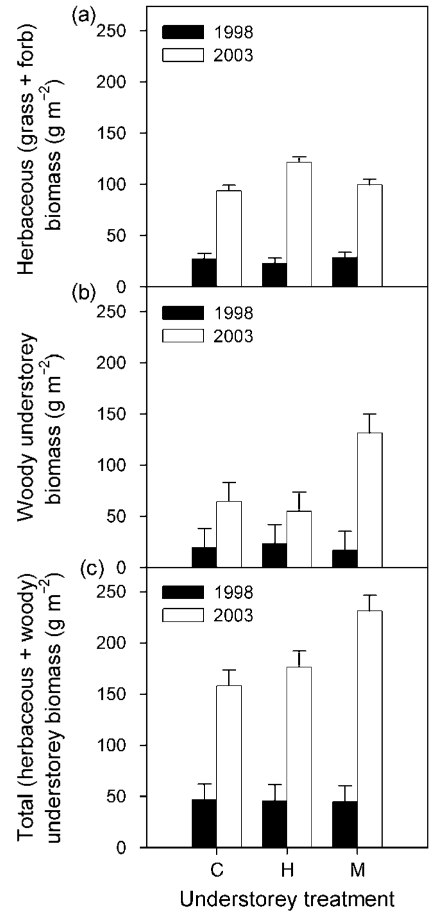

Fig. 5. Herbaceous above-ground biomass (a) increased most in the herbicide treatment, while the greatest increase in woody biomass (b) occurred in the mowing treatment over time. Total biomass (c) increased most in the mowing treatment, which is probably the result of the substantial increase in woody biomass. Understorey treatments represented by C (control), H (herbicide) and M (mowing).

restoration plots confirmed movement of vegetation composition toward reference conditions. This directional movement was not dependent on overstorey basal area treatments or vegetation management treatment effects (mixed models analysis; $P = 0{\cdot}5812$ and $P = 0{\cdot}9682$, respectively).

RELATIVE BIOMASS AND WOODY STEM COUNT

Total ground cover biomass (grasses, forbs and woody species) increased more than threefold across all overstorey retention ($P = 0{\cdot}0446$) and understorey treatments ($P = 0{\cdot}0383$) between 1998 and 2003 (Table 2). The rate of biomass accumulation increased with decreasing overstorey retention ($P = 0{\cdot}0011$). Among understorey treatments, total biomass was greatest in response to mowing ($P < 0{\cdot}0001$). For woody species only, the mowing treatment resulted in greater biomass response than with herbicide or control treatments ($P < 0{\cdot}0001$). However, for herbaceous species, biomass was greater with the herbicide treatment than either of the other treatments ($P < 0{\cdot}0001$) (Fig. 5). Overall, the results suggest a slight trend of increasing herbaceous: woody biomass ratio in the herbicide treatment ($P = 0{\cdot}0687$).

Total stem count of woody stems increased between 1998 and 2003 ($P < 0{\cdot}0001$) (Table 3). This increase was observed in the control understorey treatment (28% increase; $P = 0{\cdot}0004$) and most prominently in the mowed treatment (46% increase; $P < 0{\cdot}0001$), but no change occurred due to the herbicide treatment ($P = 0{\cdot}3608$) (Fig. 6). The increase in hardwood stems was predominantly in the 1–2 m height size class. The herbicide treatment eliminated nearly all the hardwood stems 2 m or greater in height ($P = 0{\cdot}0024$). Overstorey retention treatment did not affect hardwood stem counts strongly, although there was a trend of increasing hardwood stems between 1998 and 2003 in the low and medium overstorey retention treatments ($P = 0{\cdot}0796$).

Table 2. Mixed models repeated measures analysis tests of fixed effects of total understorey biomass (grasses, forbs, woody) for 1998 (pre-treatment) and 2003 (post-treatment). Woody vegetation management treatments (treatment) include control (fire only), herbicide, and mowing. Overstorey retention treatments (density) include low (L), medium (M), and high (H) basal area. Asterisks denote significance at α = 0·05

	Tests of fixed effects			
	n.d.f.	d.d.f.	*F*	*P*
Treatment	2	15·2	2·40	0·1247
Density	2	46·9	7·88	0·0011*
Year	1	21·7	155·42	< 0·0001*
Treatment × year	2	21·7	3·80	0·0383*
Density × year	2	66·6	3·26	0·0446*

	Contrasts of woody vegetation management treatments and overstorey retention treatments for 1998 and 2003			
	1998		2003	
Treatments	*t*	*P*	*t*	*P*
Control vs. herbicide	0·03	0·9742	–0·83	0·4106
Control vs. mowing	0·07	0·9418	–3·31	0·0023*
Herbicide vs. mowing	0·04	0·9676	–2·48	0·0188*
Basal area: L vs. M	0·07	0·9407	2·28	0·0255*
Basal area: L vs. H	0·14	0·8893	4·36	< 0·0001*
Basal area: M vs. H	0·07	0·9411	2·36	0·0213*

Table 3. Mixed models analysis tests of fixed effects for total stem count of woody stems. Stems increased between 1998 and 2003 and these increases were detected in the control and mowing treatments. Asterisks denote significance at α = 0·05

	n.d.f.	d.d.f.	*F*	*P*
Treatment	2	15·2	0·53	0·5997
Density	2	97·9	0·08	0·9246
Year	1	178	31·29	< 0·0001*
Treatment × year	2	178	4·60	0·0113*
Density × year	2	137	2·58	0·0796

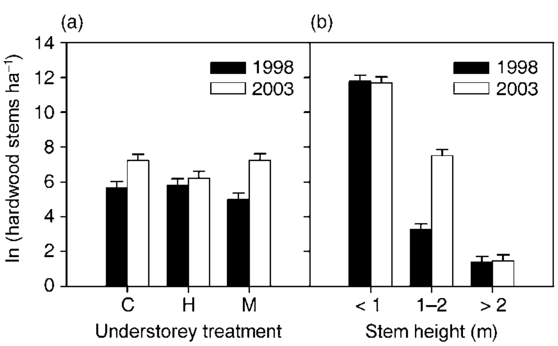

Fig. 6. (a) Hardwood stem density increased from 1998 to 2003 with the greatest change occurring in the mowing treatment ($P < 0{\cdot}0001$). Understorey treatments include control (C), herbicide (H) and mowing (M). (b) Hardwood stem density increased most in the 1–2 m height class ($P < 0{\cdot}0001$), while the other height classes (< 1 m and > 2 m) showed little change over time.

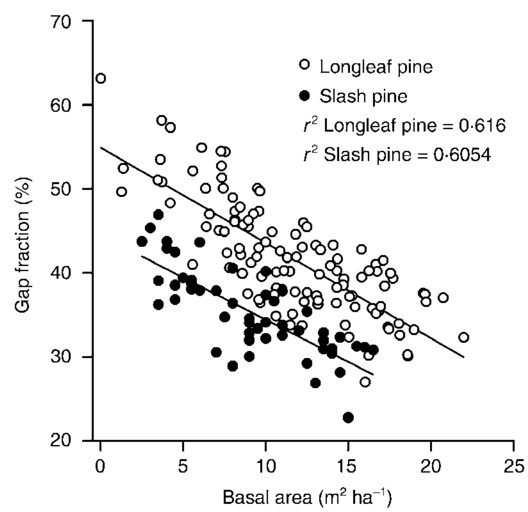

Fig. 7. Gap fraction increased with decreasing overstorey retention (basal area) and availability of light was higher in longleaf pine forests than in slash pine forests.

LIGHT AVAILABILITY AND SEEDLING RESPONSE

For both longleaf and slash pine canopies, light (expressed as percentage of gap fraction) increased with decreasing overstorey retention (basal area). However, this measure of light availability was consistently higher in longleaf pine forest stands than in slash pine stands for a given basal area ($P < 0{\cdot}0001$) (Fig. 7).

Longleaf pine seedling survival (2 years after planting) was relatively high across the range of basal area

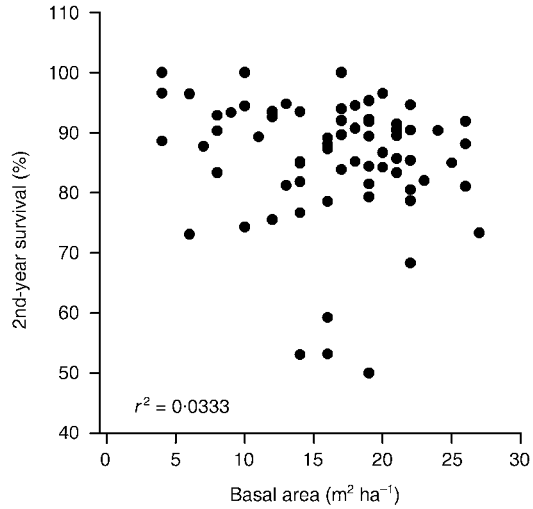

Fig. 8. Two-year survival of longleaf pine seedlings was similarly high across stocking conditions in the slash pine forest.

conditions (5–28 m^2 ha^{-1}) and did not vary as a function of stocking (P = 0·1251) (Fig. 8). During the course of the study, few planted longleaf seedlings emerged from the grass stage, a characteristic life stage lasting 1–10 years after germination during which no height growth occurs (Boyer 1993).

Discussion

Given the large-scale conversions of natural pinelands to pine plantations throughout the south-eastern United States, much of the restoration of the longleaf pine ecosystem will be focused upon sites where canopy conversion is a necessary part of the long-term process (Kirkman & Mitchell 2006). The vegetation change and seedling establishment results reported here indicate that retaining slash pine canopy with its gradual replacement to longleaf pine is an effective restoration strategy to promote the desired state of recovery, i.e. a multi-aged forest with a diverse, herbaceous, fire-maintained ground cover. Our adaptive management study does not include the extreme management treatments of burn exclusion or large-scale canopy harvest followed by aggressive application of herbicide or mechanical methods to control hardwood competition. Evidence from other studies indicates that such approaches may actually set back, rather than facilitate conservation goals (McGuire *et al.* 2001; Jack, Mitchell & Pecot 2006).

The need for multistep approaches to attain structural and functional attributes crucial to achieving a desired trajectory has been recognized for other ecosystems (Suding, Gross & Houseman 2004). In numerous cases, the reliance on successional recovery alone has been insufficient for restorative change because legacies of past management can divert ecological dynamics in degraded systems to very different paths from those of reference conditions (Bakker & Berendse 1999; Zedler & Callaway 1999; Anderson, Schwegman & Anderson 2000; Hardesty *et al.* 2000; van Auken 2000; many others). Thus, in some situations, restoration requires management that disrupts abiotic or biotic feedbacks that constrain the rate or direction of change in the degraded system (Young, Chase & Huddleston 2001; Mayer & Rietkerk 2004; Suding *et al.* 2004). This approach may be particularly important in a fire-maintained ecosystem such as longleaf pine where natural ecosystem processes, including pine regeneration, occur in a state of a perpetual forest with frequent low intensity fire, as opposed to forest types that naturally reassemble following stand replacing disturbances (Mitchell *et al.* 2005).

WOODY BIOMASS, FUELS AND ADVANCED REGENERATION

This study demonstrates how advanced regeneration can be established under an overstorey of mature slash pine while maintaining essential fuels for prescribed fire. The establishment of planted longleaf pine seedlings across a wide range of canopy conditions in this study is consistent with earlier findings of Mitchell *et al.* (2006) in which establishment conditions occur under canopy gap fractions greater than 30%. Greater seedling establishment is promoted in more open portions of the savanna because these areas tend to have less adult competition and lower fire intensity (Grace & Platt 1995; Palik *et al.* 1997, 2003; Mitchell *et al.* 2006). The absence of height initiation of planted seedlings beneath the canopy treatments during this study period was not surprising, because all the treatments in our study resulted in a gap fraction of less than 60%. Early growth of longleaf pine seedlings is controlled strongly and positively by light in canopy openings (Boyer 1993; Palik *et al.* 1997, 2003) and conditions sufficient for height initiation are observed only when canopy gap fraction exceeded 70% (Mitchell *et al.* 2006).

The degree of pine canopy cover also may have indirect effects on longleaf pine seedling growth through the release of woody understorey plants and the accumulation of fuels necessary to control hardwood encroachment. The significant, but modest, response differences in hardwood encroachment due to canopy retention in this study was due to the conservative range of basal area conditions of the treatments (all less than 50% canopy gap fraction). However, in other timber harvests in natural longleaf pine stands with greater than 70% gap fraction, a much greater increase in hardwood growth through reduction of below-ground competition has been reported (McGuire *et al.* 2001; Jack, Mitchell & Pecot 2006). Consequently, if increased resources in large overstorey gaps are pre-empted by established woody understorey plants, seedling growth may be diminished through competition with the understorey vegetation (Pessin 1938, 1939; Pecot *et al.* in press). Furthermore, the loss of litterfall fuel with canopy removal may have important negative feedback consequences for controlling hardwood encroachment (Williamson & Black 1981), particularly in the absence of wiregrass (Hendricks, Wilson & Boring 2002). Thus, overstorey removal resulting in large openings without advanced regeneration of longleaf pine can release hardwoods that eventually dominate the site and potentially jeopardize the long-term option of perpetuating the stand through frequent prescribed fire.

LIGHT AVAILABILITY AND CANOPY RETENTION

In this study, the differences in light availability to the understorey and ground cover between longleaf pine and slash pine canopies for a given basal area suggest that optimal stocking densities for canopy retention may differ for the two species. Canopy gap fraction has been shown to be strongly correlated with and is an unbiased predictor of seasonal light availability to the understorey (Battaglia *et al*. 2003). Arguably, because canopy gap fraction is greater for longleaf pine than for slash pine, the basal area retained during thinning of slash pine might be less than that necessary to achieve similar canopy conditions in a longleaf pine stand. However, inherent differences in the fuel quality of slash and longleaf may argue otherwise (Fonda 2001). A comparison of burning characteristics of a southern Florida variety of slash pine (*P. elliottii* var. *densa*) and longleaf pine needles found that this variety of slash pine was somewhat less flammable than those of longleaf pine. South Florida slash pine has life-history and leaf characteristics more similar to that of longleaf pine than the more northern variety, *P. elliottii* var. *elliottii*. Consequently, the difference in fuel qualities may be even greater between longleaf pine and the northern variety of cul-tivated slash pine. Thus, fuel consideration may require that more basal area of slash pine be retained than in a comparable longleaf pine stand.

VEGETATION CHANGE

Although we did not find differences in plant species richness or compositional change due to canopy retention or woody vegetation management treatments, the aggressive use of prescribed fire and overall canopy thinning resulted in plant communities in the restoration plots that resemble reference sites more closely after 5 years. One underlying reason for the increased similarity is clearly due to the introduction and establishment of wiregrass in all plots. However, the directional change in restoration plots toward reference plots when wiregrass is excluded from the analysis was not driven strongly by a single species response, but by the addition and deletion of more species in the restoration sites than in the reference sites.

The increase rather than decrease of woody biomass in response to mowing suggests that not only is this treatment ineffective in reducing abundance of woody cover, but it may actually serve to increase hardwood encroachment, especially when used in the absence of a subsequent herbicide treatment of resprouting woody vegetation. Substantial changes in species richness or composition in response to hardwood reduction may not become apparent for many years and numerous successive fire events, if ever. Our findings of vegetation response are similar to other short-term studies in which mechanical or chemical treatments were used in combination with burning to reduce hardwood encroachment (Kush, Meldahl & Boyer 1999; Provencher *et al*. 2001). However, Brockway & Outcalt (2000) report a stronger response in reduction of hardwoods following the use of broadcast or spot application of hexazinone. If a more aggressive rate of hexazinone application or greater canopy removal had been employed in our study, differences in treatment responses would probably be more dramatic over a shorter period.

Conclusion

Based on the findings of this study, coupled with knowledge of the complex interactions of fire, fuels and biotic components of the longleaf pine ecosystem, we recommend that a variable canopy retention approach be used as a restoration alternative to clearcuts in the conversion of single-age slash pine plantations to a multi-age longleaf pine savanna. The establishment of longleaf pine seedlings as advanced regeneration, which will be released in the next timber harvest, is a method to maintain pine cover for needle cast for fuel. Retention of the forest canopy during the restoration process allows the use of the undesirable species as a functional surrogate for fuels. This effort, coupled with wiregrass establishment, will help to provide the fuels necessary for the frequent prescribed fires that are essential for hardwood control and for encouraging the development of an abundance of other fine fuels and diversity in the ground cover. The use of an undesirable species as a structural or functional bridge to foster ecological processes during restoration may be an appropriate strategy for other ecosystems. However, evaluating the suitability of retaining an undesirable species as a temporary surrogate will require a keen understanding of the natural history and disturbance complexities of the particular ecosystem.

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References

Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M. & Klingel, J.T. (2002) Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications*, **12**, 1418–1433.

Anderson, R.C., Schwegman, J.E. & Anderson, M.R. (2000) Micro-scale restoration: a 25 year history of a southern Illinois barrens. *Restoration Ecology*, **8**, 296–306.

Aronson, J., Floret, C., Le Floc'h, E., Ovalle, C. & Pontanier, R. (1993) Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands. I. A view from the south. *Restoration Ecology*, **7**, 8–17.

van Auken, O.W. (2000) Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics*, **31**, 197–215.

Bakker, J.P. & Berendse, F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution*, **14**, 63–68.

Battaglia, M.A., Mitchell, R.J., Mou, P.O. & Pecot, S.D. (2003) Light transmittance estimates in a longleaf pine woodland. *Forest Science*, **49**, 752–762.

Boyer, W.D. (1993) Long-term development of regeneration under pine seedtree and shelter wood stands. *Southern Journal of Applied Forestry*, **17**, 10–15.

Brockway, D.G. & Outcalt, K.W. (2000) Restoring longleaf pine wiregrass ecosystems: hexazinone application enhances effects of prescribed fire. *Forest Ecology and Management*, **137**, 121–138.

Clewell, A.F. (1989) Natural history of wiregrass (*Aristida stricta* Michx., Gramineae). *Natural Areas Journal*, **9**, 223–233.

Covington, W.W., Fulé, P.Z., Hart, S.C. & Weaver, R.P. (2001) Modeling ecological restoration effects on ponderosa pine forest structure. *Restoration Ecology*, **9**, 421–431.

Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S. & Wagner, M.R. (1997) Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry*, **95**, 23–29.

Dixon, W.N., Corneil, J.A., Wilkinson, R.C. & Foltz, J.L. (1984) Using stem char to predict mortality and insect infestation of fire-damaged slash pines. *Southern Journal of Applied Forestry*, **8**, 85–88.

Fonda, R.W. (2001) Burning characteristics of needles from eight pine species. *Forest Science*, **47**, 390–396.

Frelich, L. & Puettman, K. (1999) Restoration ecology. *Maintaining Biodiversity in Forest Ecosystems* (ed. M. Hunter), pp. 499–524. Cambridge University Press, Cambridge, UK.

Fulé, P.Z., Covington, W.W. & Moore, M.M. (1997) Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications*, **7**, 895–908.

Glitzenstein, J.S., Streng, D.R. & Wade, D.D. (2003) Fire frequency effects on longleaf pine (*Pinus palustris* Miller) vegetation in South Carolina and Northeast Florida, USA. *Natural Areas Journal*, **23**, 22–37.

Goebel, P.C., Palik, B.J., Kirkman, L.K., West, L., Drew, M.B. & Pederson, D.C. (2001) Forest ecosystems of a lower gulf coastal plain landscape: multifactor classification and analysis. *Journal of the Torrey Botanical Society*, **128**, 47–75.

Grace, S.L. & Platt, W.J. (1995) Effects of adult tree density and fire on the demography of pre-grass stage juvenile longleaf pine (*Pinus palustris* Mill.). *Journal of Ecology*, **83**, 75–86.

Hardesty, J., Adams, J., Gordon, D. & Provencher, L. (2000) Simulating management with models. *Conservation Biology Practice*, **1**, 26–31.

Hendricks, J.J., Wilson, C.A. & Boring, L.R. (2002) Foliar litter position and decomposition in a fire-maintained longleaf pine-wiregrass ecosystem. *Canadian Journal of Forest Research*, **32**, 928–941.

Jack, S.B., Mitchell, R.J. & Pecot, S.D. (2006) Silvicultural alternatives in a longleaf pine/wiregrass woodland in southwest Georgia: understorey hardwood response to harvest-created gaps. *Proceedings of the 13th Biennial Southern Silvicultural Research Conference, February 28–March 3, 2005, Memphis, TN* (ed. K.F. Conner), pp. 85–87. General Technical Report. Southern Research Station, USDA Forest Service, Asheville, NC.

Johnson, R. & Gjerstad, D. (2006) Restoring the overstorey of longleaf pine ecosystems. *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration* (eds S. Jose, E.J. Jokela & D.L. Miller). Springer, New York, NY.

Kenward, M.G. & Roger, J.H. (1997) Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics*, **53**, 983–997.

Kirkman, L.K., Coffey, K.L., Mitchell, R.J. & Moser, E.B. (2004) Ground cover recovery patterns and life-history traits: implications for restoration obstacles and opportunities in a species-rich savanna. *Journal of Ecology*, **92**, 409–421.

Kirkman, L.K. & Mitchell, R.J. (2006) Conservation management of *Pinus palustris* ecosystems from a landscape perspective. *Applied Vegetation Science*, **9**, 67–74.

Kirkman, L.K., Mitchell, R.J., Helton, R.C. & Drew, M.B. (2001) Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany*, **88**, 2119–2128.

Kush, J.S., Meldahl, R.S. & Boyer, W.D. (1999) Understorey plant community responses after 23 years of hardwood control treatments in natural longleaf pine (*Pinus palustris*) forests. *Canadian Journal of Forest Research*, **29**, 1047–1054.

Lemon, P.C. (1949) Successional responses of herbs in the longleaf-slash pine forest after fire. *Ecology*, **30**, 135–145.

Lindenmayer, D.B. & Franklin, J.F. (2002) *Conserving Forest Biodiversity – a Multi-Scaled Approach*. Island Press, Washington, DC.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute, Cary, NC.

Luken, J.O. (1990) *Directing Ecological Succession*. Chapman & Hall, London, UK.

Macchiavelli, R.E. & Arnold, S.F. (1994) Variable order antedependence models. *Communications in Statistics – Theory and Methods*, **23**, 2683–2699.

Mayer, A.L. & Rietkerk, M. (2004) The dynamic regime concept for ecosystem management and restoration. *Bioscience*, **54**, 1013–1020.

McGuire, J.P., Mitchell, R.J., Moser, E.B., Pecot, S.D., Gjerstad, D.H. & Hedman, C. (2001) Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understorey response to tree removal in longleaf pine savannas. *Canadian Journal of Forest Research*, **31**, 765–778.

McNab, W.H. & Avers, P.E. (1994) *Ecological Subregions of the United States: Section Descriptions*. Administrative Publication WO-WSA-5. United States Department of Agriculture Forest Service, Washington, DC.

Mitchell, R.J., Franklin, J.F., Palik, B.J., Kirkman, L.K., Smith, L.L., Engstrom, R.T. & Hunter, M.L. Jr (2005) *Natural Disturbance-Based Silviculture for Restoration and Maintenance of Biological Diversity*. National Commission on Science for Sustainable Forestry, Washington, DC. Available at: http://ncseonline.org/NCSSF/cms.cfm?id=425 #synthesis (accessed June 2006).

Mitchell, R.J., Hiers, J.K., O'Brien, J.J., Jack, S.B. & Engstrom, R.T. (2006) Silviculture that sustains: the nexus between silviculture, frequent prescribed fire and conservation of biodiversity in longleaf pine forests of the southeastern United States. *Canadian Journal of Forest Research*, **36**: 2724–2736.

Mitsch, W.J. & Wilson, R.F. (1996) Improving the success of wetland creation and restoration with know-how, time, and self-design. *Ecological Applications*, **6**, 77–83.
Noss, R.F. (1989) Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Natural Areas Journal*, **9**, 211–213.
Palik, B.J., Mitchell, R.J. & Hiers, J.K. (2002) Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. *Forest Ecology and Management*, **155**, 347–356.
Palik, B.J., Mitchell, R.J., Houseal, G. & Pederson, N. (1997) Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. *Canadian Journal of Forest Research*, **27**, 1458–1464.
Palik, B.J., Mitchell, R.J., Pecot, S.D., Battaglia, M.A. & Pu, M. (2003) Spatial distribution of overstorey retention influences resources and growth of longleaf pine seedlings. *Ecological Applications*, **13**, 674–686.
Pecot, S.D., Mitchell, R.J., Palik, B.J., Moser, E.B. & Hiers, J.K. (in press) Competitive responses in longleaf pine woodlands: above and below ground effects on seedlings and understorey plants. *Canadian Journal of Forest Research*, in press.
Peet, R.K., Wentworth, T.R. & White, P.S. (1998) A flexible multipurpose method for recording vegetation composition and structure. *Castanea*, **63**, 262–274.
Pessin, L.J. (1938) The effect of vegetation on the growth of longleaf pine seedlings. *Ecological Monographs*, **8**, 115–149.
Pessin, L.J. (1939) Density of stocking and character of ground cover as factors in longleaf pine reproduction. *Journal of Forestry*, **37**, 255–258.
Provencher, L., Herring, B.J., Gordon, D.R., Rodgers, H.L., Galley, K.E.M., Tanner, G.W., Hardesty, J.L. & Brennan, L.A. (2001) Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. *Restoration Ecology*, **9**, 13–27.
Schabenberger, O. & Pierce, F.J. (2002) *Contemporary Statistical Models for the Plant and Soil Sciences*. CRC Press, Boca Raton, FL.
Schulte, L.A., Mitchell, R.J., Hunter, M.L. Jr, Franklin, J.F., McIntyre, R.K. & Palik, B.J. (2006) Evaluating the conceptual tools for forest biodiversity conservation. *Forest Ecology and Management*, **232**, 1–11.
Suding, K.N., Gross, K.L. & Houseman, G.R. (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*, **19**, 46–53.
Swetnam, T.W., Allen, C.D. & Betancourt, J.L. (1999) Applied historical ecology: using the past to manage for the future. *Ecological Applications*, **9**, 1189–1206.
Taylor, A.H. (2004) Identifying forest reference conditions on early cut-over lands, Lake Tahoe Basin, USA. *Ecological Applications*, **14**, 1903–1920.
Waldrop, T.A., White, D.L. & Jones, S.M. (1992) Fire regimes for pine–grassland communities in the southeastern United States. *Forest Ecology and Management*, **47**, 195–210.
Williamson, G.B. & Black, E.M. (1981) High temperature of forest fires under pines as a selective advantage over oaks. *Nature*, **293**, 643–644.
Wright, S.P. (1998) Multivariate analysis using the MIXED procedure. Paper 229. *Proceedings of the Twenty-Third Annual SAS Users Group International Conference*. SAS Institute, Cary, NC. Available at: http://www2.sas.com/proceedings/sugi23/Stats/p229.pdf. Accessed January 2006.
Young, T.P., Chase, J.M. & Huddleston, R.T. (2001) Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration*, **19**, 5–18.
Zedler, J.B. & Callaway, J.C. (1999) Tracking wetland restoration: do mitigation sites follow desired trajectories? *Restoration Ecology*, **7**, 69–73.

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