# Chapter 5

# Plant Competition, Facilitation, and Other Overstory–Understory Interactions in Longleaf Pine Ecosystems

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## Introduction

Many of the stand structural characteristics of longleaf pine (*Pinus palustris* Mill.) forests that existed prior to European colonization have been altered or lost from past disturbance histories (Frost this volume). For example, often missing are the widely spaced, large-diameter trees, the all-aged stand structure that included a vigorous cohort of grass-stage longleaf pine seedlings, and the understory community composed of numerous woody and herbaceous species of short stature embedded within the flashy fuels of a wiregrass (*Aristida beyrichiana* Trin. & Rupr.) or bluestem (*Andropogon* spp.) matrix. Some of these structural features, such as the understory community, can be restored through modern silvicultural methods, vegetation management, prescribed fire, pine thinning, and artificial regeneration (i.e., planting or seeding) (Johnson and Gjerstad this volume; Walker and Silletti this volume). Other structural features, such as an all-aged distribution of longleaf pines, must be allowed to develop over time given appropriate disturbance regimes and the presence of keystone species (i.e., longleaf pine and wiregrass or bluestem) to "jump-start" the system. A mechanistic understanding of overstory and understory interactions will provide a sound basis for prescribing treatments designed to restore and maintain longleaf pine communities.

Overstory trees in forest stands affect understory vegetation by modifying growing conditions, either directly or indirectly. These modifications are manifested in a variety of ways, including consumption of growth-limiting resources (i.e., light, soil water, and nutrients) and alteration of other physical characteristics that impact growing conditions (i.e., temperature, litterfall accumulation, and fire behavior). In a similar way, understory vegetation can influence the growing conditions of overstory trees, potentially affecting their survival, stem growth, and crown morphology.

This chapter will focus on two common interactions in forest communities, competition and facilitation, and their potential influences on overstory and understory responses in southern pine forests, with emphasis on longleaf pine. First I will discuss basic concepts of plant interactions, including types and associated responses, and attempt to classify overstory and understory interactions commonly observed in longleaf pine forests. Implications of plantation silviculture to these interactions will be considered. Next I will review previous

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research on overstory and understory interactions with emphasis on southern pine communities. Finally I will discuss overstory and understory interactions observed in two case studies conducted in longleaf pine plantations at the Savannah River Site, a National Environmental Research Park near Aiken, SC. The discussion will conclude with implications of these interactions to restoration and maintenance of longleaf pine communities.

The plant interactions that are the primary focus of this chapter imply a stand structure of at least two canopy layers, the overstory and the understory. To simplify the discussion, I will define "overstory" as the pine trees that comprise the upper canopy of a forest stand, where the minimum height of a "tree" is equal to 6 m (Daniel et al. 1979). "Understory" will be defined as herbaceous species (forbs and grasses) plus woody species (vines, shrubs, hardwoods, and pines) that have a stem diameter at breast height (1.37 m) less than 2.5 cm growing under or in the proximity of overstory trees. Midstory layers also are possible strata in this hypothetical stand structure but are not the focus of this chapter.

## Concepts of Plant Interactions

Plant interactions encompass a broad variety of positive and negative relationships that can exist when plants are grown in close proximity such that they influence each other's survival, growth, or reproduction (Harper 1977). In this section, I will rely on the conceptual framework proposed by Goldberg (1990) to characterize plant interactions, with emphasis on competition and facilitation. Most interactions between plants are indirect (i.e., they do not physically injure one another) and occur through an intermediary such as resources, natural enemies, or plant-produced toxins. The net result from a plant interaction (i.e., is it positive or negative and what is the magnitude of the effect?) is the combination of one plant's effect on abundance of the intermediary and the "target" plant's response to abundance of the intermediary (Goldberg 1990).

Interference includes those negative plant interactions that result either from competition for limited resources or allelopathy (production of chemical toxins by one plant that inhibit the functions of another). Because of differences in plant size or other traits, competition is often asymmetrical such that one plant is negatively affected while the other may show little or no signs of a response (Grace 1990). Resource gradients, such as spatial differences in soil nitrogen availability, can change competitive relationships that exist among plants to favor species or individuals that are most effective at resource capture (Goldberg and Miller 1990; Kalmbacher and Martin 1996). Such modifications in competitive relationships often result in declines in plant species diversity because of dominance by a few species.

Table 1 provides examples of plant interactions that have been observed in southern pine communities, classified according to the conceptual framework proposed by Goldberg (1990). The simple case of exploitation of a limiting resource has been defined as "uptake effects" of competition. "Nonuptake effects" of competition occur when an intermediary, such as litterfall from overstory trees, changes resource availability indirectly. In southern pine communities, both uptake and nonuptake effects of competition from overstory pines play a prominent role in limiting abundance and species diversity of the understory (Monk and Gabrielson 1985; Harrington and Edwards 1999; Harrington et al. 2003). These effects on the understory occur largely through direct exploitation of light, soil water, and nitrogen resources by the overstory, but also indirectly by accumulation of overstory needle litter that limits light availability to forest floor plants.

"Apparent competition" results when the intermediary is not a growth-limiting resource but rather it is a natural enemy, such as fire, disease, or herbivory, that is promoted by one plant so that the net effect of the enemy on the target plant is similar to that resulting from exploitation competition. For example,

TABLE 1. Examples of plant interactions observed in southern pine communities as classified according to the framework of Goldberg (1990).[a]

| | | Overstory → understory interactions | | | | Understory → overstory interactions | | | |
|---|---|---|---|---|---|---|---|---|---|
| Interaction | Intermediary | E | R | N | References | E | R | N | References |
| Exploitation competition (uptake effects)[b] | light | − | + | − | Monk and Gabrielson 1985; Means 1997; Harrington and Edwards 1999; McGuire et al. 2001; Harrington et al. 2003 | | | | |
| | soil water | − | + | − | Monk and Gabrielson 1985; Harrington et al. 2003 | − | + | − | Harrington and Edwards 1999 |
| | nitrogen | − | + | − | Palik et al. 1997; McGuire et al. 2001; Harrington et al. 2003 | | | | |
| Exploitation competition (nonuptake effects)[c] | light | − | + | − | Monk and Gabrielson 1985; Shelton 1995; Harrington et al. 2003 | | | | |
| Apparent competition[d] | fire | + | − | − | (1) Grace and Platt 1995; Brockway and Outcalt 1998; Glitzenstein et al. 1995 | − | + | − | (2) Richardson and Williamson 1988 |
| Allelopathy[e] | toxin | | | | | + | − | − | Richardson and Williamson 1988 |
| Positive facilitation[f] | soil water | + | + | + | (3) Ginter et al. 1979; Boyer and Miller 1994 | | | | |
| | nitrogen | + | + | + | (4) Harrington et al. 2003 | + | + | + | (6) Hendricks and Boring 1992; Hendricks and Boring 1999; Wilson et al. 1999; Hiers et al. 2003 |
| | fire | + | + | + | (5) Streng et al. 1993; Brewer and Platt 1994; Anderson and Menges 1997 | + | + | + | (7) Platt et al. 1988a |

[a] The influence of overstory pines on understory vegetation (overstory → understory interactions) are shown as the direction (+ or –) of effects (E) of the overstory on abundance of an intermediary, response (R) of the understory to abundance of the intermediary, and net effect (N) to the understory. Understory → overstory interactions follow in a similar manner. Numbers in parentheses are explained in the footnotes.

[b] Plant consumption of a limiting resource (light, soil water, or nitrogen) restricts its availability to "target" plants.

[c] Litterfall of overstory pines limits light availability to ground-layer vegetation.

[d] Apparent competition results when (1) pine litterfall increases fire intensity causing mortality of longleaf pine seedlings and injury of hardwoods, and (2) understory scrub vegetation decreases frequency of ground fires needed to regenerate longleaf pine.

[e] Above- or belowground exudates from understory scrub vegetation chemically suppress growth of pine seedlings.

[f] Positive facilitation results when pine litterfall (3) protects soil structure needed to maintain its water-holding capacity, (4) provides nitrogen inputs to the soil, and (5) promotes frequent ground fires that stimulate growth and flowering of herbaceous species, and when understory plants (6) provide nitrogen inputs to the soil through symbiotic nitrogen fixation and (7) promote frequent ground fires needed to regenerate longleaf pine.

accumulations of needle litter near overstory trees can support fire intensities capable of killing grass-stage seedlings of longleaf pine to create a vegetation-free zone similar in appearance to what would occur from intense resource competition (Grace and Platt 1995; Brockway and Outcalt 1998).

"Allelopathy" is a direct interaction in which plants produce a toxin in their foliage or roots that chemically alters the functions of the target plant. For example, in scrub vegetation communities of Florida, rosemary (*Ceratiola ericoides* Michx.) and false rosemary (*Conradina canescens* [Torr. & Gray] A. Gray) shrubs can limit seedling growth of bluestem, wiregrass, longleaf pine, and sand pine (*Pinus clausa* [Chapm. ex Engelm.] Vasey ex Sarg.) when grown together in noncompetitive environments (Richardson and Williamson 1988). This allelopathic relationship fosters the development of a fire-tolerant community that favors survival of shrubs at the expense of fire-dependent species, such as wiregrass and longleaf and sand pines.

"Facilitation" is a plant interaction in which one or both plants benefit from their relationship with each other. For example, needle litter from overstory pines is a source of nitrogen to understory plants that may aid their survival and growth (Harrington et al. 2003). Similarly, needle litter can act as a mulch to conserve soil water (Ginter et al. 1979) and it can protect soil structure needed to preserve water-holding capacity (Boyer and Miller 1994). Greater first-year survival of longleaf pine seedlings under uncut forest versus seedlings in experimentally created gaps suggests a beneficial effect of the overstory (McGuire et al. 2001). Note that, in contrast to the common plant interaction of facilitation, "mutualism" implies an obligatory relationship between plant species such that each benefits when grown in proximity to the other and each suffers when grown separately (Radosevich and Holt 1984).

As indicated by the majority of the plant interactions listed in Table 1, competition in southern pine communities is asymmetric with the overstory having the predominant influence in its relationship with understory vegetation. However, fire, as a common disturbance agent in these communities, has a dual role in regulating interactions between overstory and understory vegetation. It has a negative effect (apparent competition described above) in directly injuring or killing understory species incapable of tolerating its influence (Glitzenstein et al. 1995; Grace and Platt 1995; Brockway and Lewis 1997; Brockway and Outcalt 1998). But fire also has a positive effect (facilitation) in stimulating vegetative growth and flowering of specific understory species (Streng et al. 1993; Brewer and Platt 1994; Anderson and Menges 1997) and in maintaining wiregrass, a critical keystone species in longleaf pine communities (Platt et al. 1988a).

Overstory and understory interactions may operate differently in even-aged plantations than in natural stands because of differences in structural attributes (Oliver and Larson 1996). Even-aged plantations generally have uniform spacing and size of trees, similar crown morphologies and shapes largely dictated by spacing, and complete crown coverage when the stands are at full stocking. Stem size distributions are usually unimodal, and with time, they develop increasing positive skewness indicative of stand differentiation into different crown classes. Depending on spacing among trees, rates of crown closure and overall productivity of even-aged plantations often exceed those of natural stands.

Structure of understory vegetation in even-aged forest plantations is often symptomatic of overstory structure and site history, including previous land use and silvicultural treatments. Thus, an understory in an even-aged plantation is often uniform in plant size and species composition due to the homogeneity of the overstory and associated limitations in understory resource availability. At crown closure of the overstory, the stand enters the "stem exclusion stage" during which recruitment of new trees into the overstory ceases and understory abundance of shade-intolerant species and vigor of tolerant species decline (Oliver and Larson 1996). Invigoration of existing species and recruitment of new species in the understory may not occur until the "understory reinitiation stage" when canopy coverage of the overstory begins to decline.

The transition to the understory reinitiation stage may be delayed in even-aged plantations because their uniform spacing and size of trees prevents large canopy gaps from forming until late in stand development.

Given these differences in structural attributes and rates of development, it seems likely that some interactions between overstory trees and understory vegetation are likely to occur sooner, at greater intensity, and with increased duration in even-aged plantations versus natural stands. Exclusion or suppression of understory species as a result of overstory competition probably will occur more rapidly than in natural stands, depending on spacing among trees. However, understory reinitiation may be delayed substantially because of the prolonged uniformity of stand structure, even with the onset of density-dependent mortality of overstory trees. Although plantation silviculture can provide an effective means for reestablishing stands of a desired species composition and spacing, in its conventional usage it may impede restoration of understory species that rely on a heterogeneous stand structure. Thus, a complete understanding of overstory and understory interactions is needed to properly direct development of longleaf pine plantations toward the desired stand structure of the overstory and species composition of the understory.

## Previous Research on Overstory and Understory Interactions

Early research on overstory and understory interactions in longleaf pine communities focused on factors influencing the rate at which longleaf pine seedlings exited the grass stage. Pessin (1938) compared 3-year growth of grass-stage longleaf pines growing at various densities (2470 to 247,000 seedlings $ha^{-1}$) with or without manual removal of herbaceous vegetation. Scrub oaks, primarily blackjack (*Quercus marilandica* Muenchh.) and post oaks (*Quercus stellata* Wangenh.), were removed in all but one plot. Height growth varied inversely with pine seedling density and also according to the presence (1–7 cm $yr^{-1}$) versus absence (2–31 cm $yr^{-1}$) of herbaceous vegetation. Emergence of pine seedlings from the grass stage clearly was limited by availability of belowground resources, because light availability (estimated by evaporation rates) was 60% of maximum intensity or greater in all but the scrub oak plot (34% of maximum). Not surprisingly, height growth of longleaf pine seedlings in the scrub oak plot (1 cm $yr^{-1}$) was among the lowest values observed in this study.

Research on production of grazing forage in longleaf pine rangelands has quantified the extent to which overstory trees limit abundance and biomass of understory herbaceous species. Abundance of understory vegetation varied inversely with increasing density of overstory longleaf pines (Wolters 1973, 1981). Pine thinning and prescribed burning combinations increased forage yields in natural stands of longleaf pine to about half that observed for treeless rangeland (Grelen and Enghardt 1973). Although these studies provide empirical evidence of the competitive effects of overstory longleaf pines on understory vegetation, they do not identify the primary mechanisms responsible for them.

Much of the research on overstory and understory interactions in forest communities has focused on the effects of three primary factors: shade, root competition, and litterfall. Overstory and understory competitive interactions have been studied effectively by trenching around experimental plots to eliminate belowground competition for soil water and nutrients while maintaining light availability in the understory at nominal levels. In an early study, Fricke (1904, cited in Spurr and Barnes 1992) cut the roots of overstory Scots pine (*Pinus sylvestris* L.) in a closed canopy forest and observed dramatic increases in growth of understory pines, indicating that soil moisture, and perhaps nutrients, were limiting their growth. Other trenching studies have demonstrated similar results with eastern white pine (*Pinus strobus* L.) in New Hampshire (Toumey and Kienholz 1931), loblolly pine (*Pinus taeda* L.) in North Carolina (Korstian and Coile 1938),

grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.) in Montana (McCune 1986), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) in eastern Oregon (Riegel et al. 1992). Using a different experimental approach, Riegel and Miller (1991) demonstrated for ponderosa pine that eliminating some of the overstory competition for soil water and nitrogen via irrigation and fertilization, respectively, stimulated a 36% increase in aboveground biomass of the understory relative to nontreated areas.

Of the three factors mentioned previously, litterfall is perhaps the one least studied in forest communities. Southern pines shed their needles throughout the year, and this accumulation forms a physical barrier that can prevent seeds from reaching mineral soil and seedlings from emerging into sunlight (Shelton 1995). In general, herbaceous species with erect, semiwoody growth habits can tolerate moderate levels of litterfall (Sydes and Grime 1981a,b). Litterfall can intercept, absorb, and facilitate evaporation of rainfall before it reaches mineral soil layers, but it also can act as a mulch to reduce evaporation from the soil and as a substrate for protecting soil structure for retention of its water-holding capacity (Ginter et al. 1979; Boyer and Miller 1994). Litterfall can reduce temperature fluctuations in the surface soil layers, and it can act as both a source and sink of nitrogen for plant nutrition. In addition, needle litter of longleaf pines is an important fuel component that can influence fire intensity and spread, especially where it accumulates around individual trees (Grace and Platt 1995; Brockway and Outcalt 1998). Monk and Gabrielson (1985) studied dynamics of species turnover in old-field herbaceous communities using treatments that combined artificial shade, presence or absence of litterfall, and trenching around isolated loblolly pines. The normal progression of changes in species composition during the 2-year study was an increase in density of perennials and a decrease in density of annuals. Presence of shade (4% of full sunlight) or litterfall accelerated the turnover or loss of annuals but only slowed the rate of succession to perennials resulting in fewer species and lower densities of individual plants. Combined effects of shade and litterfall stimulated the greatest reductions in plant density. Litterfall probably limited germination of annuals; however, the upright growth form of many of the perennial species enabled them to shed litter, especially when grown in full sun. In trenched plots, presence versus absence of litterfall strongly limited abundance of annuals but it had no detectable influence on perennials. However, in the absence of trenching, litterfall did not influence abundance of either annuals or perennials because apparently their populations were already being regulated by shade and root competition.

Recent research on longleaf pine communities has attempted to identify the critical factors limiting pine seedling development; however, as Harper (1977) points out, study design can strongly influence experimental outcomes. For example, in both natural and experimentally created gaps within longleaf pine forest, competition for light was identified as the primary factor limiting growth of longleaf pine seedlings (Palik et al. 1997; McGuire et al. 2001). Nitrogen availability increased with decreasing density of overstory trees, but the magnitude of its effect on seedling growth was secondary to light availability. Soil water availability did not vary in a systematic way with overstory density, perhaps because of broad fluctuations in rainfall. In these studies, understory vegetation either was not manipulated (McGuire et al. 2001) or it was eliminated up to 1.2 m around individual pine seedlings (Palik et al. 1997). Perhaps soil water availability did play a more prominent role in affecting seedling responses in these studies, but background effects of understory competition prevented its detection, either as edge effects in the study by Palik et al. (1997) or by varying inversely with overstory density in the study by McGuire et al. (2001).

In another example, abundance of longleaf pine natural regeneration in an uneven-aged stand did not increase substantially until the distance from overstory trees exceeded 12 m, and maximum seedling densities occurred at distances of 16 m or greater (Brockway and Outcalt 1998) (Fig. 1). Absence of strong differences in light availability and the limited size of the zone of higher fire intensity from needle

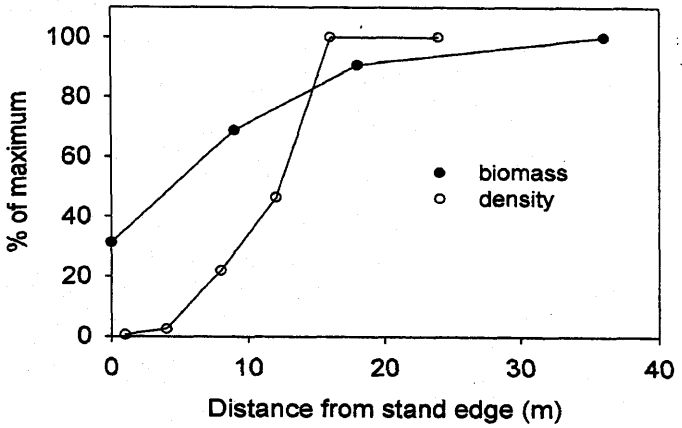


FIGURE 1. Relationships of average biomass (data from McGuire et al. 2001) and density (data from Brockway and Outcalt 1998) of longleaf pine seedlings growing within a gap versus distance from the edge of mature longleaf pine forest. Maximum values for these variables were approximately 9 g and 6700 seedlings $ha^{-1}$ for biomass and density, respectively.

litter accumulations (up to 4 m away from individual trees) prompted the authors to conclude that competition for belowground resources was the primary factor limiting pine regeneration within gaps. In the study by McGuire et al. (2001), growth of planted longleaf pine seedlings was maximized when they occurred at least 18 m from overstory trees (Fig. 1). Results of these studies imply that gaps of radius 16 m or greater (0.08 ha or larger) are needed to eliminate overstory influences. Palik et al. (1997) advocated gap sizes of 0.14 ha or larger (i.e., a radius of 21 m or larger for circular gaps) to promote growth of pine seedlings free of overstory influences. However, in each of these examples, the experimental approaches did not adequately separate and quantify overstory and understory effects to determine if consumption of belowground resources by understory vegetation was a key factor limiting pine seedling development.

Results of the canopy gap research on longleaf pine indicate that group selection is an appropriate method of regeneration. For a given stand basal area, forest stand structures that have an aggregated distribution of overstory trees will provide a higher percentage of area in larger gaps than those that retain trees evenly dispersed across a given area of land (Palik et al. 1997). Such stand structures provide a higher percentage of area with sufficient availabilities of light and nitrogen to support regeneration of longleaf pine seedlings (Battaglia et al. 2002; Palik et al. 2003). The shape and orientation of individual gaps also will influence the duration of sunlight and spatial distribution of root competition from overstory trees.

Fire is an essential feature of longleaf pine forests because of their pyrogenic characteristics of needle drape, grass-stage pine seedlings, and uniformly distributed wiregrass and bluestem (*Andropogon* spp.) (Platt et al. 1988a). Numerous studies have affirmed the benefits of fire for reducing competition from hardwoods and shrubs and for reducing needle litter accumulations that can impede establishment of longleaf pine seedlings (Boyer 1990, 1993; Glitzenstein et al. 1995; Brockway and Lewis 1997). Where wiregrass forms a dense and continuous cover under longleaf pines, variability in fire intensity may play a role in generating gaps in ground-layer vegetation that promote expansion of surviving species and colonization of new species, such as golden aster (*Pityopsis graminifolia* [Michx.] Nutt.) (Brewer et al. 1996). Because they affect burn intensity, frequency and timing of prescribed fire influence the abundance, size, and composition of understory species (Boyer 1995) as well as the timing of their flowering and seed production (Platt et al. 1988b; Brewer and Platt 1994). Hardwood mortality also varies with frequency and timing of prescribed fire. Over an 18-year period, Boyer (1993) found that stand basal area of midstory hardwoods increased following winter biennial burns (from 0.8 to 2.2 $m^2$ $ha^{-1}$), while it decreased following spring biennial burns (from 0.9 to 0.3 $m^2$ $ha^{-1}$). Van Lear and Waldrop (1991) reported that over 80% of oak (*Quercus* spp.) and sweetgum (*Liquidambar styraciflua* L.) rootstocks were killed by 10 annual burns, while only 50% of rootstocks were killed by 10 biennial burns.

The research reviewed here indicates a complex suite of factors regulates overstory and understory interactions in longleaf pine forests. Overstory effects on understory vegetation can be direct, such as competition for

limited resources or physical smothering from needle litter. These effects also can be indirect, such as spatial variation in fire intensity that results from variable rates of needle litter accumulation. Two case studies are discussed below to illustrate some of the overstory and understory interactions that occur in even-aged plantations of longleaf pine. As discussed previously, the uniform size and spatial distribution of overstory trees in even-aged plantations probably create a more homogeneous environment for studying effects of competition and facilitation than would be expected in a naturally regenerated, uneven-aged stand.

## Case Studies on Overstory and Understory Interactions in Longleaf Pine Plantations

Two case studies are presented to illustrate responses to asymmetrical competition that occur between the overstory and understory of longleaf pine plantations. The studies provide a basis for prescribing silvicultural treatments aimed at restoring plant species native to longleaf pine communities. In the first study, community-level responses (abundance and diversity) of understory vegetation were investigated in response to pine thinning and hardwood and shrub control (Harrington and Edwards 1999). In the second study, a controlled experiment was established to separately quantify competition and needle litter effects of a longleaf pine overstory on fitness and fecundity of planted populations of several perennial herbaceous species native to longleaf pine forests (Harrington et al. 2003).

## Study I: Understory Community Responses to Pine Thinning and Hardwood and Shrub Control

Initial research at the Savannah River Site on overstory and understory interactions in longleaf pine plantations focused on community responses (understory vegetation abundance and diversity) to thinning of overstory pines and control of hardwoods and shrubs with herbicides (Harrington and Edwards 1999). These silvicultural treatments were selected for study because they provided a wide range of light, soil water, and needle litter conditions in which to study understory responses. Six 8- to 11-year-old plantations of longleaf pine growing on sandhill sites were selected having average stand basal areas of 9.3 and 1.1 $m^2\ ha^{-1}$ of pines and hardwoods, respectively. Soils included loamy sands of the Blanton, Lakeland, or Troup series that were well drained to excessively well drained resulting in low to very low available water-holding capacities (Rogers 1990). A prescribed fire of moderate to high intensity was applied to each site in February 1994 and 1998. Each of the six sites was divided into four treatment areas of similar size (3 to 7 ha) and one of the following treatments was randomly assigned to each: (1) nontreated, (2) pine thinning in May 1994 to leave approximately half of the original stem density, (3) control of hardwoods and shrubs with herbicides in 1995 (grid application of hexazinone) and 1996 (spot treatments of triclopyr, imazapyr, and glyphosate), and (4) combined treatments of pine thinning and hardwood and shrub control. The experimental design is a randomized complete block with six replications (sites) of the four treatments arranged as a 2 × 2 factorial.

Within each of the 24 treatment areas, 10 sample points spaced on a 40-m grid were permanently marked for periodic vegetation measurements. At each sample point, cover was estimated for each understory species by the line intercept method (Mueller-Dombois and Ellenberg 1974) in August 1994–1996 and by visual estimation within 10 $m^2$ plots in August 1998. The data were pooled by categories of herbaceous (forbs and grasses) and woody species (hardwoods and shrubs). At the end of the 1994–1996, 1998, and 2002 growing seasons, stem diameter at breast height (millimeters at 1.37 m above ground) was measured on each pine and hardwood stem rooted within 6 m of a sample point. Height (centimeters) and crown width (centimeters

in north–south and east–west directions) also were measured annually starting in 1995 on approximately 20% of measurement trees per sample point.

Periodic annual increments in individual-tree stem basal area, height, and crown width were calculated separately for pines and hardwoods. Understory vegetation and tree growth data were averaged first by sample point and then by treatment area. Data for each measurement year were subjected to analysis of variance to identify whether main effects (pine thinning or hardwood and shrub control) or their interaction were significant ($\alpha = 0.05$). Multiple comparisons of means were conducted with either Bonferroni adjusted probabilities (for significant interactions) or Tukey's test (if only main effects were significant) (Sokal and Rohlf 1981).

## Understory Plant Abundance

Abundance of herbaceous vegetation responded dynamically to changes in stand structure, with initial decreases following the herbicide treatments, moderate increases following pine thinning, and, ultimately, large increases following the combination treatment (Fig. 2). In 1995, cover of both woody and herbaceous species varied significantly as a result of the interaction of pine thinning and hardwood and shrub control treatments. Of the four treatments, the combination treatment had the lowest overall abundance of vegetation probably because activity of hexazinone herbicide (a photosynthetic inhibitor) increased as a result of the greater light availability in the pine-thinning treatment. In 1996 and 1998, cover of understory hardwoods and shrubs was substantially less in the presence versus absence of the herbicide treatments (Fig. 2A). Cover of herbaceous species in 1996 and 1998 demonstrated strong increases in response to pine thinning. In addition, herbaceous cover in 1998 was greater in the presence versus absence of hardwood and shrub control. Pine thinning increased light availability throughout the study duration; however, it increased soil water availability only during May 1995 and 1996. In contrast, hardwood and shrub

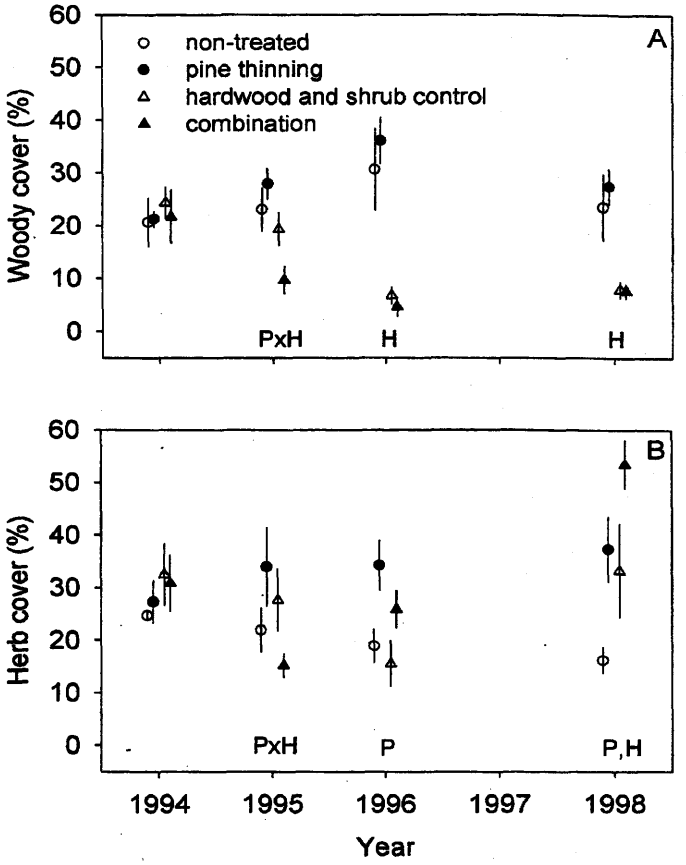


FIGURE 2. Average cover (± standard error) of (A) nonpine woody species (hardwoods and shrubs) and (B) herbaceous species during 4 to 5 years after combinations of thinning of overstory pines and control of hardwoods and shrubs with herbicides. Letters along the *x*-axis indicate factors and their interactions from the analysis of variance that were significant ($P \leq 0.05$) for a given year of the study: P = pine thinning and H = hardwood and shrub control.

control was associated with increases in soil water throughout the entire 1996 growing season. Relative differences in the magnitude of herbaceous cover responses to these treatments in 1998 indicated that light availability was the most influential factor limiting herbaceous cover (21% absolute cover reduction), although its effects were similar in magnitude to those resulting from differences in soil water availability (16% cover reduction) (Fig. 2B). Because needle litter accumulations were limited by the prescribed burns of 1994 and 1998, this factor did not appear to play a strong role in limiting development of herbaceous cover.

## Herbaceous Species Diversity

Herbaceous species density (number of species per 40 $m^2$ sample area) in 1998 varied according to the interaction of pine thinning and hardwood and shrub control (Harrington and Edwards 1999). Pine thinning alone had a greater effect on species density (33 species) than either of the hardwood and shrub control or combination treatments (30 species), and each of these responses was greater than observed for nontreated areas (25 species). A comparison of relative differences in species density resulting from pine thinning versus hardwood and shrub control main effects indicated that only thinning (increased light availability) stimulated increased diversity of herbaceous species.

## Tree Growth

Overstory and understory interactions were found to operate in both directions. That is, not only did the overstory influence understory vegetation abundance and species diversity, but the understory also influenced overstory tree growth. In each of the measurement years after 1994, pine thinning and/or hardwood and shrub control treatments were associated with growth increases in stem basal area and crown width of longleaf pine trees (Fig. 3). However, in 1995 and 1996, pine thinning was associated with reductions in height growth. Hardwood and shrub control was associated with marginal increases ($P = 0.07$) in height growth in 1996, a year noted for sustained increases in soil water from this treatment. However, 1998 height growth was less in the presence versus absence of hardwood and shrub control. Increased allocations of tree growth to stem diameter and crown width at the expense of growth in height also have been observed for loblolly pine soon after thinning an 8-year-old plantation (Ginn et al. 1991). Such shifts in growth allocation have been attributed to tree responses associated with the capture of newly available growing space rather than those associated with "thinning shock." In 1995, 1996, and 1998, pine thinning was associated with 67% to 91% increases in average basal area growth of individual hardwood trees ($P \leq 0.08$; data not shown). In 2002, pine thinning was associated with a 117% increase in average height growth of hardwoods ($P = 0.05$); however, high levels of variability among plots prevented detection of significant growth increases for stem basal area ($P = 0.11$).

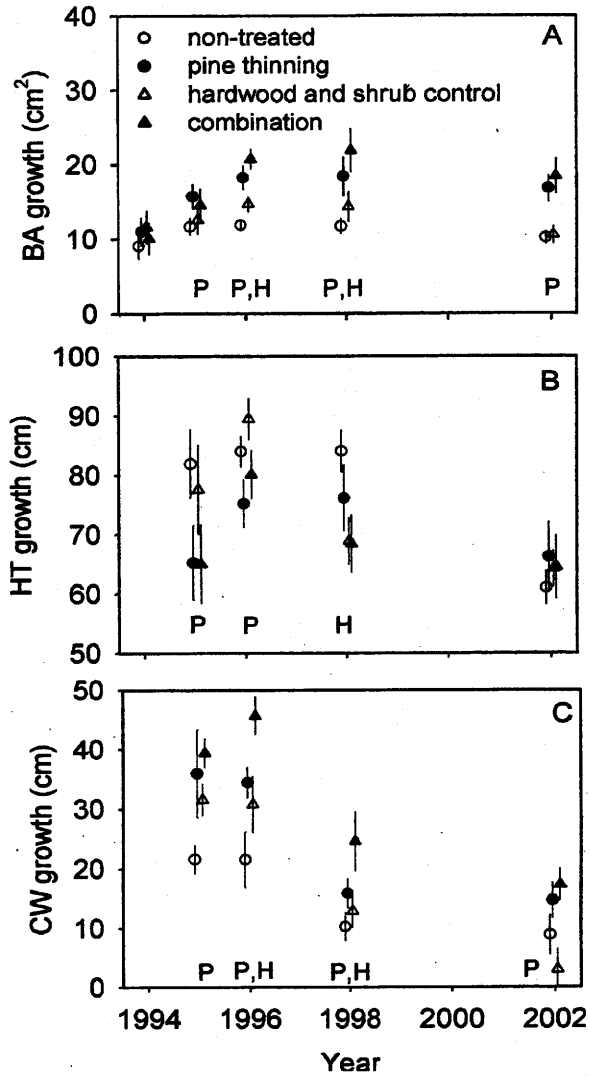


FIGURE 3. Average periodic annual growth (± standard error) in (A) stem basal area, (B) height, and (C) crown width of individual longleaf pine trees 7 to 8 years after combinations of thinning of overstory pines and control of hardwoods and shrubs with herbicides. Letters along the *x*-axis indicate factors from the analysis of variance that were significant ($P \leq 0.05$) for a given year of the study: P = pine thinning and H = hardwood and shrub control.

## Conclusions

Results of Study I indicate that availabilities of both light (via pine thinning) and belowground resources (via hardwood and shrub control) play prominent roles in maintaining abundance of herbaceous species, while perhaps only availability of light influences diversity of herbaceous species. Similarly, availabilities of both light and belowground resources played similar roles in stimulating growth increases in stem basal area and crown width of longleaf pine trees. Height growth responses to treatment varied inversely with the stem and crown responses. Although this research may only be applicable to longleaf plantations of similar age, it demonstrates a useful approach for studying community dynamics in response to silvicultural treatments.

# Study II: Effects of Above- and Belowground Competition and Needle Litter from Overstory Pines on Fitness and Fecundity of Reintroduced Herbaceous Species

A limitation of Study I was the confounding that existed between overstory competition (availability of light versus belowground resources) and needle litter because treatments were conducted at the stand level, making it impossible to separate the relative influence of each factor on understory vegetation. For example, understory conditions in nonthinned stands included growth limiting effects of competition for both light and belowground resources, making it impossible to distinguish which had the greatest influence on herbaceous vegetation. To isolate above- and belowground components of overstory competition from needle litter effects, a controlled experiment was established in 1998 according to methods described in Harrington et al. (2003). Nonsampled portions of three of the six sites from Study I were used in Study II (i.e., areas away from the sample points in the hardwood and shrub control and combination treatments). Four 0.09-ha plots (30 m × 30 m) were established in each of the 13- to 15-year-old plantations. Each plot was randomly assigned a thinning to 0, 25, 50, or 100% of the average basal area of nonthinned stands (20 $m^2$ $ha^{-1}$). In order to focus the research on overstory effects, plots were kept free of all nonpine vegetation with periodic applications of non-soil-active herbicides and hand weeding.

In the interior 20-m × 20-m area within each plot, four split-plot treatments were established to vary belowground resources and needle litter independently of pine stocking. Each of the following split-plot treatments was randomly assigned to one of four 1.2-m × 13.7-m strips in each plot: (a) trenching plus needle litter, (b) trenching minus needle litter, (c) absence of trenching plus needle litter, and (d) absence of trenching minus needle litter. Trenching was conducted in October 1998 with a Ditch Witch® (Perry, OK), aluminum flashing 0.51 m wide was installed along the vertical wall of the trench to an average depth of 0.43 m to prevent encroachment of pine roots, and the soil was replaced. In needle litter-present split plots, stand-produced needle litter was supplemented with monthly applications to result in a standardized rate (7893 kg $ha^{-1}$ $yr^{-1}$) equal to twice that predicted for nonthinned stands of 20 $m^2$ $ha^{-1}$ basal area using data from Study I. In needle litter-absent split plots, needle litter was removed manually each month. The experimental design of Study II was a randomized, complete block with three replications (sites) of the split-plot arrangement of treatments. Pine stocking was the whole-plot factor and split-plot factors were trenching and needle litter.

Fourteen perennial herbaceous species native to longleaf pine forests were selected for intensive study to represent different growth forms (e.g., upright versus prostrate) of forbs and grasses. One herbaceous species was randomly assigned to each of 10 1-$m^2$ quadrats per split plot. Containerized seedlings of the 14 species were grown in a greenhouse and

planted at a fixed density (11 to 36 plants $m^{-2}$, depending on success of greenhouse propagation) in May 1999, 2000, or 2001. Containerized seedlings of longleaf pine were purchased from International Forest Company (Statesboro, GA) and planted at a density of 36 plants $m^{-2}$ within a randomly assigned quadrat of each split plot.

Fitness of each herbaceous species was assessed as survival (%) and visually estimated cover (percentage) in October. Fecundity of each herbaceous species was assessed as inflorescence count (number of flower clusters per square meter), seed production (number of seeds produced per square meter; estimated from subsamples of 20 or more inflorescences), seed weight (grams per 1000 seeds), and seedling emergence (percentage) from standard germination tests (45 days of cold stratification followed by 3 weeks of germination in a greenhouse). In fall 2001, surviving longleaf pine seedlings growing in their assigned quadrat were severed, counted, and returned to the laboratory for biomass estimation. Fitness of longleaf pine was assessed as survival (percentage), average stem height (centimeters), average biomass (grams), and percentage of surviving trees that were exiting the grass stage, defined as those with stems 12 cm or greater in height (Haywood 2000).

To highlight the basic findings of Study II, this chapter covers responses of two perennial grasses (green silkyscale, *Anthaenantia villosa* [Michx.] Beauv., and pineywoods dropseed, *Sporobolus junceus* [Michx.] Kunth, planted May 1999 and assessed in October 2000), a perennial forb (beggar's ticks, *Desmodium ciliare* [Muhl. Ex Willd.] DC, planted May 2001 and assessed October 2001), and seedlings of longleaf pine (planted December 1998 and assessed October 2001). Analysis of variance was conducted to identify significant ($\alpha = 0.05$) treatment effects. Multiple comparisons of means were conducted with either Bonferroni adjusted probabilities (for significant interactions) or Tukey's test (if only main effects were significant) (Sokal and Rohlf 1981). Linear regression was used to quantify the relationship between average aboveground biomass and average height of longleaf pine seedlings.

## *Anthaenantia villosa* Responses

Average survival of *Anthaenantia villosa* exceeded 90% in all treatments at the end of the second year after planting, although a slight reduction was observed in the presence of needle litter (Fig. 4A). In the absence of trenching (i.e., in the presence of root competition from overstory pines), cover, number of inflorescences, and number of seeds decreased with increasing pine stocking at a more rapid rate than in the presence of trenching (Fig. 4B–D). Cover in trenched plots averaged about 80% and it did not vary among pine stockings. Cover was greater in the presence of needle litter, an effect likely attributable to nitrogen inputs associated with this treatment (Harrington et al. 2003). Seed weight did not vary significantly among treatments (Fig. 4E). Seedling emergence was less at 0% pine stocking than at 25, 50, or 100% stockings (Fig. 4F). Although plant size, flowering, and seed production each were greatest in the absence of overstory pines (0% stocking), seed viability was not. Apparently some level of overstory competition stimulated increased seed viability; thus, total reproductive effort (i.e., the product of seed production and seedling emergence) was greatest at 25% pine stocking. *A. villosa* had an interactive response pattern in which its fitness and fecundity were maximized at specific combinations of above- and belowground competition. The species was able to survive in a wide range of competitive environments, it produced the most vegetation when belowground resources were not limiting, and it produced the most viable seed in a mildly competitive environment.

## *Sporobolus junceus* Responses

In contrast to *Anthaenantia villosa, Sporobolus junceus* displayed a very different set of responses. Average survival of this species exceeded 60% for all treatments, but it decreased in the presence of either trenching or needle litter (Fig. 5A). Needle litter most likely caused shading and eventual death of suppressed individuals. Cover of *S. junceus* did not vary significantly among any of the treatments,

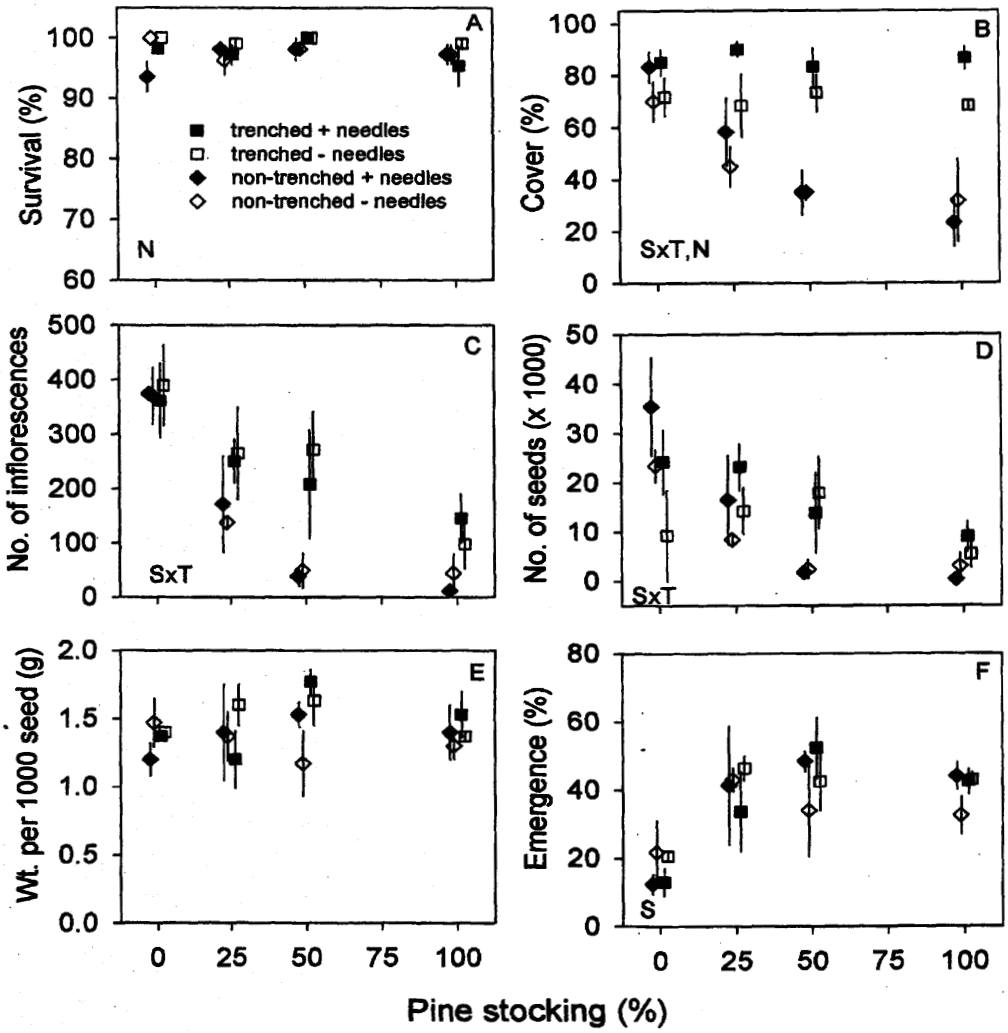


FIGURE 4. Average indices of fitness and fecundity (± standard error) of the perennial grass *Anthaenantia villosa* as influenced by stocking of overstory pines (basal area as a percentage of nonthinned stands) and presence or absence of trenching and needle litter. Letters in the lower left corner of each graph indicate factors and their interactions from the analysis of variance that were significant ($P \leq 0.05$): S = pine stocking, T = trenching, and N = needle litter.

suggesting that the species was relatively tolerant to the experimental range of resource availabilities and needle litter levels (Fig. 5B). For the trenching effects on survival, increases in belowground resources might have stimulated greater amounts of density-dependent mortality (i.e., "self-thinning"). This explanation was supported by the fact that, although survival declined slightly from trenching and needle litter effects, surviving individuals occupied the newly available growing spacing resulting in the absence of treatment effects on cover. These fitness responses contrasted sharply with the species' fecundity responses. In the presence of needle litter, inflorescence number was less than a third of that observed in its absence (Fig. 5C). In the absence of trenching, inflorescence number at 100% pine stocking was less than at the other stocking levels; however, in the presence of trenching, inflorescence number did not vary significantly among stocking levels. Seed number at 100% stocking was less than at the other stocking levels (Fig. 5D). Presence of needle litter greatly limited seed number, seed weight (Fig. 5E), and seedling emergence (Fig. 5F). *S. junceus* demonstrated a fitness response that was relatively tolerant of

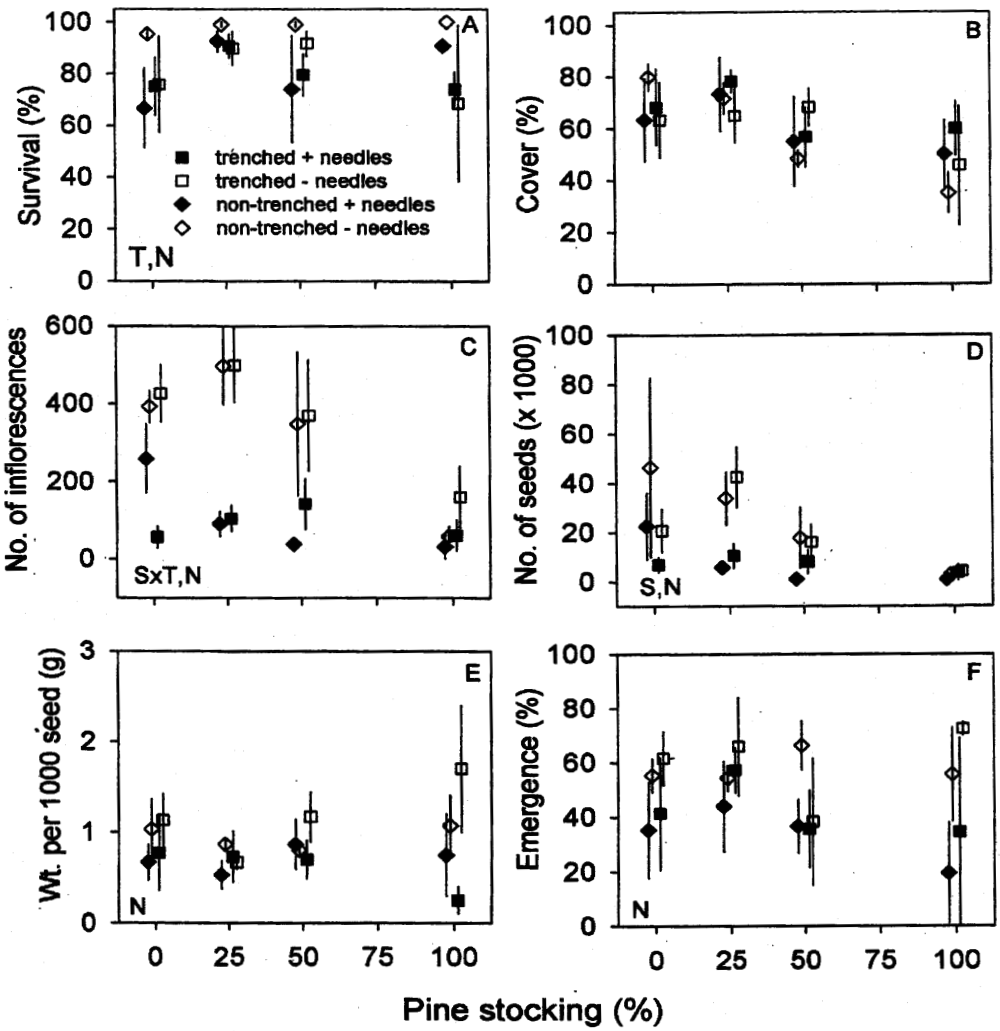


FIGURE 5. Average indices of fitness and fecundity (± standard error) of the perennial grass *Sporobolus junceus* as influenced by stocking of overstory pines (basal area as a percentage of nonthinned stands) and presence or absence of trenching and needle litter. Letters in the lower left corner of each graph indicate factors and their interactions from the analysis of variance that were significant ($P \leq 0.05$): S = pine stocking, T = trenching, and N = needle litter.

competition from overstory pines. The species was able to recover growing spacing through increases in plant size and fully occupy the site regardless of density-dependent mortality or needle litter. However, fecundity was greatly impacted primarily by needle litter (via reductions in flowering, seed production, seed size, and seed viability) and secondarily by stocking (via reductions in flowering and seed production). The mechanism underlying the strongly negative effects of needle litter on fecundity was not clear since similar effects on plant fitness were not apparent until October 2001 (Harrington et al. 2003). The species was able to thrive vegetatively in the wide range of growing conditions present in the study. Observed increases in nitrogen concentration of *S. junceus* foliage in the presence of needle litter (Harrington et al. 2003) suggested that improvements in plant nutrition might have stimulated vegetative growth at the expense of reproductive allocation. However, a more likely explanation for the fecundity responses could be the shading effects of needle litter. Fecundity responses to stocking indicated that a threshold in light availability existed below which flowering and seed production were strongly curtailed. This threshold

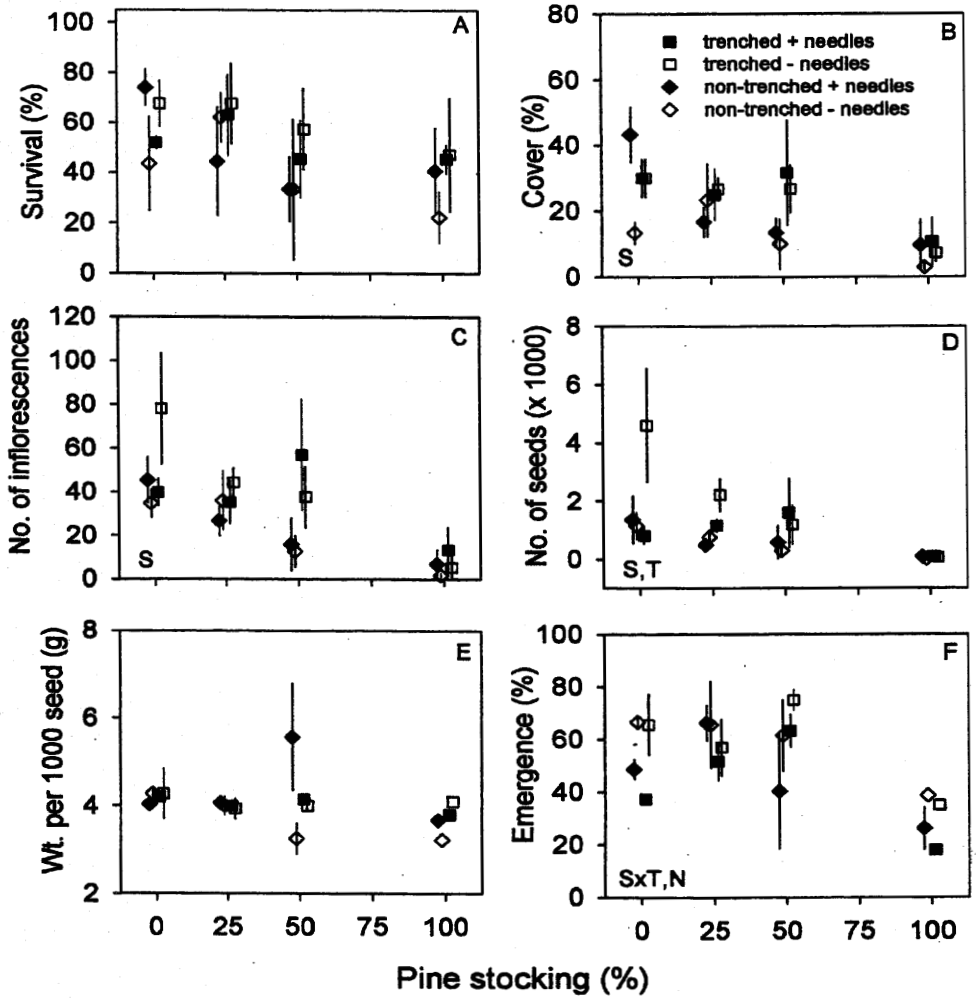


FIGURE 6. Average indices of fitness and fecundity (± standard error) of the perennial forb *Desmodium ciliare* as influenced by stocking of overstory pines (basal area as a percentage of nonthinned stands) and presence or absence of trenching and needle litter. Letters in the lower left corner of each graph indicate factors and their interactions from the analysis of variance that were significant ($P \leq 0.05$): S = pine stocking, T = trenching, and N = needle litter.

occurred between 50% and 100% stocking of overstory pines, because at lesser stockings, responses of these variables were relatively stable.

## *Desmodium ciliare* Responses

*Desmodium ciliare* responses to overstory conditions were similar to those observed for other perennial forbs in that they indicated a strong degree of intolerance to both shade and root competition from overstory pines (Harrington et al. 2003). In general, these experimental effects were additive and not interactive, suggesting that the species was able to respond to a variety of growing conditions. Although survival of *D. ciliare* declined somewhat with increasing pine stocking, these responses were not statistically significant (Fig. 6A). Cover decreased systematically with increasing pine stocking and it was especially limited at 100% pine stocking (Fig. 6B). Trenching effects on cover were marginally significant ($P = 0.06$), indicating a mild additive effect resulting from increased availability of belowground resources. Flowering and seed production responses were similar to those for cover (Fig. 6C,D): a decline with increasing stocking and

a small to moderate increase from trenching. Seed weight did not vary significantly among treatments (Fig. 6E). The interaction of stocking and trenching was significant for seedling emergence because increases from trenching were observed only at 50% stocking; all other stockings demonstrated neutral effects from trenching (Fig. 6F). In addition, there was less seedling emergence in the presence versus absence of needle litter. These results suggested that seed viability of *D. ciliare* was regulated largely by light availability determined by either or both of overstory density and needle litter. In summary, *D. ciliare* had a strong requirement for light to survive, grow, and reproduce; its potential responsiveness to enhanced belowground resources was secondary to that resulting from increased light availability.

## *Pinus palustris* Seedling Responses

*Pinus palustris* was able to survive but grew very little in response to shade and root competition from overstory pines. In the third year after planting (2001), seedling survival was greater in the presence versus absence of trenching, and it was reduced in the presence versus absence of needle litter (Fig. 7A). Stocking of overstory pines did not significantly influence either of these survival responses, suggesting that light availability was not a limiting factor for survival except when smothering from needle litter occurred. The fact that stocking had no detectable effect on survival of *P. palustris* seedlings probably was the result of adequate carbohydrate storage in the taproot of the nursery-grown seedlings that permitted the plant to tolerate severe growth-limiting conditions for several years. However, it remains uncertain how much longer these seedlings could have sustained themselves under these growing conditions. The moderate degree of survival (59% to 68%) observed in the absence of overstory competition and needle litter suggests that density-dependent mortality had occurred.

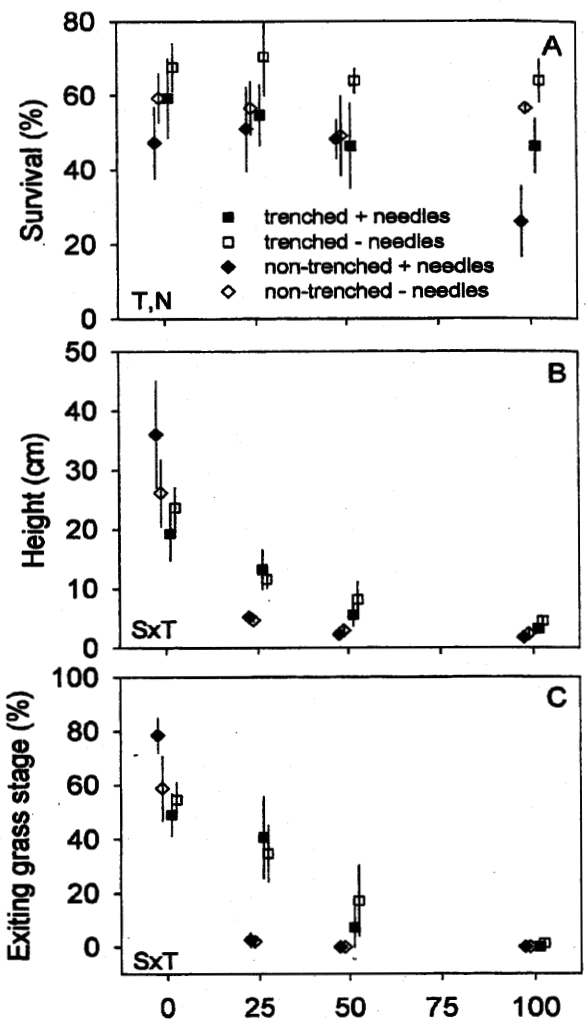


FIGURE 7. Average (A) survival, (B) stem height, and (C) percentage of survivors exiting the grass stage (± standard error) for seedlings of the tree *Pinus palustris* as influenced by stocking of overstory pines (basal area as a percentage of nonthinned stands) and presence or absence of trenching and needle litter. Letters in the lower left corner of each graph indicate factors and their interactions from the analysis of variance that were significant ($P \leq 0.05$): S = pine stocking, T = trenching, and N = needle litter.

About 97% of the variation in average aboveground biomass (grams) of longleaf pine seedlings was explained by its linear relationship with average height (centimeters) ($R^2 = 0.97; s_{y.x} = 12.2; n = 48$):

$$Y = -2.755 + 6.090(X)$$

Because of this high correlation, height and

aboveground biomass had essentially identical responses to the interaction of stocking and trenching (only height responses are shown in Fig. 7B). Both of these variables exhibited steep declines with increasing stocking but the steepness of the decline was much greater in the absence versus presence of trenching. This result indicated a strong threshold response to light availability because average height (and aboveground biomass) declined precipitously as stocking increased from 0% to 25% with subsequent increases in stocking causing only slight decreases in growth. The threshold growth response to light availability was moderated only slightly by increases in belowground resources from trenching. By the third year after planting, over half of longleaf pine seedlings growing in 0% stocking were exiting the grass stage, while less than 20% of seedlings were doing so in stockings of 50 and 100% (Fig. 7C). In contrast to the average height responses, trenching strongly increased the percentage of trees exiting the grass stage for stockings of 25 and 50%. This result is in agreement with previous research in which increased availability of belowground resources, such as resulting from control of competing herbaceous vegetation with herbicides or mulching (Haywood 2000), enabled a higher percentage of longleaf pine seedlings to exit the grass stage. However, Study II demonstrated that light availability had a much greater effect than availability of belowground resources since very few of the seedlings growing in trenched split plots at 100% stocking were exiting the grass stage. In terms of providing new saplings of *P. palustris* to ultimately replace overstory trees, only the lowest stockings (0 and 25%) averaged more than 20% of seedlings emerging from the grass stage to support their growth into the upper canopy.

## Conclusions

Results from Study II confirm some of the findings from Study I: effects of overstory competition for light and for belowground resources on understory vegetation can be of similar magnitude. Study II further illustrates the great variability in species' responses to above- and belowground competition and needle litter. However, of all the species' responses, only one indicated a positive effect of overstory shade (facilitation): seed viability of *A. villosa* was greater at pine stockings of 25% to 100% than it was at 0%. Therefore, a primary finding from Study II is that the growing conditions in gaps (i.e., full sunlight) provided the resources needed to maximize fitness and fecundity of reintroduced herbaceous species. In addition, root competition had a critically negative effect on most of the species' responses, indicating that restoration plantings will be most successful in the absence of both overstory and understory vegetation. The vigorous responses of herbaceous species observed in the relatively small gaps (30 m × 30 m or 0.09 ha) of Study II indicated that the zone of overstory root competition from neighboring 13- to 15-year-old pines extended less than 10 m into the gap. Surprisingly, plant responses to needle litter varied from positive effects (facilitation via nitrogen addition) to negative effects (apparent competition via reduced light availability). Mulching effects from needle litter (i.e., increased retention of soil water) were not detected (Harrington et al. 2003).

# Implications to Maintenance and Restoration of Longleaf Pine Communities

Previous research and the two case studies reviewed here illustrate the multiple interactions that occur between overstory pines and understory vegetation of longleaf pine forests. As indicated initially in this chapter, a mechanistic understanding of overstory and understory interactions will provide a sound basis for prescribing treatments designed to restore and maintain longleaf pine communities. In this concluding section I will discuss the implications of overstory and understory competition and facilitation to silvicultural regimes that are currently in use or being considered for longleaf pine forests. Three conditions will

be considered: new longleaf pine communities; existing herbaceous communities within natural, uneven-aged longleaf pine stands; and existing herbaceous communities within even-aged, planted longleaf pine stands.

## New Longleaf Pine Communities

Restoring all of the elements of a longleaf pine community requires coordinated establishment of longleaf pine seedlings and herbaceous species. Both vegetation components require an environment with an abundance of direct sunlight and soil water. Within existing forest, gaps 21 m in radius or larger provide such an environment. Recently harvested forest sites or old fields will have adequate light availability but not necessarily adequate soil water availability because of a potentially high abundance of competing vegetation. In order to increase soil water availability, competing vegetation abundance must be reduced significantly, at least in the individual spots where seedlings are to be established.

Spot (or banded) treatments provide a means of reducing competition without the widespread disruption in the ground layer community that can result from broadcast treatments (Brockway and Outcalt 2000). In addition, spot treatments enable existing desirable species growing between spots to be retained in an undisturbed condition. One potential technique is to create gaps in the ground layer vegetation 1 meter in radius or larger by chemical (e.g., nonsoil active herbicides, such as glyphosate or triclopyr) or mechanical methods (e.g., "Wombat" spot cultivator, Savannah Forestry Equipment, Savannah, GA).

By locating these ground-layer gaps at a spacing of 3 m or greater, the desired community components can be established over a broad area. Half of the gaps can be planted with a single longleaf pine seedling and no other vegetation, while perennial herbaceous species can be established in the remaining gaps by sowing seeds or planting containerized seedlings. The success of a spring planting of herbaceous will rely on absence of a severe frost and presence of adequate rainfall (Harrington et al. 2003); winter planting of dormant, containerized herbaceous seedlings is an untested approach that may avoid these pitfalls of spring weather.

Each ground-layer gap will have sufficient availabilities of light and soil water, at least during the first growing season, to enable establishment of the new seedlings. Alternatively, specific soil-active herbicides that are safe for pines and that provide residual control of competing vegetation (e.g., hexazinone or imazapyr) can be used specifically to create ground-layer gaps in which to plant longleaf pine seedlings. Herbaceous species susceptible to these herbicides can be established 1–2 years later after soil concentrations of such herbicides have declined sufficiently.

Nitrogen is probably the nutrient most limiting to establishment and growth of new herbaceous and pine seedlings. However, fertilizer should only be applied directly to the planting hole to avoid stimulating growth and potential dominance of other, more aggressive plant species, and the prescribed fertilizer rate should be safe for seedling roots.

Fire is a key ingredient for maintenance of new plantings, because it will suppress or kill nonadapted plant species and allow adapted species to flourish. Field observations from Study II indicated that, by the end of the first or second year after planting, most perennial herbaceous species native to longleaf pine communities can withstand dormant season fires.

## Existing Herbaceous Communities within Natural, Uneven-Aged Longleaf Pine Stands

In this forest community, many of the stand structural components already exist, and only enrichment plantings are needed to reestablish the desired native herbaceous species. Understory light availability should be adequate, although not optimum, if the uneven-aged structure of the stand is composed of

widely spaced individual trees (spacing of 11 m or greater; Platt et al. 1988a). If light availability is potentially limiting to longleaf pine seedlings and their associates, excess overstory trees should be harvested or girdled (to create wildlife habitat). As discussed previously, tree removals that result in aggregated, rather than dispersed, stand structures provide a higher percentage of growing space with high light availability. Additional canopy layers of hardwoods and shrubs cause further limitations to understory light availability, and their abundance should be reduced significantly by spot treatments that do not endanger desirable herbaceous species, such as injection with non-soil-active herbicides, girdling, or cutting.

Inherent limitations in availability of belowground resources, primarily water and nitrogen, are typical of longleaf pine communities because often they occur on sandy soils with low water-holding capacities and limited nitrogen retention. Because the pools of belowground resources can be in such short supply, full occupancy of belowground resources by overstory pines may occur at stem densities that do not provide complete crown coverage. Therefore, moderate densities of longleaf pine can be highly competitive for belowground resources. Soil water availability in this community also will be limited by understory vegetation. Although this recommendation conflicts with the findings of Palik et al. (1997) and McGuire et al. (2001) in which soil water availability did not vary systematically with overstory density, I hypothesize that if overstory and understory components were manipulated independently in natural stands of longleaf pine, their separate and significant competitive effects on soil water could be detected, as found in the longleaf pine plantations of Study II.

As discussed previously, spot (or banded) treatments can be used to create ground-layer gaps in areas at least 21 m from overstory pines. If advanced regeneration of longleaf pine is needed, mineral soil seedbeds can be created to foster germination and seedling development in years of adequate seed crops. Some of the ground-layer gaps can be located approximately 16 m from potential longleaf pine seed trees to allow pine seeds to germinate in areas of minimal competition and accumulation of needle litter from overstory trees. As discussed previously, root competition from overstory pines can create zones that exclude natural pine regeneration, and areas within 4 m of overstory pines have the potential for intense ground fires capable of killing young pine seedlings.

Reinstatement of prescribed fires in the dormant season or spring is essential for maintaining the vigor of the new plantings and to avoid overtopping by resprouting hardwoods and shrubs.

## Existing Herbaceous Communities within Planted, Even-Aged Longleaf Pine Stands

Extensive plantations of longleaf pine have been established on public lands and, as part of the Conservation Reserve Program, on former agricultural land. Often these plantations were established at spacings typical for loblolly pine (e.g., up to 1800 trees $ha^{-1}$). As mentioned previously, belowground resources may not be adequate to support long-term development of longleaf pine established at close spacings, especially on sandhill sites. Under these conditions, mortality from bark beetles (*Dendroctonus* spp. and *Ips* spp.) is likely, as has been observed recently in nonthinned stands of Study I. To foster long-term health of the forest community, densely stocked plantations can be thinned to wide spacings (5 m or more) prior to engaging in understory restoration. Within the widely spaced stands, gaps 21 m in radius or larger can be established for understory restoration. Conversely, an aggregated stand structure can be created to maintain some areas of higher stocking for timber production while providing open areas for understory restoration.

Because of uniformity of spacing and size of trees, plantations will have regions of restricted light availability even after the preceding stocking guidelines have been followed. To provide adequate light and soil water availability, ground-layer gaps can be established

away from overstory trees and on the north side of overstory gaps. Results from Study II suggest that the critical zone of root competition extends less than 10 m away from 13- to 15-year-old longleaf pines, unlike the 18-m zone observed for mature trees (Brockway and Outcalt 1998). Note that restrictions in light availability in longleaf pine plantations are likely to become more intense with decreasing space among trees and increasing site quality.

Based on Study II, reintroduced herbaceous and longleaf pine seedlings will have a wide range of fitness and fecundity responses in the understory of a longleaf pine plantation. Responses are likely to range from increases in vegetative growth at the expense of reproductive performance to gradual declines in response to needle litter accumulations. This diversity of plant responses indicates that a diversity of growing conditions would be needed to maintain a full gamut of species in the understory. Applications of prescribed fire, vegetation management, and pine thinning can be scheduled at appropriate times to create pockets of enhanced resource availability that foster flowering, seed production, and recruitment of new seedlings. In time and given appropriate maintenance treatments, reintroduced plant species are likely to form stable populations that are self-perpetuating.

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