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PERFORMANCE OF PLANTED HERBACEOUS SPECIES IN LONGLEAF PINE (*Pinus palustris* Mill.) PLANTATIONS: OVERSTORY EFFECTS OF COMPETITION AND NEEDLEFALL

by

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DEDICATION

To Tim,

"When you are inspired by some great purpose, some extraordinary project, all your thoughts break their bounds: your mind transcends limitations, your consciousness expands in every direction and you find yourself in a new, great and wonderful world. Dormant forces, faculties and talents become alive, and you discover yourself to be a greater person by far than you ever dreamed yourself to be."

--Patanjali

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Longleaf pine (*Pinus palustris* Mill.) once dominated one of the most extensive forest ecosystems in North America and has nearly vanished without notice (Landers et al. 1995, Outcalt 2000). The natural range of longleaf pine covers most of the Atlantic and Gulf Coastal Plains, from southeastern Virginia to eastern Texas and south through the northern two-thirds of Florida, with extensions into the Piedmont and mountains of northern Alabama and northwestern Georgia (Landers et al. 1995). Today, only 3% of the original acreage in longleaf pine forest remains (Landers et al. 1995, Outcalt 2000). The primary factors thought to be responsible for the near disappearance of longleaf pine forests from the Southeast are regenerative failure of longleaf, fondness of feral livestock for the seedlings, and fire suppression during the last century (Frost 1993).

Natural longleaf pine forests are distinguished by their diverse herb-dominated understory plant communities and associated animal communities (Glitzenstein et al. 1993). With fire suppression from 1920 to 1950 longleaf pine savannahs have been replaced with dense, stratified stands of overstory pines, midstory hardwoods, and understory shrubs. In many cases, loblolly pine (*Pinus taeda* L.) has replaced the longleaf because its shade tolerance and seed production are superior to those of longleaf pine (Baker and Langdon 1990). In these replacement stands, midstory hardwoods often consist of turkey oak (*Quercus laevis* Walt.), bluejack oak (*Quercus incana* Bartr.), and blackjack oak (*Quercus marilandica* Muenchh.). Understory vegetation is large and abundant comprising species such as sumac (*Rhus* spp.), sparkleberry (*Vaccinium* spp.), and waxmyrtle (*Myrica cerifera* L.). In addition, vine species such as Japanese honeysuckle (*Lonicera japonica* Thunb.), yellow jessamine (*Gelsemium sempervirens* St.Hil.), and greenbrier (*Smilax* spp.) invade longleaf pine sites. These conditions limit light availability in the understory, resulting in reductions in herbaceous plant production and species diversity (Brockway et al. 1998).

Restoration efforts and silvicultural methods

Longleaf pine can be naturally or artificially regenerated at a reasonable cost and with a high probability of success if necessary cultural measures are properly timed and executed (Landers et al.1995). However, many of the treatments used, such as herbicides and bedding can reduce abundance of herbaceous species. In addition, longleaf pine plantations are distinctly different from naturally occurring longleaf pine communities that have long been characterized by their open, grassy understories (Grelen and Enghardt 1973). Plantations, often established at densities of 1500 to 1800 trees/ha, can negatively impact understory species because of their dense canopy and needlefall. Shoot morphology and growth habit of herbaceous species can determine their ability to tolerate the smothering effects of needlefall (Sydes and Grime 1981a, 1981b). Species with erect, semi-woody growth habits are generally expected to be more tolerant of litterfall deposition than those with spreading, non-woody growth habits.

Light is an obvious ecological factor affecting understory vegetation. Numerous studies have shown that silvicultural treatments that increase light availability, such as herbicides, thinning, and burning, used individually or in combination, can promote herbaceous understory vegetation (Wolters 1981). Intensive thinning and control of woody vegetation with herbicides in 8- to 11-year-old plantations of longleaf pine resulted in increased abundance and species diversity of herbaceous species (Harrington and Edwards 1999). Increased herbaceous abundance also resulted following thinning and prescribed burning in longleaf pine stands in central Louisiana (Grelen and Enghardt 1973, Wolters 1981).

Herbicide use has been successful in restoration of longleaf pine communities because of its ability to mimic some of the effects of burning such as decreasing hardwood abundance and litterfall accumulation (Hay-Smith and Tanner 1994, Brockway and Outcalt 2000). Tolerance of plant species to specific herbicides can allow them to flourish in the absence of other competing vegetation. For example, on drier sandy sites hexazinone (Velpar®) has been shown to release species such as wiregrass (*Aristida stricta* Michx.), arrowroot (*Zamia pumila* L.), yellow jessamine (*Gelsemium sempervirens* St.Hil.), greenbriers (*Smilax* spp.), and blueberries (*Vaccinium* spp.) (Glitzenstein et al.1993). On wetter sites imazapyr (Arsenal® AC) has been shown to release blackberries (*Rubus* spp.), legumes, and elms (*Ulmus* spp.) (Boyd et al. 1995).

Although light is a critical resource to understory vegetation, it may not operate independently to facilitate survival, growth, and reproduction of understory vegetation. Under a dense forest canopy, most factors of the microclimate and soil differ from those characterizing similar but open sites, with soil moisture the most obvious of growth limiting factors (Spurr and Barnes 1992, Riegel et al. 1992).

One experimental technique for studying differences in above- and below-ground resources in forest canopies is trenching, in which roots of overstory trees are cut and excluded from specific areas under a forest canopy in order to eliminate competition for soil water and nutrients without altering light availability. In one study, trenching under an overstory of Scots pine (*Pinus sylvestris* L.) showed dramatic increases in growth of understory pine seedlings, indicating that soil moisture, and perhaps nutrients, were limiting their growth (Spurr and Barnes 1992). Other trenching studies with white pine (*Pinus strobus* L.) in New Hampshire (Toumey and Kienholz 1931), loblolly pine in North Carolina (Korstian and Coile 1938), grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.) in western Montana (McCune 1986), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in northeastern Oregon (Riegel et al. 1992) report similar results showing trenching to increase survival and growth of understory vegetation. However, the process of trenching is not practical for use as a silvicultural treatment on a large scale. Irrigation and fertilization may be more sensible approaches for increasing availability of soil water and nutrients to understory vegetation. A more recent study on ponderosa pine in eastern Oregon showed that irrigation and fertilization also increased the aboveground biomass of the understory by 36% as compared to untreated plots (Riegel and Miller 1991).

Pine needlefall is another environmental factor that has direct and indirect effects on the understory community. Southern pines shed their needles throughout the year, and their presence on the forest floor intercepts light, shades seeds and seedlings and reduces the thermal amplitude in the soil (Facelli and Pickett 1991). In addition, pine needlefall can act as a physical barrier preventing seedling and sprout emergence and seeds from reaching mineral soil layers. Litter can also act to intercept, absorb, and facilitate evaporation of rainfall before it reaches mineral soil, and it can act as a mulch to reduce evaporation from the soil (Ginter et al. 1979).

The nutrient value of pine needles is important to consider. Pine litter does help support growth, especially on infertile soils, by returning a large portion of the nutrients absorbed by the trees back to the soil (Morris et al. 1992). In the absence of pine litter, the cycle is interrupted and a reduction in tree growth may be observed (Morris et al. 1992). Pine litter removals in a single commercial harvest remove an average of about 21 kg/ha of nitrogen, 1.5 kg/ha of phosphorous, 1.2 kg/ha of potassium, 9.7 kg/ha of calcium and 2.3 kg/ha of magnesium (Morris et al. 1992). Pine litter removal can also result in increased tree water stress on dry sites (McLeod et al. 1979).

Past research on understory species in longleaf pine forests

Because of the high diversity of plant species per unit area, longleaf pine ecosystems are considered one of the most species-rich communities outside of the tropics (Peet and Allard 1993). The loss of these communities has resulted in the increased rarity of 389 plant species with 187 of them considered rare region-wide (Walker 1993). A more recent list now includes an additional 250 species (http://www.talltimbers.org/research.html).

Previous research on the reintroduction of understory species in longleaf pine forests has focused primarily on wiregrass (*Aristida* spp.). Wiregrass is often cited as a keystone species of longleaf communities because it provides essential fuel for the fire regime necessary to maintain them (Seamon et al. 1989). Research findings on wiregrass indicate that it can be regenerated from seed with relative ease (Seamon et al. 1989); however, wiregrass is dependent on fire during the growing season to stimulate its rapid vegetative growth, flowering, and seed production (Clewell 1989). Recent studies on wiregrass have been conducted to determine effects of different site preparation and fertilizer application on seedling survival and growth (Outcalt et al. 1999) and the potential seed production following prescribed burns from May through August (Outcalt 1994). Results indicate that cultivation and fertilization can decrease the time required for wiregrass to reach seed-bearing age by two years in the presence of growing season fire.

Research on other plant species includes the reintroduction of *Parnassia caroliniana* Michx., a rare forb of wet longleaf pine flatwoods and savannas (Glitzenstein et al. 1998) and *Conradina glabra* Shinners, a rare shrub of dry longleaf pine habitats (Gordon 1996). Both of these reintroductions were for conservation purposes because these species were endangered and records of known populations were at less than ten locations (Glitzenstein et al. 1998, Gordon 1996). Most recent is a study by Glitzenstein et al. (2000) that reviews methods for initiating plant populations that incorporates information from research on numerous plant species of the outer South Carolina Coastal Plain.

Further research is needed to expand our understanding of the biology of understory plant species and the effects of silvicultural treatments on their habitat and population stability. The purpose of this study was to examine the performance of reintroduced understory species to experimental manipulations of overstory competition and needlefall to determine which of these factors might be critical for their success. By increasing our understanding of overstory competition and needlefall, this research will provide better insight into how silvicultural treatments can be used in restoration efforts to stimulate increases in understory abundance and diversity.

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CHAPTER 2

PERFORMANCE OF PLANTED HERBACEOUS SPECIES IN LONGLEAF PINE (*Pinus palustris* Mill.) PLANTATIONS: OVERSTORY EFFECTS OF COMPETITION AND NEEDLEFALL[1]

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ABSTRACT

Overstory and midstory vegetation layers limit abundance and species richness of understory herbaceous plants in longleaf pine (*Pinus palustris* Mill.) plantations, yet the specific mechanisms are poorly understood. In fall 1998, we initiated research to determine the separate effects of above- and belowground competition and needlefall of overstory pines on understory plant performance. Four levels of overstory pine thinning (0, 25, 50, and 100% of unthinned basal area) were applied to 0.09-ha plots in three 13- to 15-year-old plantations at the Savannah River Site near Aiken, SC. Within each plot all non-pine vegetation was removed and four subplots were randomly assigned to receive combinations (presence or absence) of trenching to a 0.4 m depth and needlefall at twice the rate of fully stocked plots. Containerized seedlings of twelve herbaceous species were grown in a greenhouse, planted within each split plot (seven species in 1999 and five species in 2000), and their survival, height, cover, and biomass were monitored for one or two growing seasons. Periodic monitoring of overstory crown closure, soil water content, temperature, and nutrients was conducted. Crown closure varied from 0% to 80% with increasing pine stocking. In the absence of trenching, soil water decreased with pine stocking but in trenched subplots it was significantly greater and less variable despite the droughts of 1999 and 2000. Above- and belowground competitive effects of overstory pines on species performance were either interactive or additive. Species with interactive effects had similar performance with increasing pine stocking in the presence of trenching, but declining performance in its absence. The combination of 100% pine stocking, absence of trenching, and presence of needlefall generally resulted in the poorest performance. Species with additive effects had declining performance with increasing pine stocking that was independent of responses due to trenching or needlefall. Results indicate that competition for light had a more detrimental effect on performance of herbaceous species in longleaf pine plantations than that resulting from competition for belowground resources.

KEY WORDS: Restoration ecology, Understory vegetation, Containerized reproduction

INTRODUCTION

Longleaf pine (*Pinus palustris* Mill.) once dominated one of the most extensive forest ecosystems in North America (Landers et al 1995, Outcalt 2000). Today only 3% of its original distribution remains (Landers et al. 1995, Outcalt 2000). The primary factors thought to be responsible for the near disappearance of these forests are regeneration failure of longleaf pine, fondness of feral livestock for its seedlings, and fire suppression during the last century (Frost 1993).

Fire suppression since 1920 has resulted in the replacement of longleaf pine savannahs with dense, stratified stands of overstory pines, midstory hardwoods, and understory shrubs. In many cases, loblolly pine (*Pinus taeda* L.) has become dominant because its shade tolerance and seed production are superior to those of longleaf pine (Baker and Langdon 1990). In these replacement stands, midstory hardwoods often consist of the turkey oak (*Quercus laevis* Walt.), bluejack oak (*Quercus incana* Bartr.), and blackjack oak (*Quercus marilandica* Muenchh.). Understory vegetation can be large and abundant with species such as sumac (*Rhus* spp.), sparkleberry (*Vaccinium* spp.), and waxmyrtle (*Myrica cerifera* L.). In addition, vines such as Japanese honeysuckle (*Lonicera japonica* Thunb.), yellow jessamine (*Gelsemium sempervirens* St.Hil.), and greenbrier (*Smilax* spp.) can form additional layers in the canopy. Such stand structures reduce light availability in the understory, resulting in reduced abundance and species richness of understory vegetation (Harrington and Edwards 1999).

Outside of the tropics, longleaf pine ecosystems are considered to be among the most species-rich forest communities because of their high density of plant species per unit area (Peet and Allard 1993). However, decreasing acreage of the open stand structures typical of longleaf pine has resulted in habitat loss and increased rarity of 389 vascular plant species of which 187 species are considered rare region-wide (Walker 1993). Walker's list, available online (http://www.talltimbers.org/research.html), now includes 250 additional species.

To restore these communities it is often necessary to plant longleaf pine and to reintroduce certain native herbaceous species. Longleaf pine can be naturally or artificially regenerated at a reasonable cost and with a high probability of success if necessary cultural measures are properly timed and executed (Landers et al.1995). However, site preparation treatments such as herbicides and bedding can reduce abundance of herbaceous species (Outcalt 1988, Harrington and Edwards 1999). In addition, longleaf pine plantations are distinctly different from naturally occurring longleaf pine communities that have characteristic open and grassy understories (Grelen and Enghardt 1973). Plantations often contain much higher stand densities (1500 to 1800 trees/ha) that negatively impact the understory species because of their dense canopy and needlefall.

Previous research on the reintroduction of understory species in longleaf pine stands has focused primarily on wiregrass (*Aristida* spp.). Wiregrass, often cited as a keystone species of many longleaf pine communities, provides essential fuel for the fire regime necessary to maintain these communities (Seamon et al. 1989). Research findings on wiregrass indicate that it can be regenerated from seed with relative ease (Seamon et al. 1989); however, the species is dependent on fire during the growing season to stimulate rapid vegetative growth, flowering, and seed production (Clewell 1989).

Recent studies on wiregrass have been conducted to determine effects of different site preparation and fertilizer treatments on seedling survival and growth (Outcalt et al. 1999) and the potential seed production following prescribed burns from May through August (Outcalt 1994). Results indicate that cultivation and fertilization can decrease the time required for wiregrass to reach seed bearing age by two years when used in conjunction with a growing season fire.

In forest communities, light is perhaps the most obvious resource with the potential to limit growth of understory vegetation. Previous research has shown that silvicultural treatments that increase light availability (e.g., herbicides, thinning, and burning) will result in increased abundance of understory vegetation (Grelen and Enghardt 1973, Wolters 1981, Brockway et al. 1998, Harrington and Edwards 1999). However, light is not the only environmental factor affecting understory vegetation. Under a dense forest canopy, most factors of the microclimate and soil differ from those characterizing similar open sites, with soil moisture a paramount factor (Spurr and Barnes 1992, Riegel et al. 1992).

A common experimental technique for studying differences in above- and below-ground resources in forest canopies is trenching, in which roots of overstory trees are cut and excluded from specific areas under a forest canopy in order to eliminate competition for soil water and nutrients without altering light availability. Trenching studies on a variety of tree species have shown that root competition can be more limiting to growth of understory vegetation than light, even under dense canopies (Korstian and Coile 1938, Toumey and Kienholz 1931, McCune 1986, Riegel et al. 1992).

Pine needlefall is another environmental factor that potentially can influence understory vegetation. Southern pines shed their needles throughout the year, and their presence on the forest floor intercepts light, shades seeds and seedlings and reduces the thermal amplitude in the soil (Facelli and Pickett 1991). In addition, pine needlefall can act as a physical barrier preventing seedling and sprout emergence and seeds from reaching mineral soil layers. Litter can also act to intercept, absorb, and facilitate evaporation of rainfall before it reaches mineral soil layers, and it can act as a mulch to reduce evaporation from the soil (Ginter et al. 1979).

In order for community restoration to be successful, key factors that limit the establishment and maintenance of reintroduced understory vegetation must be identified. Therefore, the purpose of this study is to examine the performance of reintroduced understory species by experimentally manipulating levels of overstory competition and needlefall to determine how these factors limit understory plant performance. The primary hypotheses tested were whether performance of reintroduced understory vegetation varies among levels of pine stocking, presence or absence of trenching and needlefall, or their interaction. In addition, three other hypotheses were tested:

1) The negative effects of overstory competition on performance of reintroduced understory vegetation will exceed those of needlefall.
2) Peak performance of reintroduced understory vegetation will occur at low densities of longleaf pine, because of lessened competitive effects and potential moderation of temperature extremes and evaporative losses by the overstory.

3) At high densities of longleaf pine, negative effects of belowground competition and needlefall will combine, resulting in a disproportionate reduction in performance of reintroduced understory vegetation.

METHODS

Study sites and treatments

The study was conducted at three sites located on the Savannah River Site (SRS), a National Environmental Research Park near Aiken SC. At study initiation, the sites (Williston, Par Pond, and Dunbarton) supported 13- to 15- year-old plantations of longleaf pine previously described by Harrington and Edwards (1999). In 1994, pine density in non-thinned areas varied from 1410 to 1470 trees/ha. Soils include loamy sands of the Blanton (Grossarenic Paleudults), Lakeland (thermic, coated Typic Quartzipsamments), and Troup (loamy, siliceous, thermic Grossarenic Paleudults) series. The sites had been broadcast burned in March 1994 and January 1998 by the Savannah River Forest Station, USDA Forest Service.

At each of the three study sites (experimental blocks), four 30-m x 30-m plots were installed. Because the research focused on effects of overstory pines, plots were located in areas that had received herbicide treatments in 1995 and 1996 to control non-pine woody vegetation (Harrington and Edwards 1999). Three of the plots were located in areas that were thinned June 1994 to remove approximately half of the trees per hectare (Harrington and Edwards 1999), while the fourth plot was located in an unthinned area. Non-pine woody vegetation was removed with a September broadcast application of glyphosate in water (Accord® at 5 kg acid equivalent/ha in 124 l/ha of spray plus 0.5% surfactant) and an October spot treatment of triclopyr in oil (10% solution of Garlon® 4 in JLB improved plus oil). In October 1998-2000, diameter at breast height (1.37 m aboveground) was measured on each pine located within a given plot; these data were used to calculate stand basal area. The mean basal area of the three unthinned plots (19.8 m^2/ha) was defined as 100% stocking, and the remaining three plots were randomly assigned pine densities of 0, 25, 50% of full stocking. Pines were cut with chainsaws in October 1998, and a low thinning method was used to remove trees in the 25 and 50% stockings.

Within each plot, four split-plot treatments were established to vary belowground resources (presence or absence of trenching) and needlefall (presence or absence) independently of pine stocking. The experimental design of the study is a randomized, complete block with a split-plot arrangement of treatments. Pine stocking is the whole-plot factor and split-plot factors are trenching and needlefall (presence or absence) in a 2x2 factorial arrangement. Split-plots were oriented with their long axes in a north-south direction to eliminate possibility of systematic location effects. Each split plot, 1.2 m x 13.7 m in dimension, was located randomly within a given plot and contained a linear arrangement of eleven 1-m^2 quadrats (Figure 1). Ten of the eleven quadrats were used for two cohorts of plantings. Selected species of herbaceous vegetation were planted in the spring of 1999 (seven species) or 2000 (five species) and their performance was monitored through the end of 2000. The additional quadrat remained unplanted for the duration of the study and was used to measure soil water content and surface temperature in the absence of understory vegetation.

Trenching was accomplished mechanically with a Ditch Witch® (Perry OK), aluminum flashing 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. For the duration of the study needlefall rates in the two split-plot treatments were held constant at twice the mean monthly value (g/m^2) predicted for unthinned stands of basal area 20 m^2/ha, based on a regression equation from needlefall data collected March 1995 to February 1997 from the same study sites (Harrington and Edwards 1999). This needlefall application rate was chosen to provide a high but constant rate of needlefall similar to that of a fully stocked, mature stand of longleaf pine. Needlefall removal in the remaining two split-plot treatments was done monthly by hand to prevent damage to the planted herbaceous species. Monthly hand weeding within the split-plots was conducted for the duration of the study to eliminate the effects of interspecific competition. A 5% solution of glyphosate (Accord®) in water with 0.5% concentration of surfactant was carefully applied as needed to remove weeds from areas surrounding the split-plots.

Propagation techniques

Selections of herbaceous species for reintroduction were based upon availability of seed at time of collection, expert advice, uniqueness of species (i.e., species that vary in growth habit and include a variety of grasses and forbs), and success in propagation (Table 1). In addition, longleaf pine was included as a reintroduced species to study its potential to survive and grow in the various treatments.

Seed was collected during October and November of 1998 and 1999 at SRS. In 1999, seed was also collected at the Gopher Heritage Preserve located near Windsor SC.

With little or no past research on these herbaceous species and to ensure successful propagation, twice the amount of species needed for each cohort and many times the amount of seed needed for each species were collected. During autumn 1998 and 1999, greenhouse trials were conducted to identify a subset of the species that could be propagated successfully as containerized stock. Each herbaceous species was cultivated by germinating cold-stratified seed (45 days in dark, cool, and moist conditions at approximately 4°C) and growing the seedlings in a greenhouse for four months within containers (93 cm^3). To avoid potential injury from a late spring frost, herbaceous species were planted in early May 1999 (eight species) and 2000 (five species) with containerized dibbles (International Forest Company, Odenville AL). In December 1998, containerized seedlings of longleaf pine were purchased and planted similarly in the appropriate quadrats.

To accommodate the second cohort, three species from the first cohort were removed in May 2000 with a foliar application of glyphosate herbicide (5% solution of Accord® in water with 0.5% concentration of surfactant). For most of the species studied 36 individuals were planted per quadrat; however, limited propagation of several species resulted in planting densities as low as 11 individuals per quadrat (Table 1). Each quadrat was surrounded by a 0.10-m hand-weeded buffer to reduce competition from neighboring plants.

Vegetation measurements

Survival, maximum height (cm), and cover (%; estimated visually) were recorded for each quadrat in June, August, and October of 1999 and 2000. In August of 1999 and

2000, the average plant (estimated visually) within each quadrat was clipped, returned to the laboratory, dried at 65°C to a constant weight, and weighed (g).

Foliar samples of *S. junceus* were collected in August 2000. After determination of dry weight, the average plant was analyzed for total nitrogen (N), phosphorous (P), and potassium (K) concentrations and content. Samples were ground to pass a 2 mm screen and digested following the procedures of Isaac and Johnson (1976) to obtain % N, those of Chapman and Pratt (1961) for total K, and those of ALPKEM (1996) for total P.

Measurements of environmental conditions

Crown closure. In August 1998-2000, a vertical densitometer (Geographic Resource Solutions, Arcata CA) was used to determine presence or absence of overstory pine cover (scored as 1 or 0, respectively) above each of 60 points per plot that were located at 1-m intervals along four transects oriented at a randomly-selected azimuth. The average of these readings provided an estimate of the proportion of the plot covered by crowns of overstory pines.

Soil surface temperature. Hobo® sensors (Pocasset, MA) were used to record soil surface temperature at 1.2 hour intervals from June to October 2000 in non-trenched, needlefall-absent split plots. Sensors were placed in each of the non-vegetated and *S. junceus* quadrats. Values of soil surface temperature were averaged to provide mean daily values.

Soil water availability. Volumetric soil water content (%) at 0- to 0.45-m depth was measured monthly from May 1999 to October 2000 using a Trase® time domain reflectometry (TDR) system (Soil Moisture Equipment, Inc., Santa Barbara CA). A pair of 0.45 m stainless steel rods was inserted vertically into the center of each non-vegetated quadrat. In February 2000, an additional pair of rods was installed within each *S. junceus* quadrat. Rods remained permanently in place throughout the duration of the study. Daily precipitation was recorded by staff of the USDA Forest Service, Savannah River Forest Station at a centrally located site on SRS.

Available soil nitrogen. From June to October 2000, soil samples (25 mm cores) were collected from a 0 to 0.15-m depth within each non-vegetated quadrat. In the laboratory, 30 ml of 2 mol L^{-1} KCL were added to 5 g soil. Extraction of exchangeable ammonium and nitrate from each soil solution was performed according to the methods of Keeney and Nelson (1982). Ammonium and nitrate values were combined to provide an index (ppm) of available soil nitrogen (N).

Statistical analyses

All analyses were performed with the Statistical Analysis System (SAS Institute, Inc. 1989). Prior to analysis of variance (ANOVA), logarithmic transformations of height and biomass and angular transformations of variables expressed as proportions (survival, cover, crown closure soil water, and foliar nitrogen) were applied to ensure normality of the residual variances. Plot-level estimates of crown closure for each year were subjected to ANOVA to test for significant (α=0.05) differences among pine stockings. For each sample period, quadrat-level variables of plant performance, soil water content, and soil and foliar nutrient content were subjected to ANOVA to test for significant differences among stocking, trenching, and needlefall treatments and their interactions. Maximum observed soil water content per TDR-rod pair was used as a covariate in the soil water ANOVA (Harrington and Edwards 1999). Multiple comparisons of adjusted (least-square) means from the ANOVA were performed with Bonferroni adjusted probabilities (α=0.05) (Sokal and Rohlf 1981). To test the relationship of foliar N to available soil N (expressed in logarithms), linear regression was used to compare intercept and slope parameters among levels of stocking, trenching, and needlefall (Sokal and Rohlf 1981).

RESULTS

Pine basal area and crown closure

In the two growing seasons since thinning the pine plantations, basal area has increased by 15, 28, and 32% for the 100, 50 and 25% pine stockings, respectively (Figure 2). In contrast, crown closure increased at a slower rate, particularly in the 25 and 50% stockings, where little change occurred from 1999 to 2000.

Environmental Conditions

Precipitation

Growing season (May through October) precipitation was 55.6 and 48.3 cm in 1999 and 2000, respectively (SRFS 2000). Long-term (1965-1985) average growing season precipitation for the SRS is 62.5 cm (Rogers 1990). Although both years were drier than normal, precipitation was sufficient in 1999 at the time of planting to ensure adequate survival (see *Plant Performance* below). In contrast, rainfall for May 2000 was less than 1.1 cm, which negatively impacted survival of seedlings planted in that year.

Soil water content

For most of the 18 months in which monitoring occurred, soil water content in non-vegetated quadrats varied significantly as a result of either the interaction of pine stocking and trenching (SxT) or trenching by itself. Generally, for months in which significant differences were found, soil water content was greatest at 0% stocking and in the presence of trenching. In the absence of trenching, soil water declined consistently as stocking increased from 50 to 100% (Figure 3). However, in the presence of trenching, soil water availability was influenced very little by stocking. These responses indicate that trenching successfully partitioned competition from pine into above- and belowground components. During several periods in the 1999 and 2000 growing seasons, soil water in non-trenched plots dropped below 6%, the assumed permanent wilting point for these soils (Harrington and Edwards 1999); trenching greatly reduced the effects of soil drought during these periods (Figure 3).

Soil water content responses for *S. junceus* quadrats differed from those for non-vegetated quadrats. Significant ($P \leq 0.047$) differences due to trenching and needlefall were found for some months. For months in which treatment effects were significant, soil water content was greater in trenched split-plots and in split-plots treated with needlefall.

Of the eight months in which monitoring occurred in both the non-vegetated and *S. junceus* quadrats, significant differences existed between the two quadrats for six of these months. For five of these months, soil water content was significantly ($P \leq 0.003$) greater in the presence versus absence of vegetation (i.e., *S. junceus* versus non-vegetated quadrats). In June 2000, soil water content dropped below 6% and a significant ($P \leq 0.006$) interaction between stocking and vegetation presence was detected. Closer evaluation of this interaction indicated that soil water content decreased linearly with stocking and the non-vegetated quadrats contained more water than *S. junceus* quadrats at each stocking.

Soil nitrogen

Treatment responses for available soil nitrogen (N) were not consistent among the five months in which sampling took place. In June, soil N was significantly greater in the presence (1.66 ppm) versus absence (3.16 ppm) of trenching ($P \leq 0.001$). ANOVA results for July indicated a significant ($P \leq 0.047$) three-way interaction between pine stocking, trenching, and needlefall (SxTxN), but multiple comparisons indicated significant differences only between the largest and smallest treatment means. Soil N in August was less ($P \leq 0.075$) in the presence versus absence of needlefall while in September these differences were reversed ($P \leq 0.05$). Treatment effects for October were not significant ($P \geq 0.184$).

Temperature

In each sample month from June to October, soil surface temperature differed among pine stockings ($P \leq 0.06$), with mean daily values decreasing linearly with increasing stocking. Growing season averages were 27.4° C, 26.4° C, 25.6° C, and

24.9°C for 0, 25, 50, and 100% stocking levels, respectively. The long-term (1965-1985) average air temperature for the same time period is 24.4° C (Rogers 1990). No significant differences in soil surface temperature were detected between non-vegetated and *S. junceus* quadrats.

Plant Performance

General findings

The following results for understory plant survival, cover, and height are based upon measurements taken in October in the last year in which monitoring occurred for a given species. Similarly, biomass results are from August of the last year of monitoring. In general, plant performance responses for these months were consistent with those found in the other months in which monitoring took place. Height, cover, and biomass could only be analyzed for the 1999 cohort because poor survival of the 2000 cohort. For the duration of the study, only minor signs of herbivory (i.e., *L. hirta* in two main-plot treatments) were observed and these occurred at the end of the 2000 growing season after all plant performance measurements had been taken.

It is important to note that the various measures of plant performance did not differ significantly between trenched and non-trenched plots at 0% pine stocking (i.e., there was no effect of the aluminum flashing by itself). In the absence of overstory competition for light, water, and nutrients, all species of the 1999 cohort approximately doubled in cover for the duration of the study (Figure 4). In 1999, species continued to increase in cover late into the growing season. In contrast, in 2000 cover increased early in the growing season and then remained stable or declined from August to October, probably a result of the summer drought.

Survival

Initial (June) survival of the 1999 cohort was excellent (86-100%), while survival of the 2000 cohort was poor (6-17%) because of a severe spring drought. Despite these differences between growing seasons, pine stocking by itself did not significantly affect survival in October. Most species showed significant increases in survival when grown in the presence versus absence of trenching ($P \leq 0.027$) (Figures 5-6). The needlefall treatments reduced survival for some species but generally only in the second year of monitoring. One exception was the significant interaction ($P \leq 0.003$) of SxTxN found with *S. odora*. Survival of *S. odora* was significantly reduced relative to the other split-plot treatments at the 50% stocking level in non-trenched split-plots with needlefall, while at full stocking survival was significantly reduced with needlefall in both trenched and non-trenched split-plots.

Cover

In general, changes in plant cover were of greater magnitude with increases in pine stocking than they were in the presence versus absence of trenching or needlefall (Figure 7). Cover responses to the pine stocking, trenching, and needlefall treatments varied by species; however, cover was generally greatest at 0% stocking and in the presence of trenching. *A. villosa, L. elegans, P. palustris*, and *S. secundum* demonstrated an interactive type of response to the treatments, and responded significantly ($P \leq 0.003$)

to SxT. Other significant ($P \leq 0.044$) interactions included stocking and needlefall (SxN) and trenching and needlefall (TxN) for *P. palustris* and *S. secundum*, respectively.

The response pattern for *A. villosa* indicates cover was unaffected by pine stocking in the presence of trenching, however, in the absence of trenching cover decreases with increasing stocking (Figure 7). Although not as pronounced, the cover response for *P. palustris* was similar to *A. villosa*, and the presence of needlefall at 100% stocking for these two species resulted in a reduction in cover. Cover of *S. secundum* was significantly less at 100% stocking in the absence of trenching in comparison to the other stocking levels in the presence or absence of trenching. In addition, in the absence of needlefall, cover of *S. secundum* in non-trenched plots was significantly less than those of trenched plots at all stocking levels.

Cover responses of *L. hirta*, *P. graminifolia*, and *S. odora* to the treatments were additive (Figure 7). Cover of *L. hirta* and *S. odora* differed significantly ($P \leq 0.018$) among levels of pine stocking and trenching while cover of *P. graminifolia* differed significantly ($P \leq 0.001$) only between presence and absence of trenching. *L. hirta*, *S. odora*, and *P.graminifolia* exhibited superior performance in the presence versus absence of trenching at each stocking level. The cover response of *L. hirta* to stocking indicates that it is moderately shade tolerant because only the 0 and 100% stockings differed significantly from each other. In contrast, *S. odora* was less shade tolerant and exhibited significant decreases in cover at pine stockings above 25%, regardless of the presence or absence of trenching. No significant responses from the treatments were found for *S. junceus*, suggesting that this species is moderately tolerant of shade and root competition.

Biomass

With the exception of *S. junceus* and *L. hirta*, all species demonstrated an interactive type of biomass response to the pine stocking and trenching treatments (Table 2). Multiple comparisons of treatment means indicated *L. elegans* and *P. graminifolia* are relatively shade tolerant in the presence of trenching, because only at 100% pine stocking did biomass differ significantly from those of the other stockings. However, in the absence of trenching, biomass of these species at 0% stocking was significantly greater than those of the other stockings. At 25 and 50% stockings, biomass of these species was significantly greater in the presence versus absence of trenching.

The biomass responses of *S. odora* for non-trenched plots were similar to those of *L. elegans* and *P. graminifolia*. In contrast, the presence of trenching for *S. odora* only made slight improvements in its performance, and multiple comparisons indicated that biomass at 0% stocking differed significantly from those of the 50 and 100% stockings. Biomass of *S. odora* at 25% stocking was significantly greater in the presence versus absence of trenching.

The biomass responses of *A. villosa* were similar to those observed for cover (i.e., no difference between pine stockings in the presence of trenching and decreasing biomass with increasing stocking in the absence of trenching). Again, *P. palustris* responded similarly to that of *A. villosa*, however, significant differences existed between 0 and 100% stockings in the presence of trenching.

Multiple comparisons indicated that biomass of *S. secundum* at 100% pine stocking was significantly less than those of the other stocking levels in the absence of trenching while no significant differences were found between the four stocking levels in the presence of trenching. At 100% stocking, biomass of *S. secundum* was significantly greater in the presence versus absence of trenching.

Responses of *L. hirta* and *S. junceus* to the pine stocking and trenching treatments were additive. For each species, biomass was greatest at the 0% stocking level and decreased as pine stocking increased and in the presence versus absence of trenching.

Maximum height

Treatment responses of maximum height varied among species, but for many (*P. graminifolia*, *S. odora*, *L. hirta*, *S. secundum*, and *P. palustris*) significant ($P \leq 0.041$) differences were detected for the pine stocking and trenching treatments. Responding additively, height of *P. graminifolia*, *S. odora*, *L. hirta* and *P. palustris* was greater in the presence versus absence of trenching and decreased with increasing stocking. An interactive response was detected for *S. secundum* in which only minor decreases in height were observed with increasing stocking in the presence of trenching, while in the absence of trenching height was reduced by half at 100% stocking. The height response for *A. villosa* was similar to that found for its cover and biomass; however, trenching was the only significant treatment effect ($P \leq 0.016$). *S. junceus* demonstrated a significant height response to needlefall ($P \leq 0.010$). Consistent with the other species, height growth for *S. junceus* was generally greater in the presence of trenching for all levels of stocking, however, in the presence versus absence of needlefall height growth was superior. No treatment effects were significant for height of *L. elegans*, although it declined with increasing stocking.

Foliar nutrients

Foliar nutrient analysis for *S. junceus* indicated that concentrations of total N were greater ($P \leq 0.066$) in the presence versus absence of needlefall (1.020 and 0.921 %N, respectively); however, total phosphorous (P) and potassium (K) were not significantly affected by the treatments. Per-plant amounts of N, P, and K significantly ($P \leq 0.007$) increased as pine stocking decreased, however these responses were directly related to increases in plant biomass.

Intercept parameters for the linear regression of *S. junceus* foliar N versus available soil N differed significantly between presence and absence of needlefall ($P=0.040$, $r^2=0.189$, n=48). For all pine stockings, foliar nitrogen of *S. junceus* was proportionately greater (14%) in the presence versus absence of needlefall, indicating a "fertilizer" effect from application of needlefall.

DISCUSSION AND CONCLUSIONS

Plant responses

Results of this research support the hypothesis that differences would exist among levels of pine stocking, trenching, and needlefall. Species performance was greatest when pine stocking was 0%, and a more prominent response was that most species had superior performance in the presence versus absence of trenching. Likewise, the hypothesis that performance of understory species would vary more from effects of overstory competition than from those of needlefall was supported by finding that most species had significant treatment effects from stocking, trenching, or their interaction.

The hypothesis that plant performance would be greatest at low densities was supported because performance was consistently superior at 0% stocking. The hypothesis that belowground competition and needlefall would interact at 100% pine stocking causing a disproportionate reduction in plant performance also was supported by the responses of *A. villosa*, *P. palustris*, and *L. elegans.* For these species, performance was greater in the presence versus absence of needlefall, except at full stocking in non-trenched plots where needlefall negatively impacted their performance.

The survival differences between the two cohorts demonstrated the importance of timing of rainfall. Although both years were drier than normal, the lack of rainfall at the time of planting severely impacted the survival of the 2000 cohort. However, despite the differences, both cohorts demonstrated better survival in the absence of root competition (trenched split-plots) in their first growing season. Second year results from the 1999 cohort indicated a decrease in survival in the presence of root competition and needlefall which could be due to either the added stress from drought or the accumulation of needlefall.

Cover, biomass, and height responses for the species often demonstrated either an interactive or additive type of response to the stocking, trenching, and needlefall treatments. *A. villosa*, *P. palustris*, *L. elegans*, and *S. secundum* generally exhibited an interactive type of response to stocking and trenching treatments which resulted in an increase in performance in the absence versus presence of root competition. In addition, the absence of root competition diminished the effects of stocking. *L. hirta*, *S. junceus*, *S. odora*, and *P. graminifolia* generally demonstrated an additive response resulting in increasing performance with decreasing pine stocking, and greater performance in the absence versus presence of root competition. Foliar nutrient analysis for *S. junceus* indicated total N concentrations to be greater in the presence versus absence of needlefall.

Environmental conditions

Research results demonstrate that crown closure alone is not a significant factor influencing soil water availability, although values generally increased as stocking decreased. Soil water responses were analyzed in three different ways: in non-vegetated quadrats, in *S. junceus* quadrats, and in the comparison of vegetated and non-vegetated quadrats. Soil water content in non-vegetated quadrats was not affected by stocking in the absence of root competition (i.e., trenched plots). However, in the presence of root competition soil water content decreased as pine stocking increased. These results are straightforward, simply suggesting that tree roots, if present, consume soil water in proportion to their stocking or basal area. Statistically, no significant differences in soil water content existed in the presence versus absence of needlefall, suggesting that there is no mulching effect. However, differences may not be detectable due to the depth (0 to 0.45 m) at which measurements were taken. One reason for finding no differences between vegetated and non-vegetated quadrats could be due to the low retentivity of the soil in which self mulching occurs rapidly under high evaporativity, thus having little benefit (Jalota and Prihar 1998). Realistically, we would expect a mulching effect from needlefall, but in order to test for this a measurement of surface soil water content would be needed.

Similarly, the results of the *S. junceus* quadrats showed greater amounts of water in the absence of root competition. However, soil water content was also found to be greater in the presence of needlefall. This suggests that, in vegetated quadrats, the presence of needlefall can act as a mulch to reduce evaporation from the soil. In the comparison of vegetated and non-vegetated quadrats, more water was found in the *S. junceus* quadrats for 5 of the 8 months in which monitoring occurred. This could be due to the roots of *S. junceus* bringing in more water from other areas or the roots holding in moisture, both of which could be detected by the TDR. During 1 of the 8 months, soil water content dropped below the assumed permanent wilting point of 6%, soil water decreased with increasing stocking, and the non-vegetated quadrats contained more water than the *S. junceus* quadrats, suggesting that during extremely dry periods consumption of soil water at 0- to 0.45-m depth by both overstory and understory vegetation could be detected.

Soil nitrogen results indicated there were treatment effects; however, inconsistencies in the response patterns among the five months limit our ability to make definite conclusions. Although the nutrient removals associated with pine litter removal vary from site to site, we would expect soil nitrogen to be greater in the presence versus absence of needlefall and trenching.

Soil surface temperature decreased as pine stocking increased. No significant differences existed between the non-vegetated and *S. junceus* quadrats within a given stocking level. Results simply indicate soil surface temperature is reduced by the presence of an overstory canopy but not by the presence of ground-layer vegetation.

SILVICULTURAL IMPLICATIONS

This research has increased our understanding of the complexity by which overstory pines affect understory vegetation through resource competition and needlefall. In general, competition for light had a more detrimental effect on understory plant performance than did competition for belowground resources. However, performance of most species was increased when availability of belowground resources was elevated, regardless of availability of light. In addition, effects of trenching and needlefall interacted with pine stocking for certain species, indicating that limiting effects of shade can be either moderated or exacerbated by variation in belowground resources or presence of needlefall. The two response patterns, interactive or additive, provide a means of classifying herbaceous species according to their potential performance in longleaf pine community restoration, given specific overstory, understory, and needlefall conditions of longleaf pine plantations.

Research results indicate that containerized reproduction can be a successful method for restoring herbaceous species if rainfall is adequate at the time of planting. Optimal performance of planted species is likely to occur in large openings in the overstory where root competition from associated woody and herbaceous species is minimal.

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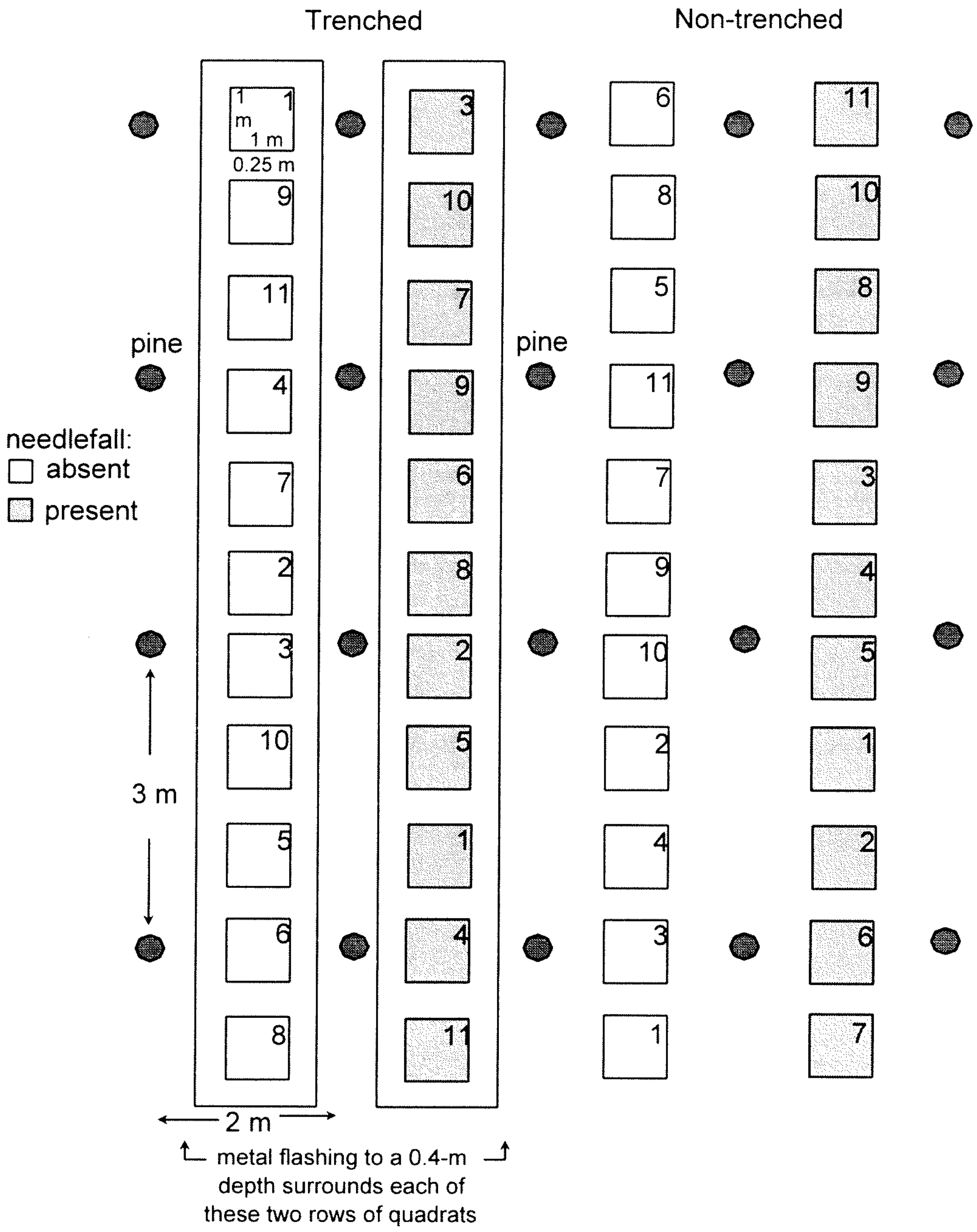
Figure 1. Example layout of a 0.09-ha plot having 100% stocking of longleaf pine. Split-plots that vary levels of trenching and needlefall were oriented north to south and their locations within the plot were randomly assigned. Within each split-plot, understory species were randomly assigned to each of ten 1-m^2 quadrats where they were planted at densities of up to 36 plants/m^2. The eleventh quadrat was used to monitor soil water and nutrient content in the absence of vegetation.


Trenched
Non-trenched
1 m
1 m
1
0.25 m
9
11
4
7
2
3
10
5
6
8
3
10
7
9
6
8
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5
1
4
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5
11
7
9
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3
1
11
10
8
9
3
4
5
1
2
6
7
pine
pine
needlefall:
☐ absent
▨ present
3 m
2 m
metal flashing to a 0.4-m depth surrounds each of these two rows of quadrats

Table 1. Characteristics of understory species used to study overstory competition and needlefall effects of longleaf pine plantations.

Scientific Name	*n*[d]	Plant Type	Characteristics	Wildlife Value[e]	Synonyms
Anthaenatia villosa (Michx.) Beauvois[a]	36	perennial grass	ascending, forms short rhizomes	unknown	green silky scale
Lespedeza hirta (L.) Hornemann[a]	23	perennial forb	erect, nitrogen fixer	white-tailed deer forage	hairy lespedeza
Liatris elegans (Walt.) Michx.[a c]	35	perennial forb	erect, persists by corms	poor white-tailed deer forage	white featherflower
Pinus palustris Mill.[a]	36	woody tree	grass stage		longleaf pine
Pityopsis graminifolia (Michx.) Nutt.[a c]	11	perennial forb	erect, persists and colonizes by rhizomes	important gopher tortoise food	*Heterotheca graminifolia* (Michx.) Shinners
Solidago odora Aiton[a c]	36	perennial forb	erect, short rhizomes	deer, turkey, etc. eat basal rosettes in winter	fragrant goldenrod
Sorghastrum secundum (Ell.) Nash[a]	33	tufted, perennial grass	ascending, from short rhizomes or hardened bases	songbirds consume seeds	lopsided indiangrass
Sporobolus junceus (Michx.) Kunth[a]	36	perennial grass	erect to sprawling	songbirds eat seeds	pineywoods dropseed
Andropogon ternarius (Michx.)[b]	36	perennial grass	erect, from short rhizomes or hardened bases	stems eaten by cotton rat, nesting sites for quail	splitbeard bluestem, silver bluestem
Carphephorus bellidifolius (Michx.) T. & G.[b]	36	perennial forb	ascending	unknown	sandywoods chaffhead
Chrysopsis gossypina (Michx.) Ell.[b]	36	perennial forb	erect, decumbent, or ascending	unknown	*Heterotheca gossypina* Michx. Shinners
Desmodium ciliare (Muhl. Ex Willd.) DC.[b]	36	perennial forb	erect	quail eat seeds	beggar lice, beggar's ticks
Eragrostis spectabilis (Pursh) Steudel[b]	36	perennial grass	erect, from short rhizomes	songbirds and gamebirds eat seeds	purple lovegrass

[a] 1999 cohort. [b] 2000 cohort. [c] Removed May 2000. [d] *n* = number planted per quadrat. [e] Miller and Miller 1999.

Figure 2. Average basal area (solid lines) and crown closure (dashed lines) of longleaf pine plantations following thinning in October 1998 to three stocking levels (0, 25, and 50% of the basal area of a fully stocked stand, 19.8 m^2/ha).

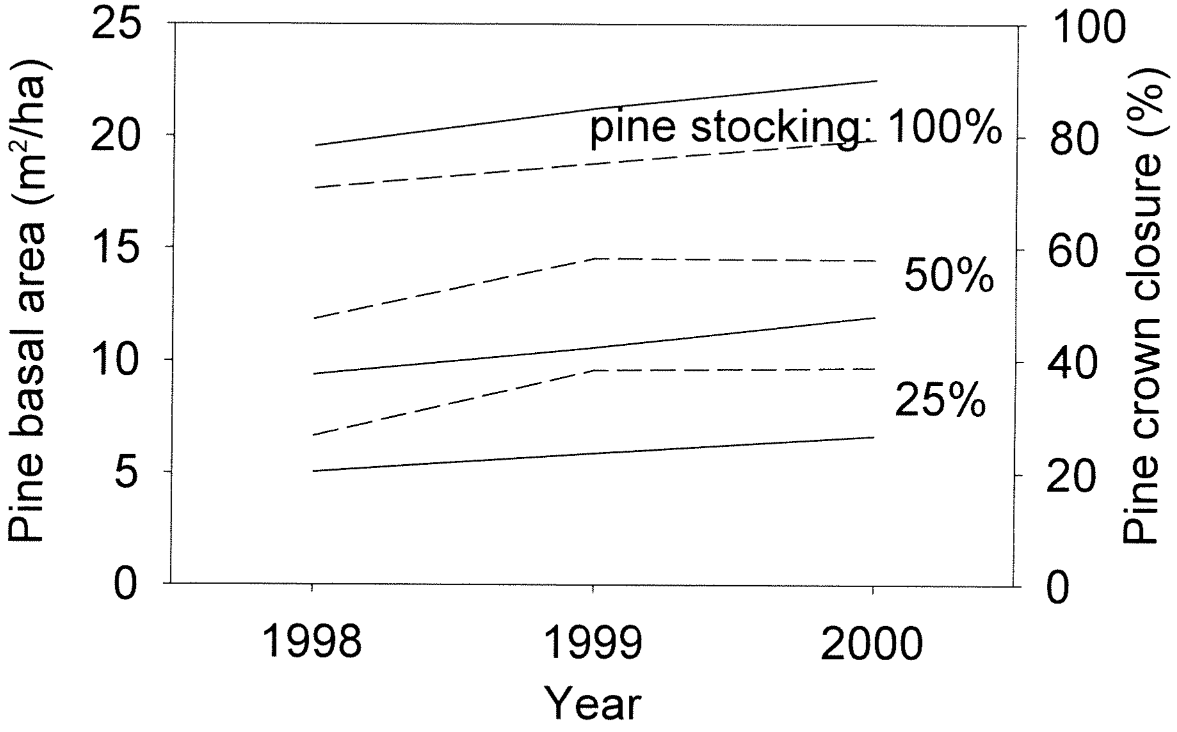
Pine basal area (m^2/ha)
0
5
10
15
20
25
Pine crown closure (%)
0
20
40
60
80
100
1998
1999
2000
Year
pine stocking: 100%
50%
25%

Figure 3. Average soil water content (0- to 0.45-m depth) during 1999 and 2000 in the four pine stocking levels in the presence (transparent surface) or absence (shaded surface) of trenching.

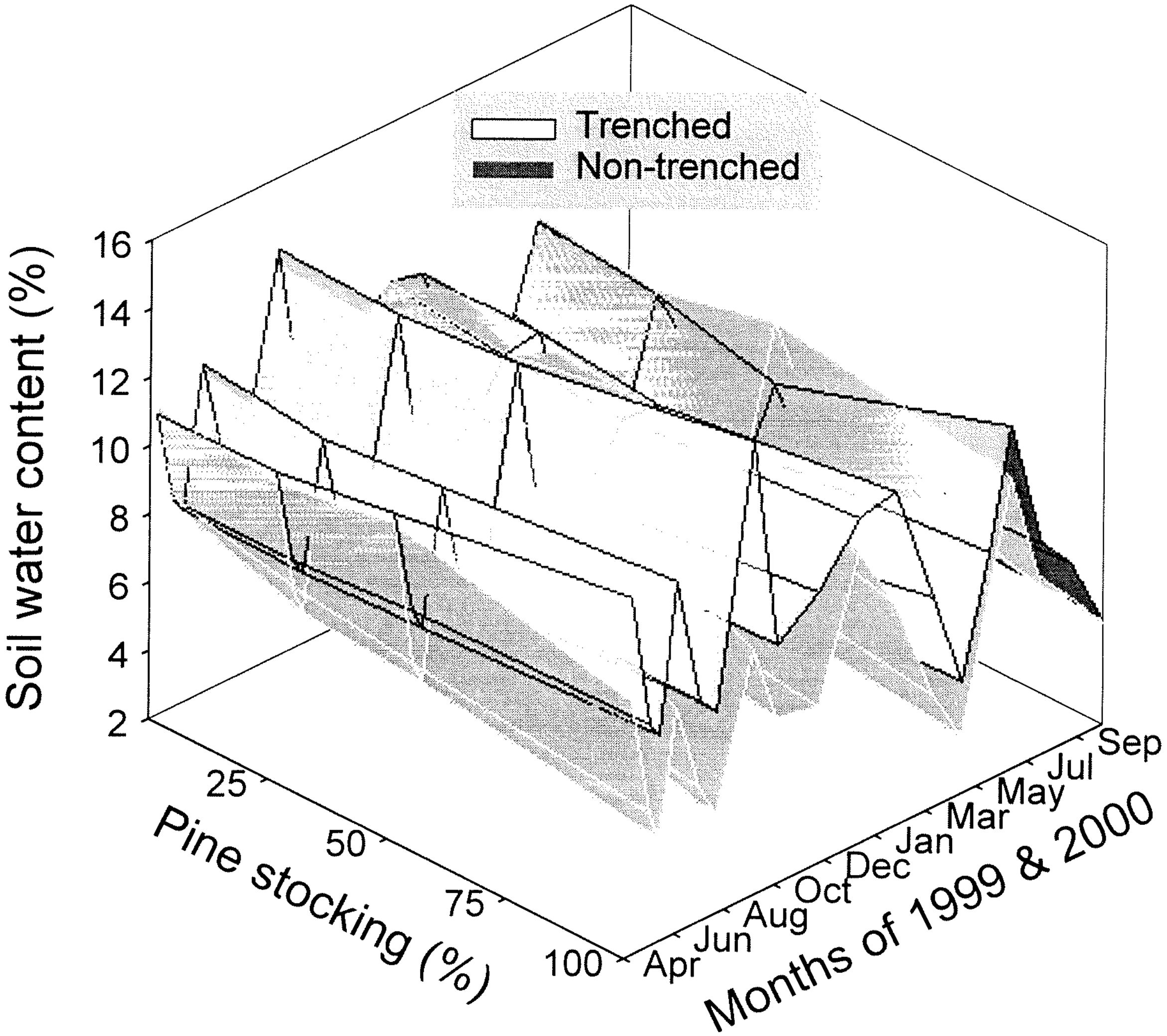
☐ Trenched
▨ Non-trenched
Soil water content (%)
16
14
12
10
8
6
4
2
Pine stocking (%)
25
50
75
100
Months of 1999 & 2000
Apr
Jun
Aug
Oct
Dec
Jan
Mar
May
Jul
Sep

Figure 4. Average cover over two growing seasons of eight species of understory vegetation planted in 1999. These data are for plantings within plots with 0% pine stocking in the absence of trenching and needlefall; thus, they illustrate vegetation development free of overstory competition and needlefall effects.

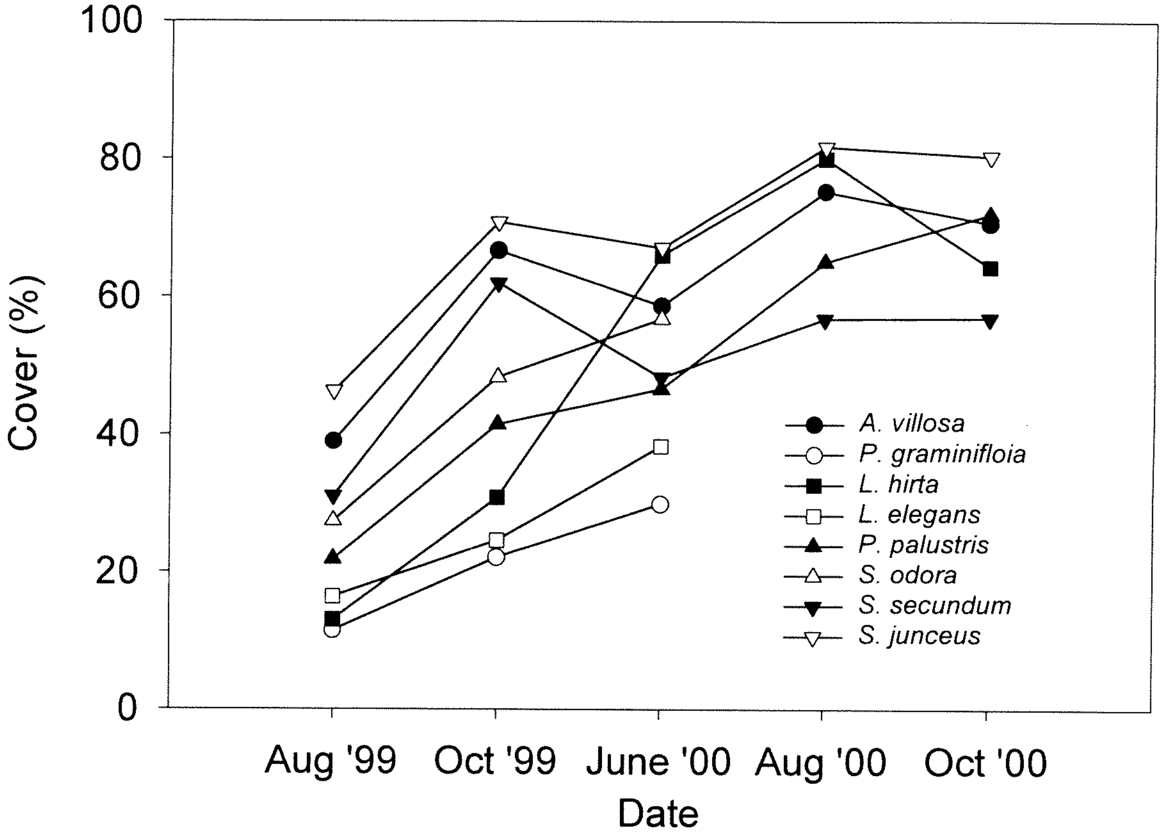
100
80
60
40
20
0
Cover (%)
Aug '99
Oct '99
June '00
Aug '00
Oct '00
Date
A. villosa
P. graminifloia
L. hirta
L. elegans
P. palustris
S. odora
S. secundum
S. junceus

Figure 5. Average survival of eight species of understory vegetation planted in 1999 in the four pine stockings and four combinations of trenching and needlefall. Responses for *L. elegans, P. graminifolia, and S. odora* are for October 1999 while those of the remaining species are for October 2000.

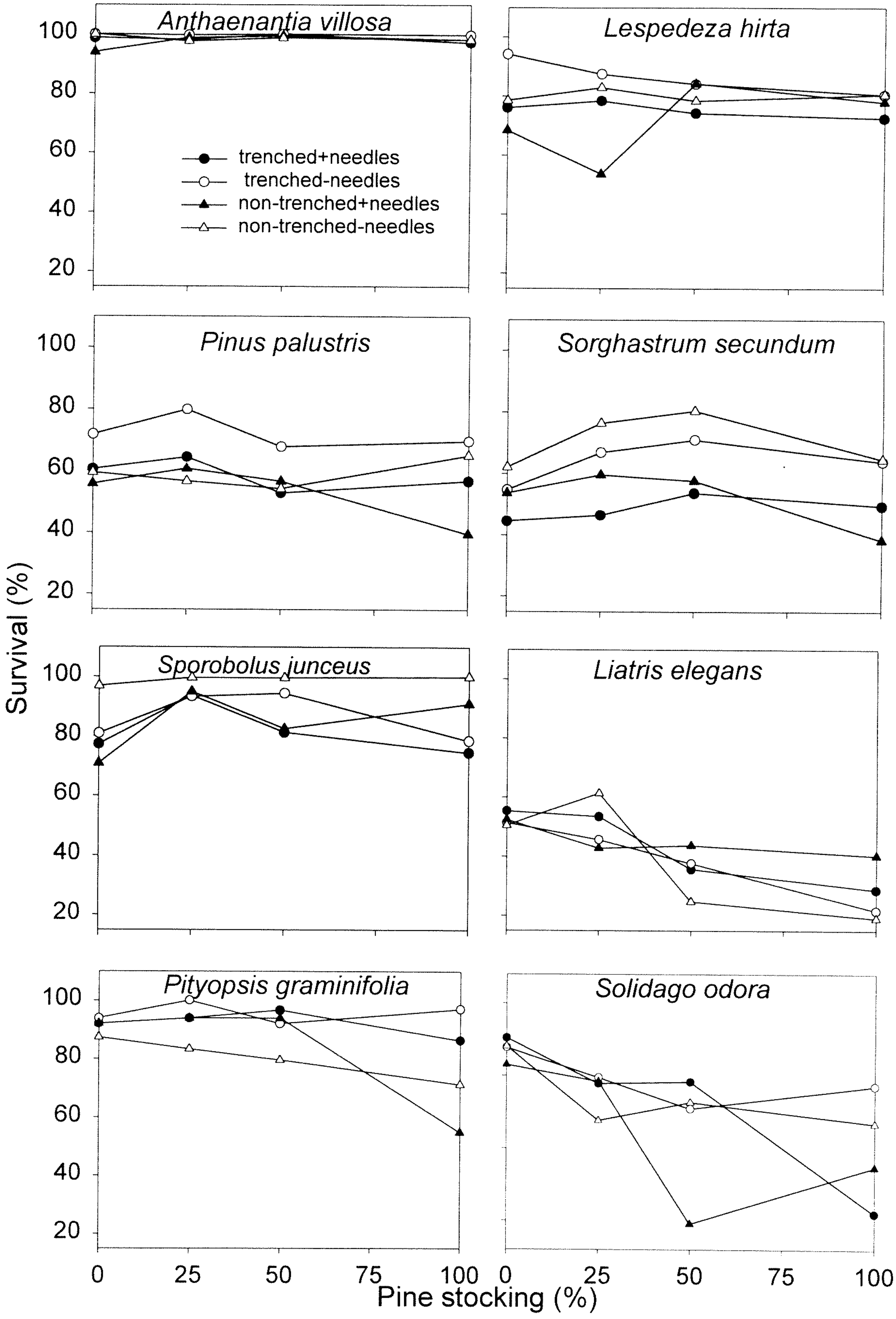
Anthaenantia villosa
Lespedeza hirta
Pinus palustris
Sorghastrum secundum
Sporobolus junceus
Liatris elegans
Pityopsis graminifolia
Solidago odora
trenched+needles
trenched-needles
non-trenched+needles
non-trenched-needles
Survival (%)
Pine stocking (%)
100
80
60
40
20
0
25
50
75
100

Figure 6. Average survival of five species of understory vegetation planted in 2000 in the four pine stockings and four combinations of trenching and needlefall. Responses are for October 2000.

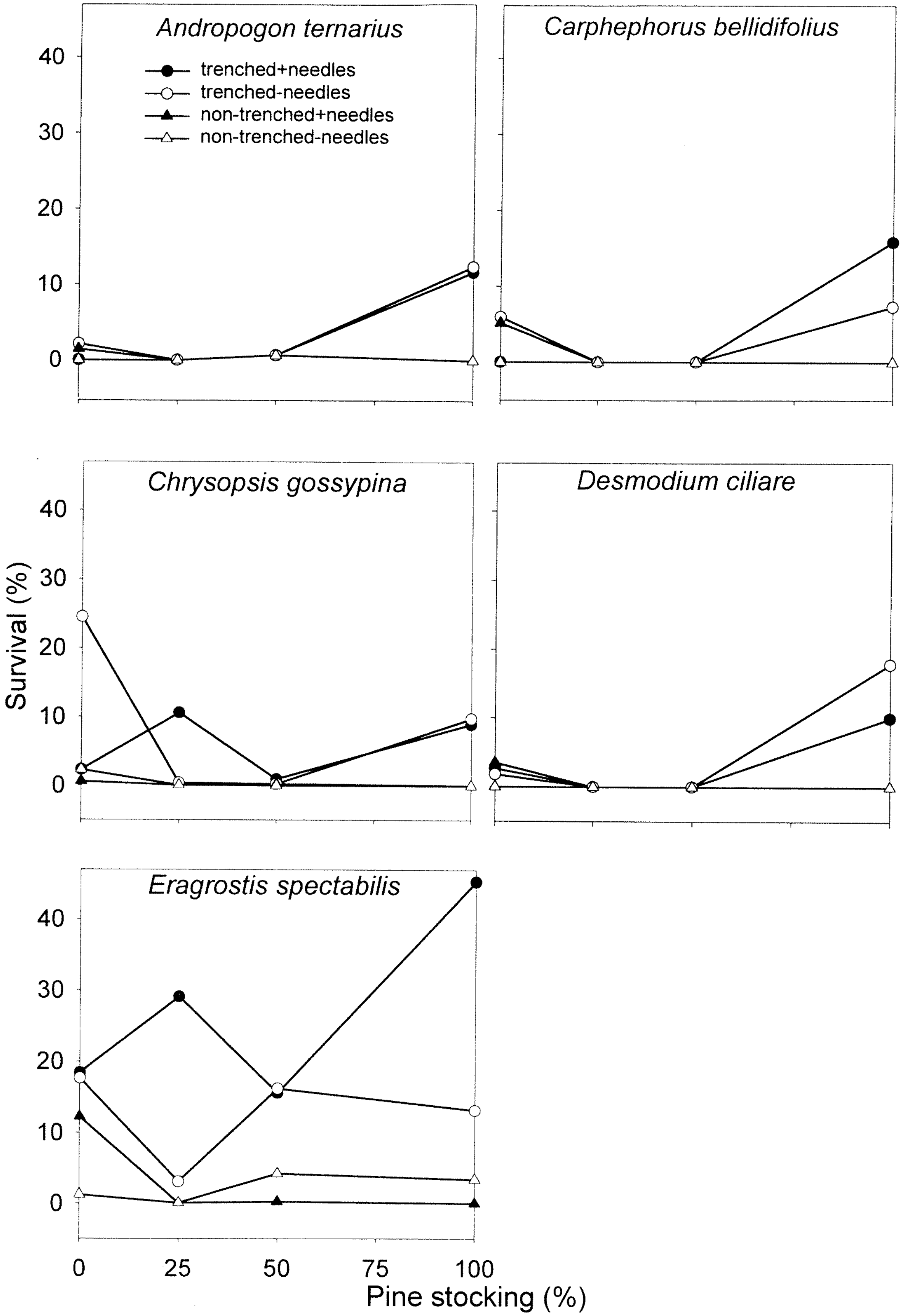
Andropogon ternarius
Carphephorus bellidifolius
Chrysopsis gossypina
Desmodium ciliare
Eragrostis spectabilis
● trenched+needles
○ trenched-needles
▲ non-trenched+needles
△ non-trenched-needles
Survival (%)
0
10
20
30
40
Pine stocking (%)
0
25
50
75
100

Figure 7. Average cover of eight species of understory vegetation planted in 1999 in the four pine stockings and four combinations of trenching and needlefall. Responses for *L. elegans, P. graminifolia, and S. odora* are for October 1999 while those of the remaining species are for October 2000.

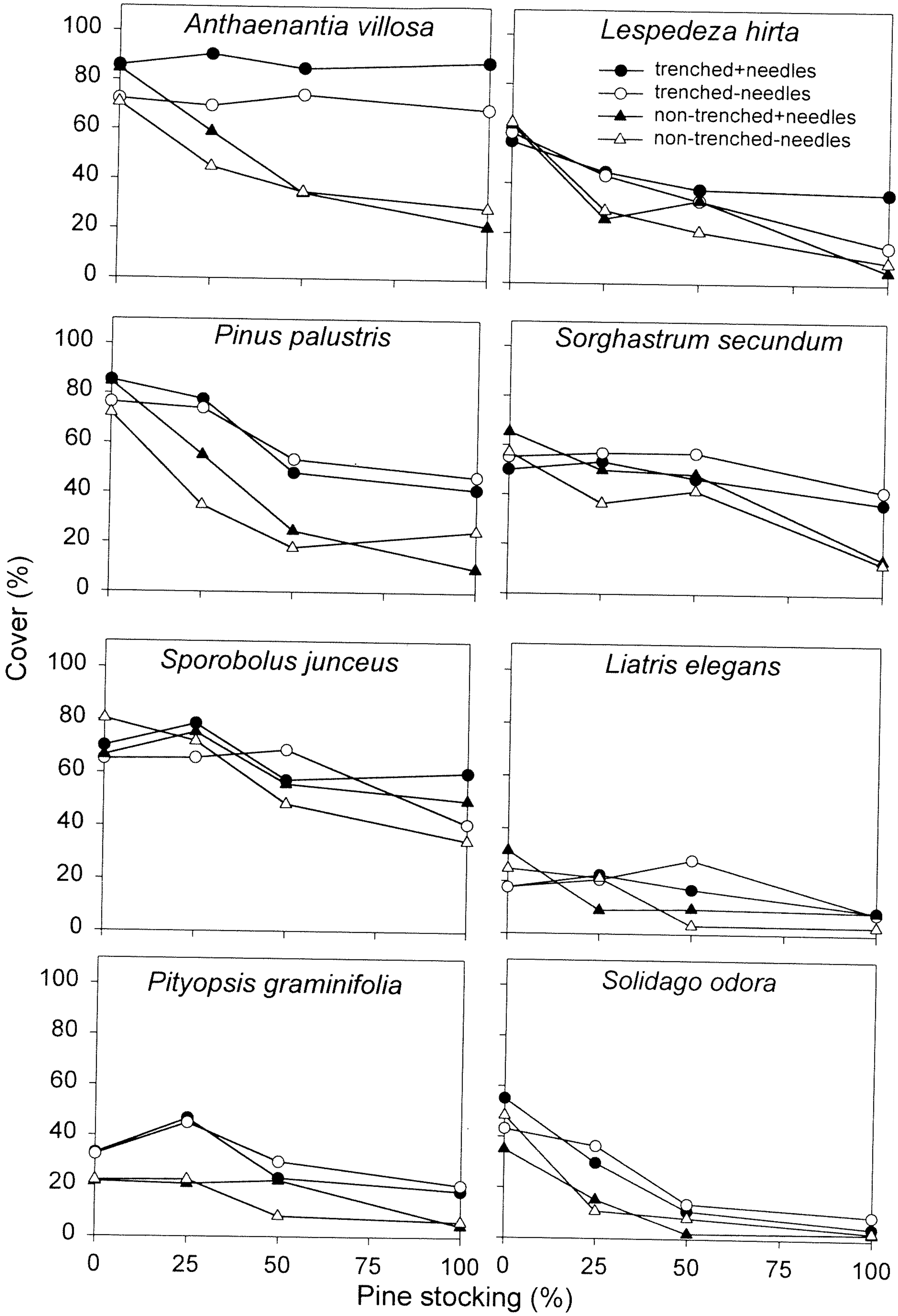
Anthaenantia villosa
Lespedeza hirta
Pinus palustris
Sorghastrum secundum
Sporobolus junceus
Liatris elegans
Pityopsis graminifolia
Solidago odora
trenched+needles
trenched-needles
non-trenched+needles
non-trenched-needles
Cover (%)
Pine stocking (%)
0
20
40
60
80
100
0
25
50
75
100

Table 2. F –test probabilities from the analysis of variance of August 2000 biomass for the eight species of understory vegetation planted in 1999.

		Herbaceous species							
Source	df	*A. villosa*	*L. hirta*	*P. palustris*	*S. secundum*	*S. junceus*	*L. elegans*	*P. graminifolia*	*S. odora*
Stocking (S)	3	0.001	0.006	0.001	0.012	0.004	0.001	0.002	0.001
Trench (T)	1	0.001	0.004	0.001	0.001	0.014	0.001	0.001	0.002
Needles (N)	1	0.069	0.040	0.974	0.764	0.465	0.029	0.936	0.528
T*N	1	0.428	0.224	0.771	0.517	0.935	0.960	0.418	0.130
S*T	3	0.004	0.074	0.001	0.021	0.154	0.001	0.041	0.015
S*N	3	0.156	0.196	0.694	0.164	0.052	0.130	0.977	0.241
S*T*N	3	0.904	0.446	0.873	0.547	0.879	0.160	0.733	0.151

CHAPTER 3

SILVICULTURAL IMPLICATIONS

Overstory and midstory vegetation layers strongly limit abundance and species richness of understory herbaceous plants in longleaf pine (*Pinus palustris* Mill.) plantations often resulting in failed efforts to restore native plant species. In addition silvicultural practices such as bedding and herbicide use that are often associated with plantation silviculture are known to negatively impact herbaceous vegetation. However, the mechanisms by which overstory competition and needlefall limit understory vegetation are poorly understood and were the subject of this study.

An important finding from this study is that the effects of above- and belowground factors combined, either additively or interactively, to further limit understory vegetation performance. Species with interactive effects had similar performance across pine stockings in the presence of trenching, but declining performance with increasing stocking that was independent of reductions in performance due to absence of trenching or presence of needlefall. Therefore more efficient approaches would involve manipulation of the overstory to reduce both above- and belowground competition. For example, when establishing a new longleaf pine stand, planting density should be low, resulting in 740-990 pines/ha. These stand densities are likely to create conditions similar to the 25 and 50% pine stockings of this study, allowing understory vegetation to establish and maintain itself. A thinning to reduce the number of pine and non-pine woody stems may also be necessary. This prescription coincides with the non-trenched plots at the 25% stocking level in our study where most often the performance of understory species did not significantly differ from the 0% stocking plots (i.e., where performance was optimal). If the stand is already established and of high density (1500 to 1800 trees/ha) a heavy thinning or group selection method may help to stimulate growth in the understory. Thinning should be conducted in a manner to leave a uniform spacing of trees to approximately a quarter or a half of the original stem density. Again, this will create similar conditions to that of the non-trenched plots at the 25% stocking level in our study. Using the group selection method to create canopy gaps of diameter twice or more than that of the height of the overstory trees will ensure that competition from the overstory trees is maintained at a level which will allow for growth of understory vegetation (Brockway and Outcalt 1998).

Research results indicate that overstory competition for belowground resources, by itself, is a strong factor capable of severely limiting performance of understory vegetation. However, the practice of trenching is not a practical method for reducing root competition on a large scale. On a smaller scale trenching could be a reasonable and cost effective option for establishing understory species, such as in establishing small "founder" populations of rare or endangered plant species. Another option for reducing belowground competition for soil water and nutrients without altering light availability could be to apply the needed water and nutrients to the stand with irrigation and fertilization. One study found 40 new vascular plant species in a 130-year-old Scots pine (*Pinus sylvestris* L.) stand after receiving 7 years of irrigation and fertilization (Kellner and Marshagen 1991). Similarly, a study on ponderosa pine (*Pinus ponderosa* Dougl. ex

Laws) in eastern Oregon showed that irrigation and fertilization increased the aboveground biomass of the understory by 36% as compared to untreated plots (Riegel and Miller 1991). However, these practices also may not be practical on a large scale due to the high costs associated with each treatment. Furthermore, there could be cause for concern for the effects of these practices on the increased growth of the overstory trees and unwanted weeds, and associated increases in competition. Similarly, increasing resources may decrease species diversity (Goldberg and Miller 1990).

In our study, the removal of all non-pine vegetation was done to avoid potential confounding factors and this treatment undoubtedly contributed to increases in plant performance. Thus, the use of herbicides, prescribed burning, and/or disking for site preparation may also be necessary to enhance restoration efforts. Areas in which understory vegetation will be planted can be treated with non-soil active herbicides, such as glyphosate or triclopyr, in early spring prior to planting. Prescribed burning can help to reduce competition from woody and herbaceous vegetation. Another option could include mechanical treatments such as single-pass disking or drum chopping which will minimize the impact on existing herbaceous vegetation (Outcalt and Lewis 1988). These treatments can help reduce competition for above- and belowground resources and facilitate establishment and long-term maintenance of planted species.

Additionally, results of this research indicate that containerized reproduction can be a successful method for restoring herbaceous species if rainfall is adequate at the time of planting. Once established, low levels of precipitation throughout the growing season did not influence seedling survival. Consequently, planting dates should not be scheduled too far in advance but should occur during a time period when precipitation is expected or has just occurred. It is also important to note that planting should not occur too early in the growing season due to potential injury from a late spring frost.

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Goldberg, D.E. and T.E. Miller. 1990. Effects of different resource additions on species diversity in an annual plant community. Ecology. 71(1): 213-225.

Kellner, O. and M. Marshagen. 1991. Effects of irrigation and fertilization on the ground vegetation in a 130-year-old stand of Scots pine. Canadian Journal of For. Res. 21(5): 733-738.

Outcalt, K.W. and C.E. Lewis. 1988. Response of wiregrass (*Aristida stricta*) to mechanical site preparation. P. 1-12 *in* Proc. of the Symposium. KBN Engineering and Applied Sciences, Inc. Gainesville, FL.

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