Competitive responses of seedlings and understory plants in longleaf pine woodlands: separating canopy influences above and below ground

Stephen D. Pecot, Robert J. Mitchell, Brian J. Palik, E. Barry Moser, and J. Kevin Hiers

Abstract: A trenching study was used to investigate above- and below-ground competition in a longleaf pine (*Pinus palustris* P. Mill.) woodland. Trenched and nontrenched plots were replicated in the woodland matrix, at gap edges, and in gap centers representing a range of overstory stocking. One-half of each plot received a herbicide treatment to remove the understory. We monitored pine survival and growth, understory productivity, light level (gap fraction), and soil resources. The overstory facilitated pine seedling survival. Pine seedling growth was reduced as overstory stocking increased. Reduced growth of seedlings was also observed in gaps when the understory was left intact. Understory plants competed with seedlings by filling the root gaps that developed as a result of overstory disturbance. Hardwood growth increased in gaps, owing to decreased belowground competition with adult pines, while growth of herbaceous plants and pine seedlings increased with light availability. Large overstory gaps are not required to initiate regeneration in longleaf pine woodlands. Retaining overstory dispersed throughout the stand but variable in density, through single-tree selection approaches, may be an alternative to gap-based approaches. This approach would allow for the fuel continuity needed to sustain the frequent fire required to maintain the diversity characteristic of this type of woodland.

Résumé : Un dispositif de tranchées a été utilisé pour étudier la compétition aérienne et souterraine dans une station forestière dominée par le pin des marais (*Pinus palustris* P. Mill.). Des placettes avec ou sans tranchées ont été répétées dans une matrice forestière, en bordure de trouées et au centre de trouées, ce qui correspondait à un gradient de densité relative du couvert. La moitié de chaque placette a été traitée à l'aide d'un herbicide pour éliminer les plantes du sous-étage. Nous avons suivi la survie et la croissance des pins, la productivité des plantes du sous-étage, la lumière (ouverture du couvert) et les ressources du sol. Les ouvertures dans le couvert dominant ont augmenté le taux de survie des semis de pin. La croissance des semis de pin a été réduite par une augmentation de la densité relative du couvert dominant. Une diminution de la croissance des semis a aussi été observée dans les trouées où les plantes de sous-étage n'avaient pas été éliminées. Les plantes du sous-étage venaient en compétition avec les semis en comblant les espaces exempts de racines qui sont apparus après la perturbation de l'étage dominant. La croissance d'espèces feuillues a augmenté dans les trouées à la suite d'une diminution de la compétition racinaire avec les pins adultes, alors que les plantes herbacées et les semis de pin ont augmenté leur croissance avec une augmentation de la disponibilité de la lumière. Les grandes trouées dans le couvert dominant ne sont pas nécessaires pour l'établissement de la régénération dans les stations forestières dominées par le pin des marais. Le maintien d'un couvert dispersé à travers le peuplement, mais de densité variable, à l'aide d'une approche de jardinage par pied d'arbre peut constituer une solution de remplacement aux approches basées sur les trouées. Cette approche favoriserait la production régulière des combustibles nécessaires pour soutenir les feux fréquents requis pour maintenir la diversité caractéristique de ce type de forêt.

[Traduit par la Rédaction]

Introduction

The extent to which competition and facilitation regulate the structure of woodlands in general, and longleaf pine (*Pinus palustris* P. Mill.) – wiregrass (*Aristida stricta* Michx.) woodlands in particular is not well understood. The mechanisms regulating seedling growth and survival in longleaf pine woodlands have been the subject of recent debate (Brockway and Outcalt 1998; McGuire et al. 2001; Palik et al. 2003) and have given rise to opposing views of

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adult–juvenile interactions. The first view, which we refer to as the hypothesis of belowground competitive seedling exclusion, suggests that survival of naturally regenerated longleaf pine seedlings (those not exhibiting height growth) in sandhill ecosystems is largely controlled by competition with adult pines' root systems, resulting in a seedling competitive exclusion zone extending 12–16 m from the adults (Brockway and Outcalt 1998). This hypothesis is based on observations that light levels were not correlated with seedling growth or survival response. It was speculated that overstory competition for soil moisture was high owing to the xeric nature of the soil and the density of pine roots within 15 m of mature trees relative to their density in areas of lower overstory abundance. However, no measures of soil moisture or seedling water stress were reported.

The second view of adult–juvenile interactions in longleaf pine woodlands, which we call the hypothesis of light-limited seedling response, is based on recent reports suggesting that growth of longleaf pine seedlings is largely related to light availability. Abundance of adult longleaf pine strongly influences the variation in the amount of light reaching the understory, both spatially (Battaglia et al. 2002; McGuire et al. 2001; Palik et al. 1997, 2003) and temporally (Battaglia et al. 2003). Belowground gaps that develop as a result of disturbance to the overstory, however, have been reported to be indistinct and ephemeral (Jones et al. 2003). This is due, in part, to the growth response of established understory (both herbaceous and woody) filling the root zone of seedlings and preempting access to available resources (McGuire et al. 2001). Though seedling growth has been reported to be controlled by competition for light, some studies report that survival is minimally facilitated by the overstory (Allen 1954; McGuire et al. 2001; Rodríguez-Trejo et al. 2003).

Both views speak to how the overstory might influence competition with seedlings, but no study directly addresses the mechanisms of competition and the importance of the understory in mediating seedling survival and growth responses. Moreover, the various views of competition lead to different implications for managing longleaf pine woodlands. The belowground seedling exclusion view mandates gap-based approaches (Brockway et al. 2005) because seedlings are unable to establish without the complete removal of adult trees. This has led to recommendations of clearings for group selections of up to 2 ha (Brockway et al. 2005). Since these gaps have fuel characteristics very different from those of the forest matrix, difficulties in applying prescribed fire can be exacerbated (Mitchell et al. 2006). The light-limited seedling response sees the forest as a continuum of light conditions in which seedlings respond to varying light availability (Pecot et al. 2005). In this scenario a portion of the stand has little to no seedling establishment (gap fraction (GF) 30% or less) because of low light availability, slowing growth such that seedlings do not survive the first fire. The largest portion of the stand has enough light (GF 30%–60%) for regeneration to establish, but growth is limited. These seedlings stay in the grass stage as advanced regeneration that can be released upon future disturbances. Lastly, the portion of the stand where GF exceeds 60% allows for the establishment and accelerated growth of longleaf pine seedlings (Mitchell et al. 2006). This allows for single-tree selection approaches that view the forest as continuous over time and space (Mitchell et al. 2006). The perpetual forests created using single-tree selection allow for forest influences to regulate forest dynamics, such as fuels able to sustain a 1- to 3-year fire-return interval, but forests are continually renewed through regeneration within the woodland matrix rather than in areas where the influence of adult pines is absent (Mitchell et al. 2006).

Understanding how overstory structure regulates forest dynamics, particularly the extent to which above- and below-ground competition (*i*) restricts the establishment and growth of seedlings and (*ii*) influences understory plant communities (such as herbaceous plants and hardwood seedlings) that grow with establishing seedlings, is critical to resolving which of these competing hypotheses is correct. Trenched plots have been used to empirically differentiate above- and below-ground interactions, providing a more direct means of testing the contrasting views concerning ecological controls on regeneration. Frequently burned longleaf pine woodlands are composed primarily of two distinct plant growth forms: a discontinuous layer of trees in the overstory and a continuous understory layer of grasses, forbs, and hardwood trees and shrubs kept at low stature (Jacqmain et al. 1999; Scholes and Archer 1997). It has been suggested that these two layers respond differently to belowground resources. Thus, these systems provide a good model for testing differences between above- and below-ground competitive effects and responses.

Water use by the various growth forms is hypothesized to vary because of different rooting depths (Walter 1971). For example, when burned frequently (1- to 3-year burn interval), longleaf pine woodlands typically consist of a monotypic overstory of longleaf pine and an understory comprising dominant C_4 bunchgrasses (wiregrass, *Andropogon* spp., *Schizachyrium* spp., and *Panicum* spp.) and co-occurring herbaceous species, as well as woody plants (*Quercus* spp., *Diospyros* spp., and *Sassafras* spp.) (Glitzenstein et al. 1995; Kirkman et al. 2001; McPherson 1997). If soil niche differentiation exists between woody and herbaceous plants in woodlands, we would expect that overstory tree removal to result in an increase in herbaceous plant biomass, mostly through increases in light availability. The opposite should be true for understory woody plants, i.e., decreased root competition will have a stronger effect than increased light availability if woody plants are more shade-tolerant but more deeply rooted than their herbaceous counterparts. The pine seedling growth and survival response should therefore be determined, in part, by the understory response to overstory removal, i.e., the increase in growth of the understory herbaceous and woody components may fill root gaps created by the overstory disturbance (McGuire et al. 2001).

Soil trenching is a field-based approach that can directly isolate mechanisms of plant–plant interactions (Coomes and Grubb 2000; Lewis and Tanner 2000; Toumey 1929). With trenching, belowground competition is removed but aboveground competition for light persists. We carried out an experiment using trenching and understory removal to better understand the influence of above- and below-ground competition on longleaf pine regeneration across a gradient of overstory longleaf pine. The regeneration response is related not only to competitive interaction from adult pines, but also

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to the resource-capturing ability of understory plants (Mitchell et al. 1999*b*). To investigate this, we examined the response of longleaf pine seedlings in the presence and absence of understory vegetation within our trenching experiment.

In this experiment we tested the following hypotheses: (1) facilitation by the overstory has a stronger influence on survival of longleaf pine seedlings than competition for water, (2) shallow-rooted shade-intolerant herbaceous plants respond positively to increases in light, whereas deep-rooted shade-tolerant understory hardwoods respond mostly to the removal of overstory belowground competition, and (3) in the absence of understory vegetation, growth of longleaf pine seedlings is related to light level and availability of soil N, and when the understory is left intact, belowground gaps are filled rapidly by the understory, so longleaf pine seedling growth is related to light only.

Materials and methods

Study site and experimental approach

The research was conducted at the Joseph W. Jones Ecological Research Center, a 115 km^2 reserve located in southwestern Georgia in the Coastal Plain region of the southeastern United States. The climate is subtropical with mean daily temperatures ranging from 11 to 27 °C. Annual precipitation averages 1320 mm/year and is typically distributed evenly throughout the year. Soils at the study site are of the Wagram series, a loamy, kaolinitic, thermic Arenic Kandiudult. The site is dominated in the overstory by 70- to 90-year-old cutover longleaf pine. The canopy of the longleaf pine woodland in this study is inherently open, with basal areas ranging from 0 to over 30 m^2/ha (mean 12 m^2/ha). The understory is largely composed of wiregrass, but other C_4 grasses, herbs, and woody (*Quercus* spp.) plants contribute to the species-rich ground cover (Kirkman et al. 2001). Frequent prescribed burning for more than 60 years has maintained a woodland structure, where deciduous trees and shrubs are low in stature and associated with understory vegetation. During this experiment the entire treatment area was burned in January of 1998, 2000, and 2002.

Treatment plots

This work is part of a larger study, begun in October 1997, which was described previously (Battaglia et al. 2002, 2003; Jones et al. 2003; Palik et al. 2003). For the present study, only the nonharvest and large-group (0.2 ha circular gaps) treatment areas were used.

After the overstory tree harvest in the larger study, all remaining trees were surveyed into Universal Transverse Mercator (UTM) coordinates in a GIS. We overlaid a 1 m × 1 m grid and quantified overstory competition at each intersection using an overstory abundance index (OAI), a distance-weighted measure of basal area within a circumscribed area (Jones et al. 2003; Palik et al. 2003; Stoll et al. 1994):

$$[1] \qquad \mathrm{OAI} = \sum_{i=1}^{n} A/d$$

where OAI is measured in square centimetres per square metre but is typically expressed as a dimensionless value, A is the cross-sectional area of tree i (cm^2), and d is the distance (m) of tree i from the grid point; d was constrained to be no less than 1 m to prevent giving undue weight to trees in very close proximity to the sampling point. OAI is a better index of overstory competitor abundance than basal area because it gives greatest weight to trees most likely to compete with a target plant (Stoll et al. 1994). We chose 15 m as the radius of our circumscribed area (Jones et al. 2003; Palik et al. 2003), since most plant responses to the overstory effects of longleaf pine have been observed within that distance (Brockway and Outcalt 1998; McGuire et al. 2001).

Our experiment consisted of a complete randomized block, split-split plot design with three replicates (Table 1). In each replicate we established ten 8 m^2 plots (4 m × 2 m) along north–south transects (Fig. 1). The first transect (five plots) was established through a randomly selected 0.2 ha overstory gap, starting at the intact (uncut) woodland matrix and encompassing the southern gap edge, gap center, northern gap edge, and intact matrix. The second transect (five plots) was established by randomly selecting a starting point in the nonharvest-treatment area and spacing plots similarly to those in the gap. A trench was dug around the perimeter of each plot to 1.5 m depth using a Ditch Witch® trenching machine (Perry, Okla.). This depth captures almost all of the fine-root biomass observed in longleaf pine woodlands (Hendricks et al. 2006). We placed 4-mil plastic sheeting (doubled for 8-mil thickness) in the trench to prevent overstory roots from growing into the treatment area over time. The trench was then filled with soil, leaving a small amount of plastic sheeting above the ground. OAI was then calculated for all trenched plots. Pairs of nontrenched control plots with OAI values (±5%) similar to those for the trenched plots were chosen from the larger study. Our trenching method overcame previously reported limitations, including incomplete severing of competing roots (Lewis and Tanner 2000), ingrowth into the treated plot once trenching is completed (Holl 1998), and the inability to adequately separate effects in the light and below ground (Ostertag 1998).

Each plot was further subdivided into 2 m × 2 m subplots and randomly assigned an understory / ground layer herbicide treatment that consisted of spraying the subplot in July 1998 with a 4% glyphosate solution to kill all understory vegetation. We planted ten 1-year-old containerized longleaf pine seedlings (judged to be healthy from the color of the leaves, and with a root collar diameter of 8–11 mm) in the central portion of each subplot in January 1999. Seedlings were planted such that there was at least 20 cm between individuals. Over the course of the study we controlled competing vegetation through hand-weeding or careful application of herbicide with a brush when there was little to no wind. Brown-spot needle blight caused by *Scirrhia acicola* (Dearn.) Siggers was not detected on any seedlings throughout the study.

Resource measurements

Available light in the understory was estimated using hemispherical photographs (Battaglia et al. 2003; Rich 1990; van Gardingen et al. 1999). Images were taken at

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Table 1. Results of ANOVA.

Source	df				
	Soil N concn.	Soil moisture (0–30 and 0–90 cm depths)	Understory biomass	Seedling survival	Seedling biomass
L	2	2	2	2	2
b (L)	4	4	4	4	4
TR	1	1	1	1	1
b (TR)	2	2	2	2	2
UR	1	1	—	1	1
b (UR)	2	2	—	2	2
L × TR	2	2	2	2	2
b (L × TR)	4	4	4	4	4
L × UR	2	2	—	2	2
b (L × UR)	4	4	—	4	4
TR × UR	1	1	—	1	1
b (TR × UR)	2	2	—	2	2
L × TR × UR	2	2	—	2	2
b (L × TR × UR)	4	4	—	4	4
TM	6	19	—	34	—
b (TM)	12	38	—	68	—
TM × L	12	38	—	68	—
b (TM × L)	24	76	—	136	—
TM × TR	6	19	—	34	—
b (TM × TR)	12	38	—	68	—
TM × UR	6	19	—	34	—
b (TM × UR)	12	38	—	68	—
TM × L × TR	12	12	—	68	—
b (TM × L × TR)	24	24	—	136	—
TM × L × UR	12	12	—	68	—
b (TM × L × UR)	24	24	—	136	—
TM × TR × UR	6	19	—	34	—
b (TM × TR × UR)	12	38	—	68	—
TM × L × TR × UR	12	38	—	68	—
b (TM × L × TR × UR)	24	76	—	136	—

Note: Sources of variance are as follows: location (L); trenching (TR); understory removal (UR); time (TM); and replicate block (*b*). Dashes denote effects not used in the specific analysis.

1 m height in the center of each plot under uniform sky conditions during the summer of 1998. Images were edited using Adobe PhotoShop© (version 6.0, Adobe, San Jose, Calif.) to increase the contrast between the foliage and the visible sky. Each image was analyzed using the image-analysis program HemiView© (version 2.1, Delta-T Devices, Ltd., 128 Low Road, Burwell, Cambridge, UK) to yield estimates of GF. We chose to use GF based on the work of Battaglia et al. (2003), who found that it was linearly correlated with light transmittance to the understory and overstory of longleaf pine forests, and this estimate was relatively unbiased, i.e., it fell on a 1:1 line with percent growing-season canopy light transmittance.

Soil N (NH_4^+ and NO_3^-) concentration was measured in each subplot during 1999 (May, July, August, and November) and 2000 (February, April, and May) using ion-exchange resin membranes according to the methods described by Binkley and Matson (1983) and Palik et al. (2003). The membranes consisted of sturdy surgical cloth impregnated with one layer of either cation or anion beads. The membranes were prepared by shaking them in 0.5 mol/L $NaHCO_3$ for three 20-min periods and triple-rinsing in deionized water after each charging. We installed two cation and two anion membranes in each subplot at 5 cm depth. The membranes were retrieved after 7 d, rinsed with deionized water, and extracted with 25 mL of 2 mol/L KCl per membrane. N concentrations were estimated using a Lachat QuikChem 8000 flow-injection analyzer (Lachat Instruments, Milwaukee, Wis.). Soil N concentration for each subplot was calculated as the sum of NH_4^+ and NO_3^- values for each period and standardized to a 7 d sampling interval.

We monitored volumetric soil moisture using time domain reflectometry (Topp et al. 1980) in each subplot across two soil depths (0–30 and 0–90 cm). For each depth, one pair of 30 and 90 cm long stainless-steel rods was placed vertically in the soil. Volumetric soil moisture was measured biweekly from January 1999 to December 2001 using a cable tester (Tektronix 1502B, Tektronix, Inc., Richardson, Tex.).

Plant-response measures

Seedling survival was assessed monthly throughout the study (January 1999 to December 2001). We counted a seedling as alive if we could see any live foliage. In December 2001 we measured total (above- and below-ground)

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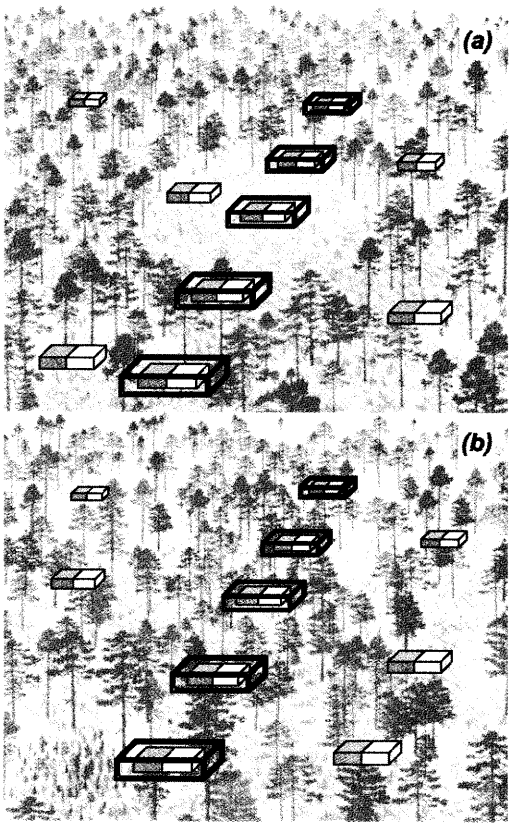
Fig. 1. Experimental design for the study. Twenty plots (in each of three replications) were installed in large-group-selection (*a*) and nonharvest (*b*) treatment areas to isolate above- and below-ground effects on seedling and understory responses. One-half of the plots received a trenching treatment (thick solid outlines). One-half of each plot received an understory herbicide treatment (shaded squares) or served as a control (open squares). For brevity, only one of the three replications is included (adapted from Riegel et al. 1992).



seedling biomass in 40 randomly selected plots, leaving 20 plots for future biomass measurements. For each seedling, we measured root-collar diameter to the nearest 0.1 mm with digital calipers and height to the top of the bud to the nearest 1 mm with a field tape. We carefully excavated and collected each root system, retrieving all structural roots and as many medium to fine roots as possible. The seedling components (foliage, stem, and roots) were then dried at 70 °C to a constant mass (at least 48 h) and weighed. Finally, we calculated the mean of total (above- and below-ground) seedling biomass for each subplot.

We measured standing understory biomass at the end of the first growing season (1999) before leaf senescence in subplots where the understory had not been removed. All understory biomass within a randomly selected 0.75 m^2 circular area adjacent to the subplot was clipped at ground level and sorted into three classes (wiregrass, other herbaceous, and woody). This material was dried at 70 °C for 48 h to a constant mass and weighed.

Data analysis

The experimental unit for this study was the plot. We analyzed data using a mixed-models analysis of variance and nonlinear regression with SAS® System for Windows version 9.1 (SAS Institute Inc., Cary, N.C.). Prior to all analyses, we determined if each variable met the assumption of a normally distributed variable. We transformed total seedling biomass and soil N concentration using the natural log and square-root transformations, respectively. Statistical differences for all tests were accepted as significant at $\alpha < 0.05$. Where interactions were present, contrasts were performed to further test for specific differences.

We used a repeated-measures mixed-models (logistic) analysis of variance using the %GLIMMIX macro to test for woodland location, trenching, understory removal, and time effects on seedling survival, soil N concentration, and soil moisture level. We determined the most appropriate covariance matrix to use for each test by maximizing a likelihood function and comparing Akaike's information criterion among potential repeated-measures structures. Consequently, survival data were fit using a spatial (power) covariance structure that accounted for the unequal sampling intervals (Littell et al. 1996). Since sampling intervals were not equally spaced through time, orthogonal polynomial coefficients were calculated using the Interactive Matrix Language (PROC IML) to generate treatment, time, and treatment by time coefficients for contrasts.

We used nonlinear regression to relate GF to OAI at the whole-plot level (n = 60) and a mixed-models analysis of covariance to test if trenching significantly affected the relationship between soil N concentration and OAI for each understory treatment. The effect of trenching on soil N concentration was significant when the understory was removed ($P < 0.001$) but insignificant when the understory was left intact ($P = 0.320$). As a result, we regressed soil N concentration and OAI for each trenching treatment separately with understory removal and we pooled data for the intact understory treatment.

Mixed-models analysis of variance and linear regression were used to test for treatment effects on understory and seedling biomass. We first tested for location and trenching effects on understory biomass (separate tests for herbaceous and woody plants) using light level (GF) as a covariate. Light level was significant as a covariate for the herbaceous plants ($P < 0.0001$), but trenching was not ($P = 0.93$). As a result, we tested the relationship of understory herbaceous biomass and GF using linear regression of the pooled (trenched and nontrenched) data. GF was not significant as a covariate for understory woody plants ($P = 0.88$), so we conducted the analysis to test for location and trench effects only. Next, we examined whether seedling biomass was related to light level and soil N concentration with different understory treatments using linear regression. All regression models were selected on the basis of our expectations of resource and seedling responses to changing overstory abundance, examination of residual plots, and the statistical significance of model coefficients (Palik et al. 2003).

To test predictions of distribution of seedlings relative to that of adults obtained from this experimental study, we measured recruitment of naturally regenerated seedlings from two monitoring programs in October 2005. We randomly selected 300 longleaf pine seedlings (less than 1.37 m tall) from a mesic site (Jones Research Center) and 100 seedlings from a xeric site (Eglin Air Force Base in

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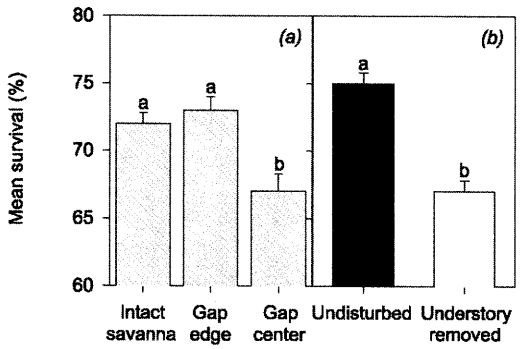
Table 2. Survival of *Pinus palustris* seedlings when the understory was removed and in areas of lower overstory abundance.

	Type 3 tests of fixed effects	
	F	*P*
Location	6.92	0.0022
Trenching	0.32	0.5761
Understory removal	28.16	<0.0001
Location × trenching	0.74	0.4844
Location × understory removal	1.46	0.2395
Trenching × understory removal	2.06	0.1565
Location × trenching × understory removal	0.16	0.8527
Time	254.06	<0.0001
Location × time	1.55	0.2212
Trenching × time	0.25	0.6224
Understory removal × time	2.71	0.1047
Location × trenching × time	0.21	0.8143
Location × understory removal × time	0.64	0.5284
Trenching × understory removal × time	0.00	0.9623
Location × trenching × understory removal × time	0.25	0.7803

Note: The output presented is from a repeated-measures ANOVA using logistic mixed models. Data are from a 70- to 90-year-old second-growth longleaf pine forest in Baker County, Georgia, USA.

Fig. 2. Survival of *Pinus palustris* seedlings in the intact woodland, the gap edge, and the gap center (*a*) and when the understory was undisturbed (*b*). Letters above the bars denote significant differences in survival rate ($\alpha < 0.05$).



northwestern Florida). The xeric site is a Lakeland soil (Typic Quartzipsamment), similar in soil-drainage class to that described in Brockway and Outcalt (1998). The distance from each seedling to the nearest adult pine was measured to the nearest 1 m to determine whether any exclusion patterns could be discerned.

Results

Hypothesis 1: Facilitation by the overstory is a stronger influence on survival of longleaf pine seedlings than competition for water

After three growing seasons and two prescribed burns, survival of planted longleaf pine seedlings declined through time and was significantly related to woodland location and understory removal (Table 2). Mean seedling survival over three growing seasons was greatest in the intact woodland and at the gap edge, lowest in the gap center (Fig. 2*a*), and greater when the understory was left intact (Fig. 2*b*). Removing belowground competition from mature pine trees through trenching did not affect pine seedling survival (Table 2).

The response of soil moisture to trenching and understory removal was generally opposite to that of seedling survival (Table 3). Soil moisture increased with trenching at both soil depths (Fig. 3) but did not vary with location or understory treatment (Table 3). However, there was an interaction between understory removal and time at 0–30 and 0–90 cm depth, with greater soil moisture in the understory-removal treatment (data not shown).

Hypothesis 2: Shallow-rooted shade-intolerant herbaceous plants respond positively to increases in light; deep-rooted shade-tolerant understory hardwoods respond mostly to a decrease in belowground competition through removal of overstory

We observed opposite growth responses of the two main understory plant guilds of herbaceous and woody (mostly *Quercus* spp.) plants to competition in the light and below ground. Aboveground herbaceous biomass increased significantly with light level ($r^2 = 0.33$, $P < 0.0001$) (Fig. 4*a*) but not as a result of trenching (Table 4). The opposite was true for woody understory plants, whose responses did not vary with light level ($P = 0.47$) but increased with trenching (Fig. 4*b*; Table 4). With trenching, woody biomass increased sevenfold in the intact woodland ($P < 0.0001$) and fivefold at the gap edge ($P = 0.02$), but no differences were noted in the gap center ($P = 0.92$) (Fig. 4*b*).

Hypothesis 3: In the absence of understory vegetation, growth of longleaf pine seedlings is related to levels of light and available soil N, and when the understory is left intact, belowground gaps are filled rapidly by the understory, so growth of longleaf pine seedlings is related to light only

When understory competition was removed, a significant curvilinear relationship accounting for 55% of the variation was observed between overstory stocking and soil N avail-

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Table 3. Effect on belowground resources (soil water and N) of removal of belowground competition and with time and location.

	Type 3 tests of fixed effects	
	F	*P*
Volumetric soil moisture at 0–30 cm depth (%)		
Location	2.43	0.0926
Trenching	36.57	<0.0001
Understory removal	0.64	0.4241
Location × trenching	0.38	0.6826
Location × understory removal	0.11	0.8931
Trenching × understory removal	0.05	0.8160
Location × trenching × understory removal	0.27	0.7665
Time	340.72	<0.0001
Location × time	2.59	<0.0001
Trenching × time	6.89	<0.0001
Understory removal × time	5.92	<0.0001
Location × trenching × time	2.06	0.0002
Location × understory removal × time	1.39	0.0564
Trenching × understory removal × time	1.54	0.0649
Location × trenching × understory removal × time	0.59	0.9783
Volumetric soil moisture at 0–90 cm depth (%)		
Location	2.43	0.0925
Trenching	23.34	<0.0001
Understory removal	0.01	0.9155
Location × trenching	0.44	0.6431
Location × understory removal	0.25	0.7803
Trenching × understory removal	0.01	0.9551
Location × trenching × understory removal	0.02	0.9754
Time	228.03	<0.0001
Location × time	1.30	0.1029
Trenching × time	5.31	<0.0001
Understory removal × time	3.00	<0.0001
Location × trenching × time	2.40	<0.0001
Location × understory removal × time	1.69	0.0054
Trenching × understory removal × time	1.14	0.3054
Location × trenching × understory removal × time	0.50	0.9959
$\sqrt{(\text{Soil N } (NH_4^+ + NO_3^-))}$ (μg·membrane^{-1}·7 d^{-1})		
Location	2.66	0.0746
Trenching	51.92	<0.0001
Understory removal	105.73	<0.0001
Location × trenching	3.35	0.0386
Location × understory removal	1.35	0.2634
Trenching × understory removal	29.68	<0.0001
Location × trenching × understory removal	2.13	0.1239
Time	62.03	<0.0001
Location × time	2.18	0.0020
Trenching × time	11.86	<0.0001
Understory removal × time	13.97	<0.0001
Location × trenching × time	1.75	0.0221
Location × understory removal × time	1.30	0.1696
Trenching × understory removal × time	7.38	<0.0001
Location × trenching × understory removal × time	2.40	0.0005

Note: The output presented is from a repeated-measures mixed-models analysis of variance. Data are from a 70- to 90-year-old second-growth longleaf pine forest in Baker County.

ability ($P < 0.0001$), with an exponential increase in soil N concentration occurring at low overstory stocking (Fig. 5*a*). When all understory competition was removed, in combination with trenching, soil N concentration was elevated and did not vary with overstory stocking ($P = 0.83$) (Fig. 5*b*). When the understory was left intact, soil N concentration did not vary with either overstory stocking ($P = 0.52$) (Fig. 5*c*) or trenching treatment ($P = 0.32$; data not shown). Levels

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Fig. 3. Effect of severing competing roots through trenching on volumetric soil moisture at depths of 0–30 cm (*a*) and 0–90 cm (*b*). Letters above the bars denote significant differences in soil moisture level ($\alpha < 0.05$) by trenching treatment.

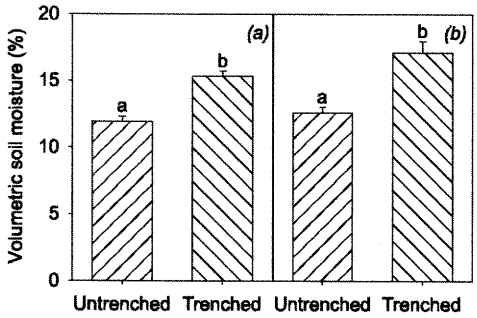
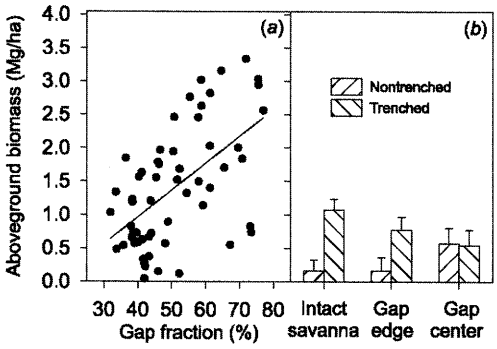


Fig. 4. Understory biomass response to overstory disturbance and severing of competing roots through trenching in a *P. palustris* woodland. (*a*) Response of herbaceous biomass to light level (biomass = –0.649 + 0.0403 × GF, $r^2 = 0.33$, $P < 0.0001$). (*b*) Response of aboveground woody biomass (mean ± 1 SE) to location and trenching.



of light reaching the understory were inversely correlated with overstory stocking ($r^2 = 0.67$, $P < 0.0001$) (Fig. 6).

The biomass of longleaf pine seedlings increased with decreased overstory stocking (Table 5) and was related to the amount of above- and below-ground resources (Fig. 7). Seedling biomass increased exponentially across the range of GF values in our study (Fig. 7). The greatest growth response occurred in areas where GF values were approximately 60% and greater. Forty-three percent of seedlings at this degree of openness had initiated height growth by the end of the study. Between approximately 35% and 60% GF, longleaf pine seedlings were able to establish and survive, but only 13% had begun height growth. No seedlings were observed in areas with GF below approximately 35%.

The response to above- and below-ground resources depended on the presence of an understory. Understory removal increased seedling biomass at all woodland locations, regardless of the trenching treatment (Table 5). The largest increase in seedling biomass was noted when the understory and belowground competition were removed. These patterns were consistent at all three woodland locations (Table 5). When the understory was removed, seedling biomass increased with both light level ($r^2 = 0.27$, $P < 0.001$) and soil N concentration ($r^2 = 0.42$, $P < 0.0001$) (Figs. 7*a* and 7*b*). When the understory was undisturbed, however, seedling biomass increased with light level ($r^2 = 0.25$, $P < 0.001$) but not soil N concentration ($P = 0.73$) (Figs. 7*c* and 7*d*).

Table 4. Response of woody understory biomass to removal of overstory belowground competition; response of herbaceous understory biomass to removal of overstory aboveground competition.

	Type 3 tests of fixed effects	
	F	*P*
Woody aboveground biomass (Mg/ha)		
Location	0.42	0.6588
Trenching	11.58	0.0013
Location × trenching	3.42	0.0406
Herbaceous aboveground biomass (Mg/ha)		
Location	10.30	0.0002
Trenching	1.37	0.2476
Location × trenching	2.82	0.0685

Note: Type 3 tests of fixed effects (mixed-models analysis of variance) are presented ($n = 60$). Data are from a 70- to 90-year-old second-growth longleaf pine forest in Baker County.

Finally, patterns of natural distribution of longleaf pine seedling relative to proximity to overstory trees for both soil types (mesic and xeric) were nearly all within the seedling-exclusion zone previously proposed by Brockway and Outcalt (1998). All of the seedlings tallied at the mesic site — and 96% of those tallied at the xeric site — were found within 16 m of overstory longleaf pine (Fig. 8).

Discussion

The direction (competition versus facilitation) and magnitude of interactions between adult longleaf pine and regenerating longleaf pine seedlings influence the manner in which the overstory can be managed to sustain regeneration. In this study, facilitation by the overstory and understory significantly increased survival of planted longleaf pine seedlings. While facilitation increased survival of longleaf pine seedlings by only 6%, it is biologically significant in that this is contrary to the prediction of the hypothesis of belowground competitive seedling exclusion (Brockway and Outcalt 1998) that seedlings would be excluded from a 12–16 m zone near adult longleaf pine trees.

Several patterns in the data suggest that competition for water did not control plant–plant interactions between adult pines and pine seedlings in our study. First, survival was greater in both the intact woodland and at the gap edge than in the center of tree gaps, suggesting that the overstory facilitated survival (Fig. 2). In fact, survival was greater well within the zone of exclusion noted in Brockway and Outcalt (1998). Second, removal of the understory resulted in significantly decreased survival of pine seedlings, suggesting that the understory also facilitated survival (Fig. 2). Third, soil moisture level responded differently than seedling survival: we observed greater soil moisture at 0–30 cm depth with trenching and understory removal, but survival was not influenced by trenching. Finally, this work was conducted during the most severe regional drought experienced in the past 50 years (Golladay and Battle 2002) with below-

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Fig. 5. Response of soil N ($NH_4^+ + NO_3^-$) concentration to overstory and understory disturbance and severing of competing roots in a *P. palustris* woodland through trenching. (*a*) The understory was removed and the plots were not trenched ($\sqrt{[\text{soil N}]} = 0.6352 + 0.5573 \times \exp(-2.5585 \times \text{OAI}$; $r^2 = 0.55$, $P < 0.0001$). (*b*) The understory was removed and plots were trenched. (*c*) The understory was left undisturbed.

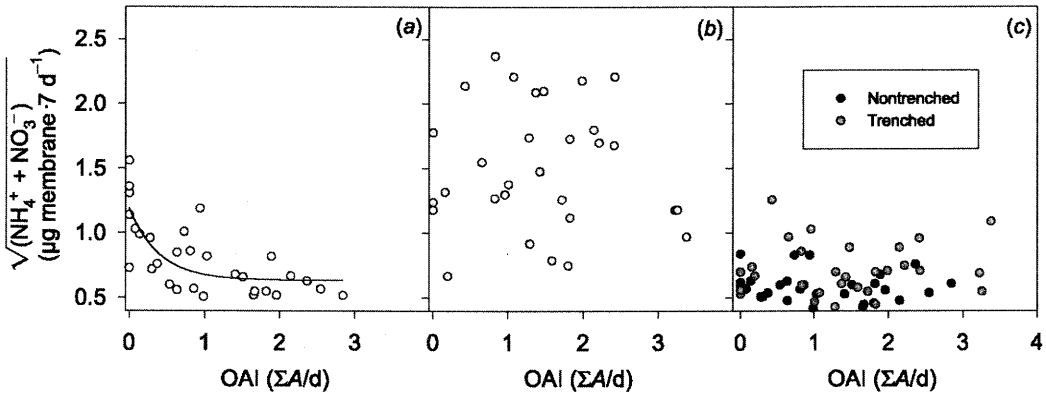
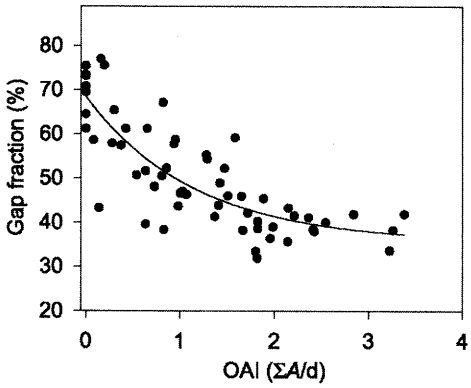


Fig. 6. Response of light level (gap fraction (GF)) to overstory stocking in a *P. palustris* woodland ($n = 60$). The equation for the fitted line is $\text{GF} = 35.56 + 32.92/(1 + (0.87 \times \text{OAI}))$ ($r^2 = 0.67$, $P < 0.0001$).



average precipitation for 19 months between November 1998 and January 2001. Thus, even though the site used in this study has greater water-holding capacity than that used by Brockway and Outcalt (1998), if competitive exclusion of seedlings due to water stress consistently reduced survival, then it likely would have been manifested during this drought.

Increased survival of planted longleaf pine seedlings in the presence of an overstory and understory may be partly explained by plant–plant interactions that ease the effect of drought conditions (Callaway and Walker 1997; Miller and Werner 1987; Mitchell et al. 1999*b*). Facilitation by the overstory or understory may only occur when the cost of maintaining adequate plant water status is greater than the physiological and morphological costs incurred under low light levels associated with greater plant cover (Holmgren et al. 1997). For example, Belsky and Canham (1994) suggest that heterogeneity in light conditions under savanna trees in Africa resulted in stomatal fluctuations that reduced transpiration and increased water-use efficiency in understory plants relative to the open-grassland matrix. A similar result was reported by Knapp and Smith (1989) and Knapp et al. (1989) in alpine regions of Wyoming, owing to light variation associated with clouds. The light environment of longleaf pine woodlands is heterogeneous spatially and temporally (Battaglia et al. 2003), and the extent to which variation in the understory light environment in longleaf pine woodlands controls physiological processes sufficiently to affect survival during drought needs further investigation.

Facilitation was observed with respect to seedling survival, while competition significantly influenced the growth of both herbaceous and woody vegetation. However, the mechanism by which growth was regulated between understory guilds differed substantively. The herbaceous community responded mainly to light, i.e., there was a positive correlation between biomass and GF (Fig. 4) and a statistically insignificant trenching effect (Table 4). The response of understory woody plants, however, was opposite to that of herbaceous plants, i.e., there was a significant trenching effect (Fig. 4) and insignificant correlation with light level. The absence of a trenching effect on woody plants in the gap center may have been due to plot location. The gap center was approximately 25 m from the gap edge, well beyond the zone of influence noted for mature, overstory longleaf pine (Brockway and Outcalt 1998; Jones et al. 2003; McGuire et al. 2001).

While understory-community productivity has been shown to be limited by soil water level at the ecosystem scale (Mitchell et al. 1999*a*), and drought exacerbated water limitations in this study, we found no positive effects of shade on productivity of herbaceous plants. Within its range, wiregrass is the dominant understory plant of natural longleaf pine ecosystems, making up nearly 50% of understory net primary productivity (Mitchell et al. 1999*a*). Wiregrass growth response increases with light level until nearly full-light conditions are reached (McGuire et al. 2001), but competition with understory cover can decrease wiregrass seedling survival and biomass (Kindell et al. 1996). Similar to our findings, Tiedemann et al. (1971) reported that growth was positively correlated with light levels (20%–80% of full sunlight) in four grass species in the southeastern United States. Monk and Gabrielson (1985) found that only 1 of 14 understory species common to old-field sites in South Carolina responded positively to shade. Positive effects of shade on grass productivity have been linked to

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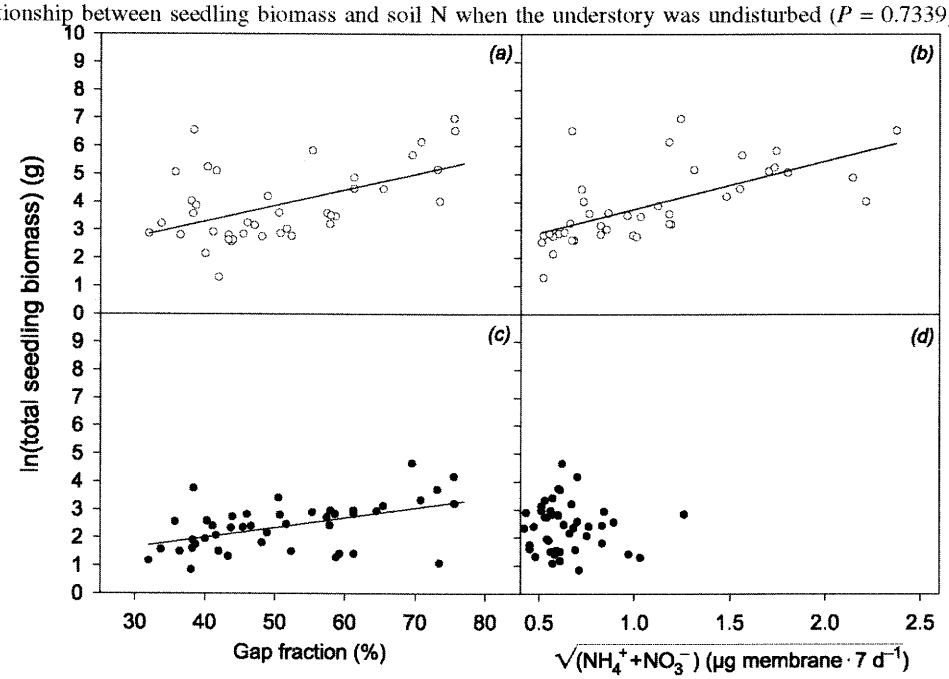
Table 5. Response of *P. palustris* seedling biomass after three growing seasons to trenching with understory removal.

		Woodland location		
Understory reatment	Trenching reatment	Intact woodland	Gap edge	Gap center
Undisturbed	Nontrenched	1.978aA (0.210)	2.757bA (0.280)	2.798bA (0.301)
Undisturbed	Trenched	1.873aA (0.246)	2.347abA (0.339)	3.304cA (0.331)
Removed	Nontrenched	2.705aB (0.208)	3.327abB (0.264)	4.582cB (0.370)
Removed	Trenched	4.284aC (0.262)	5.612bC (0.434)	6.132bcC (0.370)

Note: Values show ln(mean seedling biomass) in grams. The values in parentheses show 1 SE. Values followed by a different lower-case letter differ significantly ($\alpha < 0.05$) among locations for each treatment. Values followed by a different capital letter differ significantly ($\alpha < 0.05$) among treatments at each location.

Fig. 7. Response of *P. palustris* seedling biomass to increasing light and soil N concentration when the understory was removed (*a* and *b*) but to light alone when the understory was undisturbed (*c* and *d*). Equations are as follows: (*a*) ln(biomass) = 1.06 + 0.056 × GF ($r^2 = 0.27$, $P = 0.0005$); (*b*) log(biomass) = 2.04 + 1.71 × soil N ($r^2 = 0.42$, $P < 0.0001$); (*c*) ln(biomass) = 0.60 + 0.035 × GF ($r^2 = 0.25$, $P = 0.0005$); (*d*) there was no relationship between seedling biomass and soil N when the understory was undisturbed ($P = 0.7339$).



increased nutrient cycling due to animal droppings under tree crowns in savannas (Belsky 1994) and litterfall and throughfall inputs under blue oak trees (*Quercus douglasii* Hook. & Arn.; Callaway et al. 1991). Shading in woodlands and savannas increases grassland productivity by also reducing soil and leaf temperatures, which reduces transpiration and improves water relations of understory plants (Belsky 1994; Smith et al. 1987; Tiedemann and Klemmedson 1977; Weltzin and Coughenour 1990; Wilson 1989). However, we found no increase in productivity of grasses associated with savanna tree crowns, only an increase in survival of longleaf pine seedlings. It appears that even when these systems are water-limited (Mitchell et al. 1999*a*), shade does not generally increase understory productivity.

The contrasting growth responses of herbaceous and woody plants to overstory competition suggest that these plant types may be competing for different resources (herbaceous plants for light and woody plants for soil N). While the impact of understory plants on pine seedling growth is readily seen, how each understory type (herbaceous and woody) controls seedling growth is more difficult to discern. Our study could not isolate the individual effects of herbaceous and understory woody plants on longleaf pine seedling survival and biomass. The increased growth of pine seedlings in trenching and herbicide treatments in the gap centers compared with that in the intact woodland and gap edge (Table 5), however, suggests that advanced hardwood regeneration is preempting soil resources with established root systems, as plots in the gap centers were more than 25 m from the nearest canopy trees. Future work that is able to separate these understory components would help elucidate factors that regulate understory growth and the extent to which herbaceous and woody plants differentially control longleaf pine seedling growth.

Walter (1971) proposed a two-layer model to describe savanna structure, which generally fits the patterns observed in this study. This model suggests that niche differentiation in root zones, i.e., more superficial rooting of herbaceous plants and deeper rooting of woody plants, alters competitive responses (Bragg et al. 1993; Brown and Archer 1990;

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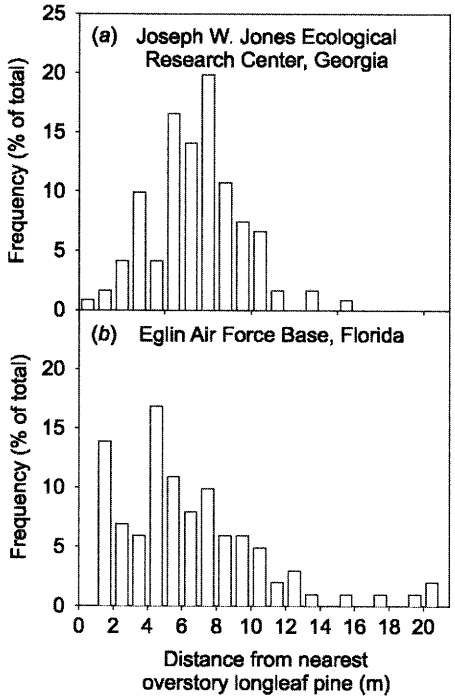
Fig. 8. Natural regeneration of *P. palustris* under parent trees on mesic sites at the Joseph W. Jones Ecological Research Center in southwestern Georgia (*a*) and xeric sites at the Eglin Air Force Base in northwestern Florida (*b*).



Scholes and Archer 1997; Vetaas 1992). This root partitioning has been shown in annual grassland systems dominated by grasses and forbs (Gordon and Rice 1992). In longleaf pine savannas and woodlands, wiregrass roots are disproportionately found in the upper 30 cm of soil (Saterson and Vitousek 1984), whereas pines and hardwoods are more deep-rooted (Jacqmain et al. 1999; Pessin 1939*b*). In this study, the deeper rooted shade-tolerant hardwood understory was more strongly influenced by belowground competition with adult pines than the understory of herbaceous plants, with as much as a sevenfold increase in biomass in the intact woodland with trenching (Fig. 4).

Longleaf pine woodlands appear to function differently than other open-canopy ecosystems noted in the literature. Rather than trees facilitating productivity underneath the canopy through greater fertility compared with the open matrix (Belsky 1994), longleaf pine root gaps show increased soil nutrient availability either when adult pine roots are severed or in the center of large gaps when understory plants are not present (Jones et al. 2003; Palik et al. 1997). This is similar to a report by Parsons et al. (1994) on closed-canopy lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) forests. If the understory is left intact, however, root gaps are ephemeral and indistinct (Jones et al. 2003; McGuire et al. 2001), even when adult tree roots are severed (Fig. 5).

Forest management implications

Frequently burned longleaf pine woodlands with an undisturbed grass-dominated understory are rich in terms of species diversity, with as many as 50 plant species/m^2 (Kirkman et al. 2001; Walker and Peet 1984). These woodlands are also home to many endemic species (Hardin and White 1989). Frequent surface fire is important for creating the conditions that sustain these species (Kirkman et al. 2004). Moreover, sufficient longleaf pine canopy cover is important for sustaining the diversity of this ecosystem (Simberloff 1999) and providing enough longleaf pine needles as the fine fuel source that carries frequent fire (Mitchell et al. 2006; Williamson and Black 1981). Yet approaches to harvesting of adult pines, even on lands where conserving biodiversity is an important goal, have often been based on an even-aged structure (Rudolph and Conner 1996) or large gaps, i.e., patch clearcuts (Brockway et al. 2005), where lack of pine fuels makes frequent surface fire more difficult to maintain.

Partly based on the hypothesis of belowground competitive seedling exclusion (sensu Brockway and Outcalt 1998), it has been reported that gap-based approaches are necessary to establish longleaf pine regeneration while maintaining an uneven-aged structure (Brockway and Outcalt 1998; Brockway et al. 2005). Gaps at least 40 m in diameter (0.125 ha) (Brockway and Outcalt 1998) and up to 2 ha in size (Brockway et al. 2005) have been suggested. Data presented in this study and those of Palik et al. (2003) demonstrate that gap-based approaches increase seedling growth and may be warranted when timber-production objectives are of greater priority than conservation or on sites in which the understory has been damaged through previous land use (Hedman et al. 2000). In this case, further intensive site preparation to control vegetation does not impede the attainment of other objectives.

The release of hardwoods in longleaf pine woodlands can be problematic when management objectives include the conservation of biodiversity. Hardwoods respond immediately to a reduction in belowground competition with the overstory and can quickly capture a site. Longleaf pine, however, requires an adequate seed year for reproduction (7–15 years between regional masting events) and an additional 2–10 years to begin height growth, owing to the stemless, grass-stage period of growth (Boyer 1990). If no seedlings are established before the gap is created, it may take a decade or longer before longleaf pine regeneration captures a site. Because hardwoods are released immediately following overstory removal, chemical or intensive mechanical vegetation management may be required, which may compromise conservation objectives (Hedman et al. 2000).

Accelerated growth of hardwoods in large gaps negatively influences the ability to apply prescribed burns in longleaf pine woodlands. Fire acts as a selective force against hardwoods, killing the aboveground portion of the plant (Williamson and Black 1981). Increased fire intensity is positively related to pine litter accumulation (Ferguson et al. 2002) and decreases with distance from adult pines (Grace and Platt 1995). Increased fire intensity is also negatively related to hardwood density (Glitzenstein et al. 1995; Williamson and Black 1981). The lack of pine fuels in the gap center coupled with the significant increase of hardwood biomass may reduce fire intensity (Mitchell et al. 2006). This increases the probability of hardwoods capturing gaps either wholly or partly.

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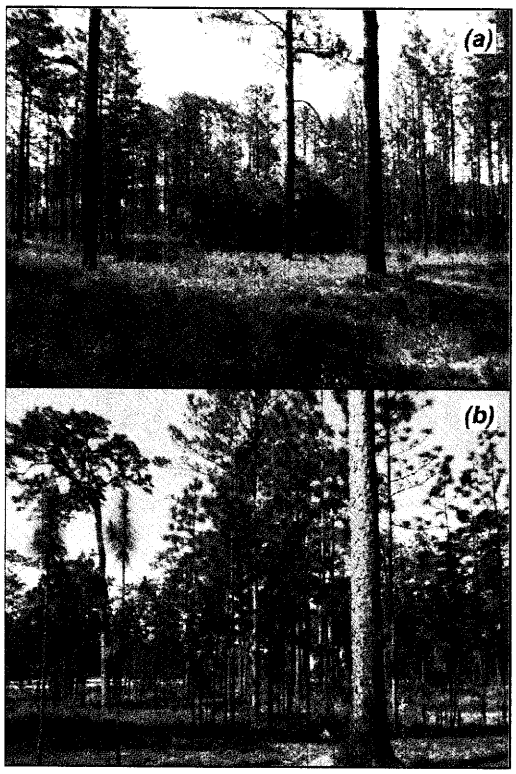
Fig. 9. The lack of a pine fine-fuel source compromises fire continuity and, combined with hardwood release from overstory competition, results in hardwood proliferation in a gap (*a*). Dispersed retention that is variable in density allows for fire continuity across the landscape, maintains low-stature hardwoods, encourages longleaf pine regeneration, and ensures a high diversity of flora and fauna (*b*). Photographs by S. Pecot.



We also showed that the presence of understory hardwoods and herbaceous plants influenced the growth of longleaf pine seedlings (Fig. 7). The growth reduction resulted from the ability of established understory plants to rapidly exploit root gaps created by overstory disturbance, thus attenuating seedling growth. Increased growth of seedlings by control of herbaceous and woody plants has been demonstrated for longleaf pine woodlands (Boyer 1989; Pessin 1938, 1939*a*) as well as several other forest systems (Brown and Archer 1989; Gordon et al. 1989; McPherson 1993). Longleaf pine has long been considered to be intolerant of competition (Boyer 1990) and, as a result, vegetative control (chemical and mechanical) has been suggested as a means of optimizing its growth (Boyer 1991; Brockway and Outcalt 2000; Brockway et al. 2005). While understory reduction can increase growth of longleaf pine seedlings, the cost may be a loss in biodiversity as well as the ability to apply fire across the landscape if it lowers fine-fuel loadings (Mitchell et al. 2006).

The ability of seedlings to survive and establish in a matrix of open-canopy pines suggests that retaining adult stands that vary in density, which is accomplished through single-tree selection, may be useful in establishing longleaf pine regeneration without adversely affecting the ability to manage prescribed burning or favoring hardwood development, as with large-gap-based approaches. Using light-distribution data from a larger study (the large-group and no-harvest plots were shared with this study), Battaglia et al. (2003) estimated the proportions of three light levels (<35%, 35%–60%, and >60% GF) in single-tree, small-group, and large-group treatments. In almost two-thirds of the area in the single-tree treatment, sufficient light was provided in the understory for the establishment of advanced longleaf pine regeneration (35%–60% GF). Once established, these seedlings can be released in future harvesting operations or by natural disturbances to the overstory. In addition, nearly one-third of the stands in the single-tree treatment had areas that were open enough to release seedlings into the rapid-growth phase (greater than 60% GF). Only 2% of the stand contained light levels that were too low for establishment of advanced regeneration or seedling release. Retaining adult pine stands that vary in density, i.e., single-tree selection, allows for a continuous supply of fuels over space and time, reducing the need for chemical and mechanical control of hardwoods while providing sufficient resources for seedling regeneration. We suggest that this approach is a viable silvicultural tool for longleaf pine woodland management.

Differences in experimental approach (such as using different seedling types and sites) may explain the opposing results between studies which suggest that competitive exclusion of seedlings requires gap-based silviculture (Brockway and Outcalt 1998; Brockway et al. 2005) and those which suggest that single-tree-selection approaches might be suitable for longleaf pine woodlands (McGuire et al. 2001; Palik et al. 2002). Using data from monitoring programs, we found that nearly all naturally regenerated longleaf pine seedlings were within 16 m of an adult longleaf pine tree, regardless of site (Fig. 8). These regeneration cohorts resulted primarily from two masting events, in 1987 and 1996, and have persisted through severe drought conditions (Golladay and Battle 2002) and three to seven prescribed burns. Thus, it appears that differences in neither regeneration type (natural versus artificial) nor site (mesic versus xeric) can explain the differences between the reports.

To summarize, (*i*) the presence of an overstory and understory facilitated survival of longleaf pine seedlings during a severe drought but lessened their growth; (*ii*) understory hardwoods competed below ground with the overstory, while herbaceous plant growth was regulated by light; (*iii*) a seedling exclusion zone caused by the longleaf pine overstory, proposed in previous work (Brockway and Outcalt 1998), was not observed; (*iv*) gap-based approaches to longleaf pine management may be best when timber objectives are more important than conservation of biodiversity, but these approaches include the possibility of hardwood release within gaps (Fig. 9*a*); and (*v*) an overstory that varies in density can be retained in longleaf pine woodlands when the importance of attaining conservation objectives is high, because it allows for establishing regeneration, sustaining frequent fire, and producing timber (Fig. 9*b*).

Acknowledgments

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