Above- and Belowground Competition from Longleaf Pine Plantations Limits Performance of Reintroduced Herbaceous Species

Timothy B. Harrington, Christa M. Dagley, and M. Boyd Edwards

ABSTRACT. Although overstory trees limit the abundance and species richness of herbaceous vegetation in longleaf pine (*Pinus palustris* Mill.) plantations, the responsible mechanisms are poorly understood because of confounding among limiting factors. In fall 1998, research was initiated to determine the separate effects of above- and belowground competition and needlefall from overstory pines on understory plant performance. Three 13- to 15-yr-old plantations near Aiken, SC, were thinned to 0, 25, 50, or 100% of nonthinned basal area (19.5 m^2 ha^{-1}). Combinations of trenching (to eliminate root competition) and needlefall were applied to areas within each plot, and containerized seedlings of 14 perennial herbaceous species and longleaf pine were planted within each. Overstory crown closure ranged from 0 to 81%, and soil water and available nitrogen varied consistently with pine stocking, trenching, or their combination. Cover of planted species decreased an average of 16.5 and 14.1% as a result of above- and belowground competition, respectively. Depending on species, needlefall effects were positive, negative, or negligible. Results indicate that understory restoration will be most successful when herbaceous species are established within canopy openings (0.1–0.2 ha) managed to minimize negative effects from above- and belowground competition and needlefall. For. Sci. 49(5):681–695.

Key Words: *Pinus palustris*, resource availability, trenching, needlefall, cover, biomass.

Longleaf pine (*Pinus palustris* Mill.) once dominated one of the most extensive forest plant communities in the southeastern United States, occupying as much as 37 million ha prior to European settlement (Frost 1993). These communities are characterized by a patchy overstory of large, open-grown pines (often fewer than 50 stems ha^{-1}), occasional hardwoods, and a species-rich herbaceous community dominated by wiregrass (*Aristida stricta* Michx. or *A. beyrichiana* Trin. & Rupr.) and bluestem (*Andropogon* spp.). Over 40 species of higher vascular plants can occur within a

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single square meter of forest floor (Peet and Allard 1993). Frequent and fast-moving ground fires set by lightning or aboriginal activity sustained these species-rich communities (Platt et al. 1991, Frost 1993).

Since 1930, fire suppression efforts have facilitated the replacement of longleaf pine communities with dense, stratified stands of overstory pines, midstory hardwoods, and understory shrubs (Frost 1993). Often loblolly pine (*Pinus taeda* L.) has become the dominant tree species because its shade tolerance and seed production are superior to those of longleaf pine (Boyer 1990). In addition, plantations of loblolly pine, slash pine (*P. elliottii* Engelm.) or sand pine (*P. clausa* [Chapm. ex Engelm.] Vasey ex Sarg.) have been established extensively by industrial and nonindustrial forest landowners on former longleaf pine sites because of their more rapid rates of early growth. In these replacement stands, midstory hardwood species include turkey oak (*Quercus laevis* Walt.), bluejack oak (*Q. incana* Bartr.), laurel oak (*Q. laurifolia* L.), and blackjack oak (*Q. marilandica* Muenchh.). Dominant understory shrubs include sumac (*Rhus* spp.), sparkleberry (*Vaccinium arboreum* Marsh.), 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 layered stand structures limit availability of light and soil water in the understory, resulting in reduced vegetation abundance and species richness (Means 1997, Harrington and Edwards 1999). A variety of silvicultural treatments, including thinning, prescribed burning, herbicide application, and fertilization, have been used successfully in southern pine stands to stimulate short-term increases in abundance of herbaceous species (Grelen and Enghardt 1973, Wolters 1973, Wolters 1981, Brockway et al. 1998, Harrington and Edwards 1999, Outcalt et al. 1999, Brockway and Outcalt 2000).

To restore longleaf pine communities, the general approach has been to first plant pine seedlings (Franklin 1997, p. 6–7) and then reintroduce the desired herbaceous species (Seamon 1998, Glitzenstein et al. 2001), some of which may be threatened or endangered (Walker 1993). As a shade-intolerant species, longleaf pine regenerates most successfully in large canopy openings with minimal competition from other woody vegetation (Boyer 1990, Palik et al. 1997, Brockway and Outcalt 1998). Site preparation typically is applied to ensure establishment and dominance of longleaf pine (Landers et al.1995); however, specific herbicide (Litt et al. 2001) and mechanical treatments (Outcalt and Lewis 1990) can reduce abundance of native herbaceous species. In addition, uniform spacing and size of trees in plantations create dense litterfall and intense competition for light (Oliver and Larson 1996, p. 195-211), further limiting efforts to re-establish desirable understory species.

Thus, a conflict exists in the current approach for restoring longleaf pine communities. Treatments that decrease woody competition to aid pine establishment can directly limit abundance of native herbaceous species. Planting pines at high densities to ensure full stocking facilitates development of dense and uniform stand structures, thereby excluding understory vegetation. Restoration techniques must be developed to avoid this conflict among component species of longleaf pine communities, and such techniques will rely on an improved understanding of overstory and understory interactions.

A common experimental technique for studying overstory and understory interactions 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 conducted in a wide range of forest communities have suggested that belowground competition can be of equal or greater importance as aboveground competition for limiting performance of understory plants (Toumey and Kienholz 1931, Korstian and Coile 1938, p. 90–92, McCune 1986, Riegel et al. 1992). In addition, recent canopy gap studies have shown that root competition from mature longleaf pines can severely limit growth of pine seedlings located less than 16 m from an adult tree (Palik et al. 1997, Brockway and Outcalt 1998, McGuire et al. 2001).

Litterfall from overstory trees is another factor that potentially can influence understory vegetation (Facelli and Pickett 1991). 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). 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 (Ginter et al. 1979). Litterfall also reduces the thermal amplitude of surface soil layers, and it is an important source of nitrogen for plant nutrition. In addition, pine needle litter is an important fuel component that can influence fire intensity and spread, especially where it accumulates around individual trees (Brockway and Outcalt 1998).

The objective of this study was to identify the primary mechanisms by which above- and belowground competition and needlefall in longleaf pine plantations limit establishment and maintenance of reintroduced understory vegetation. A variety of herbaceous species were planted in the understory of plantations that had been experimentally manipulated to separate effects of above- and belowground competition from those of needlefall. Resource availability and performance of three cohorts (1999, 2000, and 2001) of planted seedlings were monitored for 1 to 3 yr to enable the testing of four primary hypotheses:

1. *Competition versus needlefall*: understory plant performance is more strongly limited by competition than by needlefall from overstory trees.

2. *Compounding effects of competition and needlefall*: at high densities of overstory longleaf pine, competition and needlefall interact to intensify reductions in understory plant performance.

3. *Above- versus belowground competition*: understory plant performance is more strongly limited by

aboveground competition than by belowground competition.

4. *Overstory moderation*: peak performance of understory plants occurs at low overstory densities because of moderated competition effects, temperature extremes, and evaporative demands.

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. Preliminary results were presented by Harrington and Edwards (2001) and Dagley et al. (2002). At study initiation, the sites supported 13- to 15- yr-old plantations of longleaf pine previously described by Harrington and Edwards (1999). In 1994, pine density in nonthinned areas varied from 1,410–1,470 trees ha^{-1}. Soils include sands and loamy sands of the Blanton (Grossarenic Paleudults), Lakeland (thermic, coated Typic Quartzipsamments), and Troup (loamy, siliceous, thermic Grossarenic Paleudults) series (Rogers 1990). Study sites were broadcast burned during February–March 1994 and 1998.

At each of the three sites (blocks), four 30 × 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 nonpine woody vegetation (Harrington and Edwards 1999).[1] Three of the plots at each site were located in areas that were thinned in June 1994 to remove approximately half of the trees per ha (Harrington and Edwards 1999), while the fourth plot was located in a nonthinned area. Nonpine woody vegetation was removed with a September broadcast application of glyphosate herbicide (5 kg acid equivalent ha^{-1} Accord® in water plus 0.5% nonionic surfactant for a total spray volume of 140l ha^{-1}) and an October spot treatment of triclopyr herbicide (10% solution of Garlon®4 in JLB® improved-plus oil). In October 1998–2001, diameter at breast height (1.37 m aboveground) was measured on each pine, and these data were used to calculate stand basal area. The mean basal area of the three nonthinned plots (19.5 m^2 ha^{-1}) was defined as 100% stocking, and the remaining three plots were randomly assigned pine densities of 0, 25, or 50% of full stocking (basal area). Pines in tree-removal plots were cut and removed by hand in September 1998; thinning from below was used to remove trees in the 25 and 50% stockings. In winter 1999–2000, pine height averaged 11.0 m.

In the interior 20 × 20 m area within each plot, four split-plot treatments were established to vary belowground resources and needlefall independently of pine stocking (Figure 1). The experimental design of the study was a randomized, complete block with a split-plot arrangement of treatments. Pine stocking was the whole-plot factor, and split-plot factors were trenching (presence or absence) and needlefall (presence or absence) in a 2 × 2 factorial arrangement. Each split-plot treatment was randomly as-

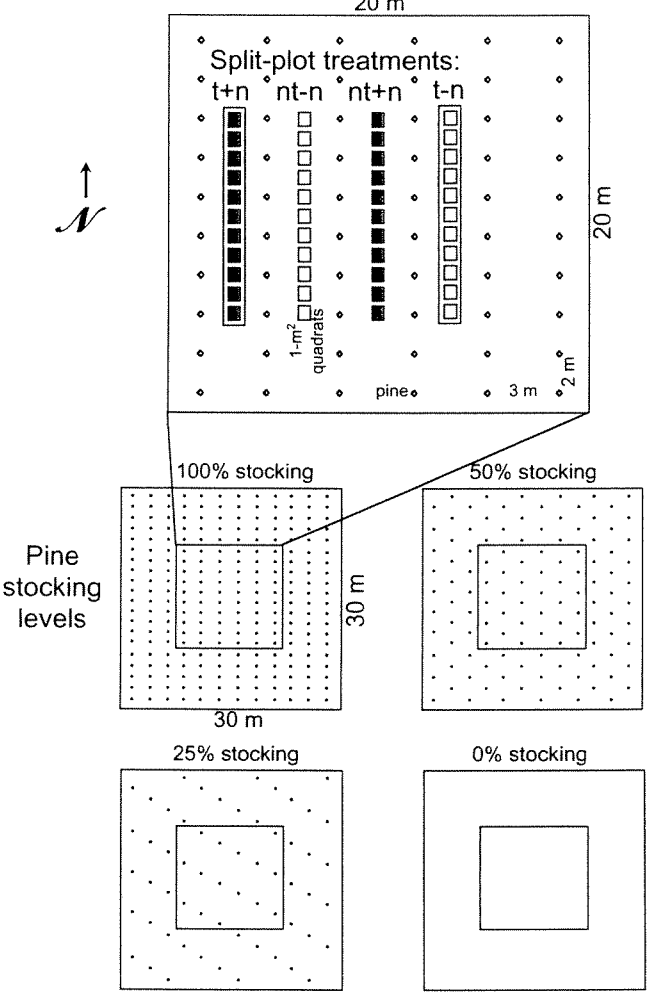

Figure 1. Diagram of experimental treatments for studying above- and belowground competition and needlefall effects of longleaf pine plantations on reintroduced herbaceous species. Split-plot treatments (t+n, trenched plus needlefall; nt-n, nontrenched minus needlefall; nt+n, nontrenched plus needlefall; and t–n, trenched minus needlefall) were randomly assigned to columns of 1–m^2 quadrats within each pine stocking level.

signed to one of four 1.2- × 13.7 m strips in each plot. Split plots were oriented with their long axes in a north-south direction to eliminate possibility of systematic location effects, and each contained a column of eleven 1 m^2 quadrats. Split plots were spaced at least 2 m apart, and a nonvegetated strip 0.25 m in width separated adjacent quadrats within a split plot. Ten of the eleven quadrats per split plot were used for three cohorts of plantings with random assignment of species locations. The pre-existing forest floor was removed from each quadrat to expose mineral soil prior to planting. Within each split plot, monospecific stands of selected herbaceous species were planted in spring 1999 (seven species), 2000 (five species), or 2001 (five species), and the performance of each species was monitored for 1 to 3 growing seasons (methods described below). The additional quadrat per split plot remained unplanted for the duration of the study (1999–2001) and was used to measure soil water content and surface temperature in the absence of understory vegetation. The split plots were hand-weeded each month for the

study duration to eliminate effects of interspecific competition. Glyphosate herbicide (5% solution of Accord® in water plus 0.5% surfactant) was applied as needed to remove the indigenous understory vegetation immediately outside the split plots.

Trenching was conducted in October 1998 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. From May 1999 to November 2001, needlefall in the two split plots receiving this treatment was held constant for each stocking level at twice the monthly value predicted for non-thinned stands of 20 m^2 ha^{-1} basal area.[2] To achieve this standardized rate, stand-produced needlefall was supplemented with monthly applications. The standardized rate (7893 kg ha^{-1} yr^{-1}), 52% higher than the maximum observed for longleaf pine plantations of similar age (Weigert and Monk 1972), was chosen to accelerate detection of potential needlefall effects during the 3 yr study. Pine needles for the monthly needlefall applications were obtained from areas adjacent to the study plots or from commercial sources; applications were based on oven dry weights. In July 1999, five laundry baskets fitted with fiberglass window screen were placed at random locations within each plot of the 25, 50, and 100% stockings to monitor monthly rates of stand-produced needlefall (needlefall was virtually absent in the 0% stocking plots). In the remaining two needlefall-absent split plots per plot, needlefall was removed manually each month.

Measurements of Environmental Conditions

Crown Closure.—In August or September of 1998–2001, a vertical densitometer (Geographic Resource Solutions, Arcata, CA) or "moosehorn" 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 randomly selected azimuths. The plot average of these readings multiplied by 100 estimates the percentage of area covered by crowns of overstory pines (crown closure) and was used as an index of light availability.

Soil Surface Temperature.—Hobo® sensors (Pocasset, MA) were used to record soil surface temperature (°C) at 1.2 hr intervals from June to October 2000 and 2001 in nontrenched, needlefall-absent split plots. Sensors were placed in the nonvegetated and *Sporobolus junceus* (Michx.) Kunth quadrats of each split plot.[3] For each of these quadrats, mean, minimum, and maximum daily values of temperature were averaged by month.

Soil Water Availability.—Volumetric soil water content (%) was measured at approximate monthly intervals from May 1999 to November 2001 (28 sample periods) using a Trase® time domain reflectometry (TDR) instrument (SoilMoisture Equipment, Inc., Santa Barbara, CA). A pair of 0.45 m stainless steel rods was inserted vertically into the center of each nonvegetated quadrat. In February 2000, an additional pair of rods was installed within each *S. junceus* quadrat to quantify vegetation effects on soil water content. Rods remained permanently in place for the duration of the study. To quantify needlefall effects on soil water in the surface layer, TDR readings were taken monthly from May to November 2001 from a pair of 0.15 m rods temporarily inserted into each nonvegetated quadrat. Soil water data from one 100%-pine-stocking plot were removed from the analyses because it was found that soil texture shifted dramatically among the four split plots from loamy sands to sandy clay loams. Monthly records of precipitation for 1999–2001 were obtained from an SRS station centrally located among the three study sites.

Available Soil Nitrogen.—At monthly intervals from June to October of 2000 and 2001, soil samples (25 mm cores) were collected from 0–0.15 m depth within each nonvegetated quadrat. In the laboratory, 30 ml of 2 mol $liter^{-1}$ KCl was added to 5 g soil from each sample. Extraction of exchangeable ammonium (NH_4^+) and nitrate (NO_3^-) sources of nitrogen from each soil solution was performed according to the methods of Keeney and Nelson (1982). Ammonium and nitrate values (ppm) were summed to provide an index of available soil nitrogen.

Plant Propagation

A variety of perennial herbaceous species native to longleaf pine communities (Peet and Allard 1993) was selected for study based on availability of seed, variation in growth habit (i.e., grasses versus forbs and erect versus prostrate growth habits), and success in propagation. Seeds were collected during October and November 1998–2000 at SRS. In 1999, seeds also were collected at the Gopher Heritage Preserve located near Windsor, SC. Each herbaceous species was cultivated by cold-stratifying seeds in flats for 45 days at 4°C, germinating them in a greenhouse, and transplanting the seedlings into plastic 93 cm^3 Hiko® containers (BCC, Landskrona, Sweden) filled with an all-purpose growing mix (45% peat moss with pine bark, perlite, and vermiculite; Fafard, Inc., Agawam, MA) for an additional 4 months of greenhouse development. A sufficient number of seedlings were grown to enable plantings of six species of grasses and eight species of forbs (Table 1).

To maximize growing season length yet avoid potential injury from a late spring frost, herbaceous species were planted in early May 1999–2001. All seedlings were planted with a containerized planting tool (International Forest Company, Odenville, AL) to minimize soil disturbance. To provide comparative data on responses of longleaf pine seedlings to the treatments, containerized seedlings were purchased (International Forest Company, Odenville, AL) and planted within randomly assigned quadrats in December 1998. For most species studied, 36 individuals were planted per quadrat; however, limited propagation of several species resulted in planting densities as low as 11 seedlings per quadrat (Table 1). To accommodate planting of the 2000 cohort, three species from the 1999 cohort were removed May 2000 with a foliar application of glyphosate herbicide (5% solution of Accord® in water plus 0.5% surfactant).[4] Survival of the 2000 cohort ranged from 3–14%; therefore, survivors were removed as done in 2000 to accommodate planting of the 2001 cohort.

Table 1. Characteristics of understory species planted into three longleaf pine plantations that were thinned to four levels of stocking with or without trenching or needlefall.

Scientific name[a]	Common name[a]	n[f]	Plant type	Characteristics
Anthaenantia villosa (Michx.) Beauv.[b]	Green silkyscale	36	Perennial grass	Ascending (slight lean); spreads by short rhizomes
Lespedeza hirta (L.) Hornemann[b]	Hairy lespedeza	23	Perennial forb	Erect; nitrogen fixer
Liatris elegans (Walt.) Michx.[b e]	White featherflower	35	Perennial forb	Erect; persists by corms
Pinus palustris Mill.[b]	Longleaf pine	36	Coniferous tree	Fire tolerant grass stage; shade intolerant
Pityopsis graminifolia (Michx.) Nutt.[b c]	Silk-grass	11	Perennial forb	Erect; spreads by rhizomes
Solidago odora Aiton[b e]	Fragrant goldenrod	36	Perennial forb	Erect; spreads by short rhizomes
Sorghastrum secundum (Ell.) Nash[b]	Lopside indiangrass	33	Perennial grass	Ascending; lacks rhizomes
Sporobolus junceus (Michx.) Kunth[b]	Pineywoods dropseed	36	Perennial grass	Erect to sprawling; bunchgrass
Andropogon ternarius (Michx.)[c]	Splitbeard bluestem	36	Perennial grass	Erect, from short rhizomes or hardened bases
Carphephorus bellidifolius (Michx.) T. & G.[c d]	Sandywoods chaffweed	36	Perennial forb	Ascending
Chrysopsis gossypina (Michx.) Ell.[c]	Golden-aster	36	Perennial forb	Erect, decumbent, or ascending
Desmodium ciliare (Muhl. Ex Willd.) DC.[c d]	Beggar's ticks	36	Perennial forb	Erect
Eragrostis spectabilis (Pursh) Steudel[c d]	Purple lovegrass	36	Perennial grass	Erect, from short rhizomes
Aristida beyrichiana Trin. & Rupr.[d]	Wiregrass	36	Perennial grass	Erect, from hardened root crowns
Eriogonum tomentosum Michx.[d]	Wild-buckwheat	36	Perennial forb	Erect

[a] Nomenclature follows Miller and Miller (1999) or Radford et al. (1968).
[b] 1999 cohort.
[c] 2000 cohort.
[d] 2001 cohort.
[e] Removed May 2000.
[f] Number of containerized seedlings planted per quadrat.

Vegetation Measurements

Surviving plants were counted and cover (%) was estimated visually for each quadrat in June, August, and October 1999–2001; however, only results from the October data were presented because they provided the most consistent treatment responses, and they summarized the cumulative responses for a given growing season. In August, at peak vegetative growth, the plant of average size (identified visually) within each quadrat was clipped, returned to the laboratory, dried to a constant weight at 65°C, and weighed (g).[5] The biomass samples of *S. junceus* and *Anthaenantia villosa* (Michx.) Beauv. were analyzed for nitrogen concentration (%) in 2000 and 2001, respectively, following the procedures of Isaac and Johnson (1976).[6] Foliar nitrogen content per quadrat was estimated by multiplying a species' nitrogen concentration by the product of aboveground biomass and quadrat density. A needlefall sample collected from each plot in October 2001 was analyzed for nitrogen concentration (%) using the foliar analysis methods described above.

Statistical Analyses

All statistical analyses were performed with SAS (SAS Institute, Inc. 1989). Analysis of variance (ANOVA) was conducted on each response variable assuming the following model

$$Y = \mu + \beta + T + \tau + (T \times \tau) + \varepsilon \qquad (1)$$

where μ represents the overall mean, β represents block effects, T represents whole-plot effects (pine stocking level), ε_1 represents whole-plot error, τ represents split-plot effects (trenching, needlefall, or their interaction), $T \times \tau$ represents the interaction of whole- and split-plot effects, and ε represents error. Data for each of the periodic samples of environmental conditions were analyzed separately. To test effects of the planted species on soil water content, only trenched plots with needlefall removal were used (to eliminate root competition and needlefall effects from overstory pines) in an analysis in which vegetation (*S. junceus*) presence versus absence was assigned to a split-plot effect as shown in Equation (1).

Prior to ANOVA, logarithmic transformations of biomass and soil nitrogen variables and angular transformations of proportionate variables (crown closure, survival, cover, soil water content, and foliar nitrogen) were applied to improve their normality (Sokal and Rohlf 1981, p. 419–421, 427–428). For each ANOVA, residuals were plotted against predicted values of the dependent variable to determine whether residual variances were relatively homogeneous. Visual inspection of scatterplots revealed that, in almost all cases, the assumptions of normality were met. If the F-test in the ANOVA indicated a significant ($\alpha = 0.05$) interaction among factors, multiple comparisons of interaction means were conducted with Bonferroni-adjusted probabilities (SAS Institute, Inc. 1989, p. 941–948). If the interaction F-test was not significant, multiple comparisons of main-effect means were conducted with Tukey's HSD test (Sokal and Rohlf 1981, p. 245). Unless indicated otherwise, treatment differences described below were significant at $P \leq 0.05$.

An equation for predicting crown closure from stand basal area of longleaf pine was developed via linear regression to enable users to estimate understory light availability for plantations of similar density. Indicator variables were specified in the regression to enable comparisons of slopes and intercepts for each year (1998–2001), and logarithmic transformations were applied to the dependent or independent variable as needed to homogenize the residual variances (Sokal and Rohlf, 1981). Regression parameters retained in the final model were significant at $P \leq 0.05$.

To illustrate effects of the experimental factors, treatment means for cover were plotted by species for October of the last year of measurement, with the exception of *Lespedeza*

hirta (L.) Hornemann and *Sorghastrum secundum* (Ell.) Nash. For these two species, data were plotted for October 2000 because their survival in 2001 declined abruptly within each treatment for unknown reasons. Cover was selected to illustrate treatment effects on plant performance because it integrates the combined responses of survival and growth.

Results

Pine Basal Area and Crown Closure

Prior to thinning to the specified pine stockings (September 1998), basal area of plots located in areas previously thinned in 1994 (10.5 m^2 ha^{-1}) was about half that of plots located in nonthinned areas (19.5 m^2 ha^{-1}). In each measurement year, basal area differed among the 25, 50, and 100% stockings (Figure 2a). From 1998 to 2001, basal area increased by 55, 46, and 23% for the 25, 50 and 100% pine stockings, respectively. Twelve out of a total of 705 longleaf pines (1.7%) died from October 1998 to November 2001, and their mortality did not appear to result from proximity to trenched areas.

In 1998, crown closure differed among each of the 25, 50, and 100% stockings; however, from 1999 to 2001 it only differed between the 25 and 100% stocking levels (Figure 2b). During the 3 yr of the study, crown closure increased by 62, 27, and 17% for the 25, 50 and 100% stockings, respectively, although little or no change occurred from 1999 to 2000. Note that in 2001 both basal area and crown closure in the 25% stocking approximately equaled those observed in 1998 for the 50% stocking.

The following regression equation was developed for predicting crown closure (Y, %) of longleaf pine from the natural logarithm of its stand basal area (X, m^2 ha^{-1}) ($n = 36$, $r^2 = 0.81$, $s_{y.x} = 7.98$):

$$Y = -18.500 + 30.687X \quad (2)$$

Measurement year did not significantly influence either the intercept or slope of the regression. Because of the limited data range, use of this equation should be restricted to 13- to 18-yr-old longleaf pine plantations of basal area 4.9-28.9 m^2 ha^{-1}.

Environmental Conditions

Precipitation.—Growing season (May through October) precipitation was 42.8, 60.1, and 64.3 cm in 1999, 2000, and 2001, respectively (USDA Forest Service–Savannah River 2002). Long-term (1964–1985) average growing season precipitation for the SRS is 62.5 cm (Rogers 1990). Although each of the years had significant drought periods (Figure 3a), precipitation in the months prior to and soon after planting in 1999 and 2001 apparently was sufficient to ensure adequate survival of planted species (described below). However, precipitation in April and May 2000 was well below average, and the resulting dry soil conditions (described below) probably caused the low survival of seedlings planted that year.

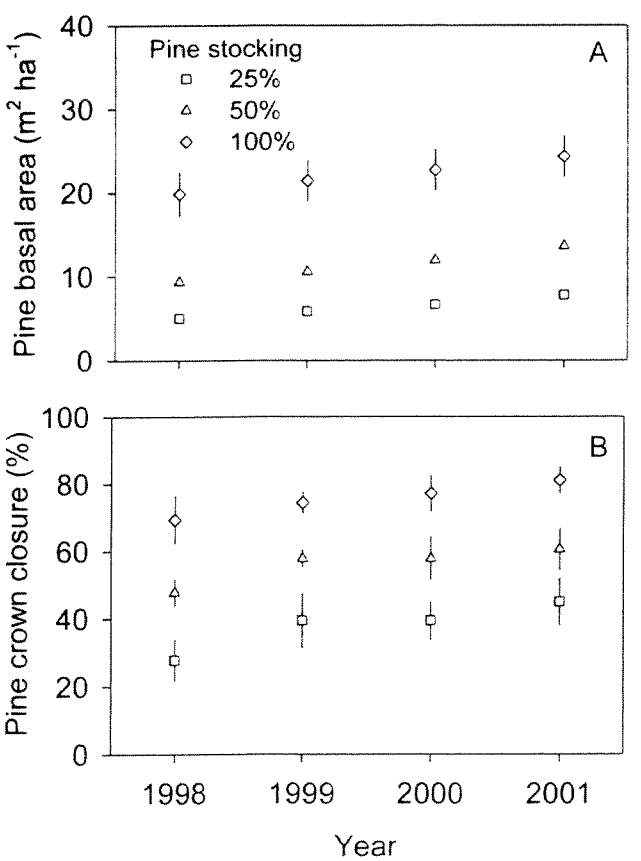

Figure 2. Average values (± standard error) for (a) stand basal area and (b) crown closure during 3 yr after a 1998 thinning of three longleaf pine plantations to three levels of stocking (0% stocking not shown).

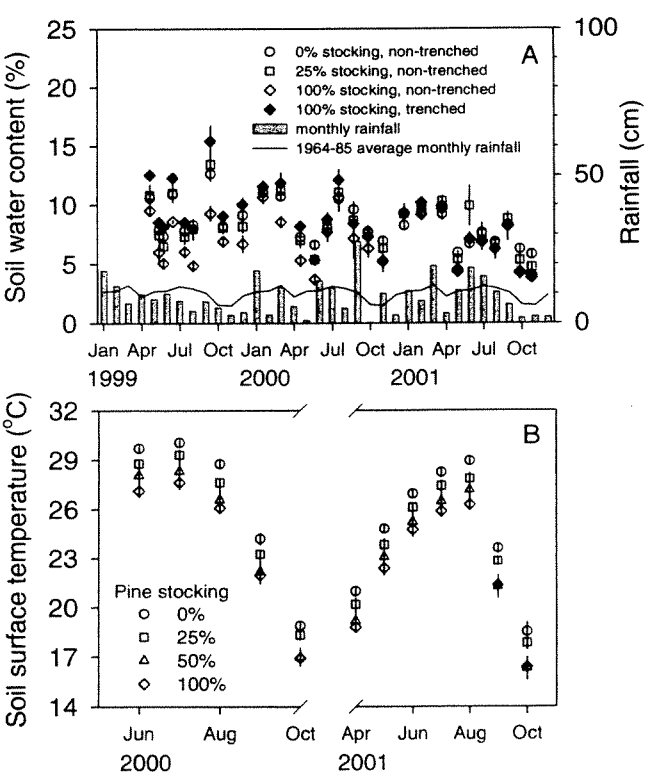

Figure 3. Average values of (a) soil water content (0–0.45 m depth) of selected treatments, monthly rainfall, and 1964–1985 monthly rainfall (Rogers 1990) and (b) soil surface temperature (± standard error) after a 1998 thinning of three longleaf pine plantations to four levels of stocking with or without trenching or needlefall. A subset of the soil water treatment means were plotted to illustrate general effects of stocking and trenching.

Soil Water.—For each of the 1999 measurements, soil water in nonvegetated quadrats varied as a result of the interaction of pine stocking and trenching (Figure 3a). During this time, soil water in trenched plots did not vary among stocking levels, indicating that trenching successfully partitioned competition from pine into above- and belowground components. However, in nontrenched plots, soil water decreased in proportion to stocking. For each of the year 2000 measurements, soil water for a given stocking averaged greater in the presence versus absence of trenching, and the stocking-by-trenching interaction was significant only in May. In 2001, significant effects of trenching were detected only in January, February, May, October, and November.

The lowest mean value of soil water observed in the study occurred in May 2000 (Figure 3a), and probably this brief period of soil drought was the primary factor limiting survival of the 2000 cohort (described below). During six periods in the 1999–2001 growing seasons, soil water in nontrenched plots dropped below 6%, the assumed permanent wilting point for these soils (Harrington and Edwards 1999). At 0% pine stocking, soil water did not vary significantly in the presence versus absence of trenching, indicating negligible background effects from trenching, such as those potentially associated with soil disturbance and presence of aluminum flashing.

In quadrats planted with *S. junceus*, soil water content did not differ among levels of pine stocking, trenching, or needlefall except in May 2001 when it was greater in the presence (5.8%) versus absence of needlefall (4.4%). In September 2001, soil water at 0–0.15 m in nonvegetated quadrats was greater in the presence (10.0%) versus absence (8.8%) of needlefall. In November 2001, a similar effect of needlefall was detected, but only in the presence of trenching. Soil water was less in the presence versus absence of *S. junceus* for 6 of the 19 measurements in 2000–2001.

Temperature.—In each sample month of 2000–2001, soil surface temperature differed among pine stockings, with mean daily values decreasing incrementally with increasing stocking (Figure 3b). In August, when surface temperatures differed most, values averaged 3°C warmer in the 0 versus 100% stockings. In August, September, and October 2000, maximum daily temperatures in the 0% stocking were 3–9°C warmer than values observed for each of the other stockings. In contrast, minimum daily temperature did not vary significantly among stockings. During the latter parts of each growing season, minimum temperatures were higher, and maximum temperatures were lower under *S. junceus*.

Needlefall.—During each year from 1999 to 2001, stand-produced needlefall was greater in the 100% pine stocking (2975–4963 kg ha^{-1}) than in either the 50% (1565–3242 kg ha^{-1}) or 25% (1330-2655 kg ha^{-1}) stockings. Stand-produced needlefall for the 100% stocking corresponded closely to those reported for longleaf pine plantations of similar age (Weigert and Monk 1972). Methodologies used to standardize needlefall rates in the needlefall treatment were effective at minimizing variation among pine stockings (Figure 4a). In 1999 and 2001, annual rates (stand produced plus supplemented) in the needlefall treatment exceeded the standardized rate (7893 kg ha^{-1} yr^{-1}) by only 49–123 kg ha^{-1} (1–2%), and they did not differ significantly among pine stockings. In 2000, annual rates in the needlefall treatment for the 100% stocking level were significantly less than standardized rates by 125 kg ha^{-1} (2%), while those in the 25% stocking level were significantly greater than standardized rates by 13 kg ha^{-1} (<1%). Nitrogen concentration of pine needles did not differ among stocking levels and averaged 0.22%. Based on this mean concentration, nitrogen inputs from the needlefall treatment (stand-produced plus supplemented) during 1999-2001 were 15–20 kg ha^{-1} yr^{-1}. In 1999 and 2001, nitrogen inputs from the needlefall treatment were significantly lower in the 0% stocking than in other stockings, while for 2000 they were significantly lower in the 100% stocking (Figure 4a).

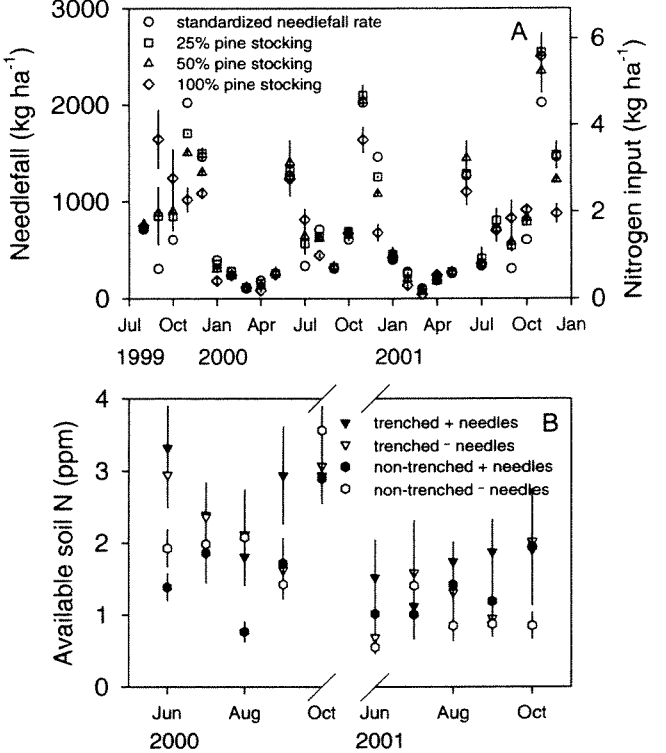

Figure 4. Average (a) stand-produced plus supplemented needlefall and resulting nitrogen inputs, and (b) available soil nitrogen (NH_4^+ and NO_3^- concentrations at 0–0.15 m depth) (± standard error) after a 1998 thinning of three longleaf pine plantations to four levels of stocking with or without trenching or needlefall (standardized needlefall rate was 7893 kg ha^{-1}yr^{-1}).

Soil Nitrogen.—In June and August 2000, available soil nitrogen was greater in the presence versus absence of trenching, while in June and August 2001 it was greater in the presence versus absence of needlefall (Figure 4b). In September 2001, the interaction of needlefall and stocking was significant. Multiple comparisons of interaction means indicated that soil nitrogen did not vary significantly in the absence of needlefall; however, in the presence of needlefall, soil nitrogen decreased from 2.4 to 0.7 ppm as pine stocking increased from 0 to 100%.

Plant Performance

Survival.—First-year survival of planted species averaged 77, 6, and 71% for the 1999, 2000, and 2001 cohorts,

respectively. Third-year survival (2001) of the 1999 cohort remained high for *A. villosa* (91%) and *S. junceus* (74%), but it was substantially less for *L. hirta* (60%), *P. palustris* (50%), and *S. secundum* (40%). Extremely dry soil conditions at the time of planting (Figure 3a) limited survival of the 2000 cohort. Frequency of herbivory was very low for the study duration and was primarily limited to *A. beyrichiana* and *Carphephorus bellidifolius* (Michx.) T. & G. in several quadrats immediately after planting the 2001 cohort.

Trenching was associated with increased survival of most species (Table 2). Although survival of the 2000 cohort was extremely low, significant increases associated with trenching were detected for each species except *C. bellidifolius*. Pine stocking, by itself, rarely was associated with reductions in survival, and no reductions from needlefall were detected for the 2000 and 2001 cohorts. A significant interaction of pine stocking and needlefall was detected for first-year survival of *A. villosa* and *Solidago odora* Aiton. Multiple comparisons of interaction means for these species indicated that, in the presence of needlefall, survival declined with increasing pine stocking, while in the absence of needlefall, survival did not vary significantly among stockings. In the second and third years after planting the 1999 cohort, a negative effect of needlefall independent of pine stocking was detected for survival of the five species.

Cover.—Cover responses to pine stocking, trenching, and needlefall varied by species; however, in general cover was greatest at 0 or 25% stockings and in the presence of trenching (Figures 5 and 6). At 0% stocking, plant cover did not vary significantly in the presence versus absence of trenching, indicating that potential effects of soil disturbance and aluminum flashing from the trenching treatment were negligible, as found for soil water. Cover of *A. villosa*, *Eragrostis spectabilis* (Pursh) Steudel, and *A. beyrichiana* was greater in the presence versus absence of needlefall, particularly at pine stockings less than 100%. All other needlefall responses observed were either negative or nonsignificant.

An important observation from this research is that, with the exception of *P. palustris* (a tree species) and *Eriogonum tomentosum* Michx. (a biennial herbaceous species), each species flowered and produced seed by the end of the first growing season after planting, although viability of the seed was not tested. Apparently when given an adequate supply of resources, the containerized seedlings were able to establish quickly and complete their life cycles.

Species' cover responses can be grouped according to several discrete patterns. *A. villosa*, *P. palustris*, *S. secundum*, *Liatris elegans* (Walt.) Michx., *A. beyrichiana*, and *E. tomentosum* each exhibited a significant stocking-by-

Table 2. ANOVA results for plant performance, including significant ($P \leq 0.05$) factors (S = pine stocking, T = trenching, and N = needlefall), and *F*-test probabilities (Prob.>*F*). Blank cells indicate variables that were not measured.

		October survival (%)		October cover (%)		August biomass (g)	
Species	Year	Factors	Prob.>*F*	Factors	Prob.>*F*	Factors	Prob.>*F*
Anthaenantia villosa [a]	1999	SxN, T	0.008, 0.026	SxT, N	0.000, 0.038	S, T	0.000, 0.000
	2000	N	0.044	SxT, N	0.000, 0.002	SxT, SxN	0.012, 0.043
	2001	N	0.014	SxT, N	0.015, 0.034	SxN, T	0.037, 0.001
Lespedeza hirta [a]	1999	T	0.021	S, T	0.038, 0.000	S, T	0.000, 0.002
	2000	N	0.007	S, T	0.017, 0.009	S, T	0.008, 0.019
	2001	N	0.002	n.s. [d]		S, T	0.011, 0.017
Liatris elegans [a]	1999	n.s. [d]		SxTxN	0.021	SxT	0.000
Pinus palustris [a]	1999	T	0.047	T, N	0.000, 0.001	SxN, T	0.018, 0.000
	2000	T, N	0.018, 0.016	SxT, SxN	0.003, 0.012	SxT	0.000
	2001	T, N	0.015, 0.001	SxT, TxN	0.000, 0.038	SxT	0.001
Pityopsis graminifolia [a]	1999	T	0.020	T	0.000	SxT	0.012
Solidago odora [a]	1999	SxTxN	0.003	S, T	0.000, 0.001	SxT	0.002
Sorghastrum secundum [a]	1999	n.s. [d]		SxT, TxN	0.001, 0.027	SxT	0.000
	2000	N	0.000	SxT, TxN	0.004, 0.045	SxT	0.041
	2001	S, T, N	0.040, 0.041, 0.000	n.s. [d]		T	0.002
Sporobolus junceus [a]	1999	T	0.049	SxT, N	0.028, 0.000	SxT	0.000
	2000	T, N	0.027, 0.012	n.s. [d]		S, T	0.003, 0.026
	2001	T, N	0.011, 0.000	N	0.000	S, T	0.005, 0.005
Andropogon ternarius [b]	2000	T	0.031	T	0.028		
Carphephorus bellidifolius [b c]	2000	n.s. [d]		n.s. [d]			
	2001	SxT	0.042	S	0.000	S	0.006
Chrysopsis gossypina [b]	2000	T	0.006	T	0.010		
Desmodium ciliare [b c]	2000	T	0.005	T	0.021		
	2001	n.s. [d]		S	0.011	S	0.000
Eragrostis spectabilis [b c]	2000	T	0.002	T, N	0.001, 0.015		
	2001	n.s. [d]		S, T	0.005, 0.002	n.s. [d]	
Aristida beyrichiana [c]	2001	T	0.032	SxT, SxN	0.008, 0.002	S, T, N	0.003, 0.001, 0.021
Eriogonum tomentosum [c]	2001	SxT	0.031	SxT	0.042	n.s. [d]	

[a] Planted 1999.
[b] Planted 2000.
[c] Planted 2001
[d] n.s.: no factors had a significant ($P \leq 0.05$) *F* –test.

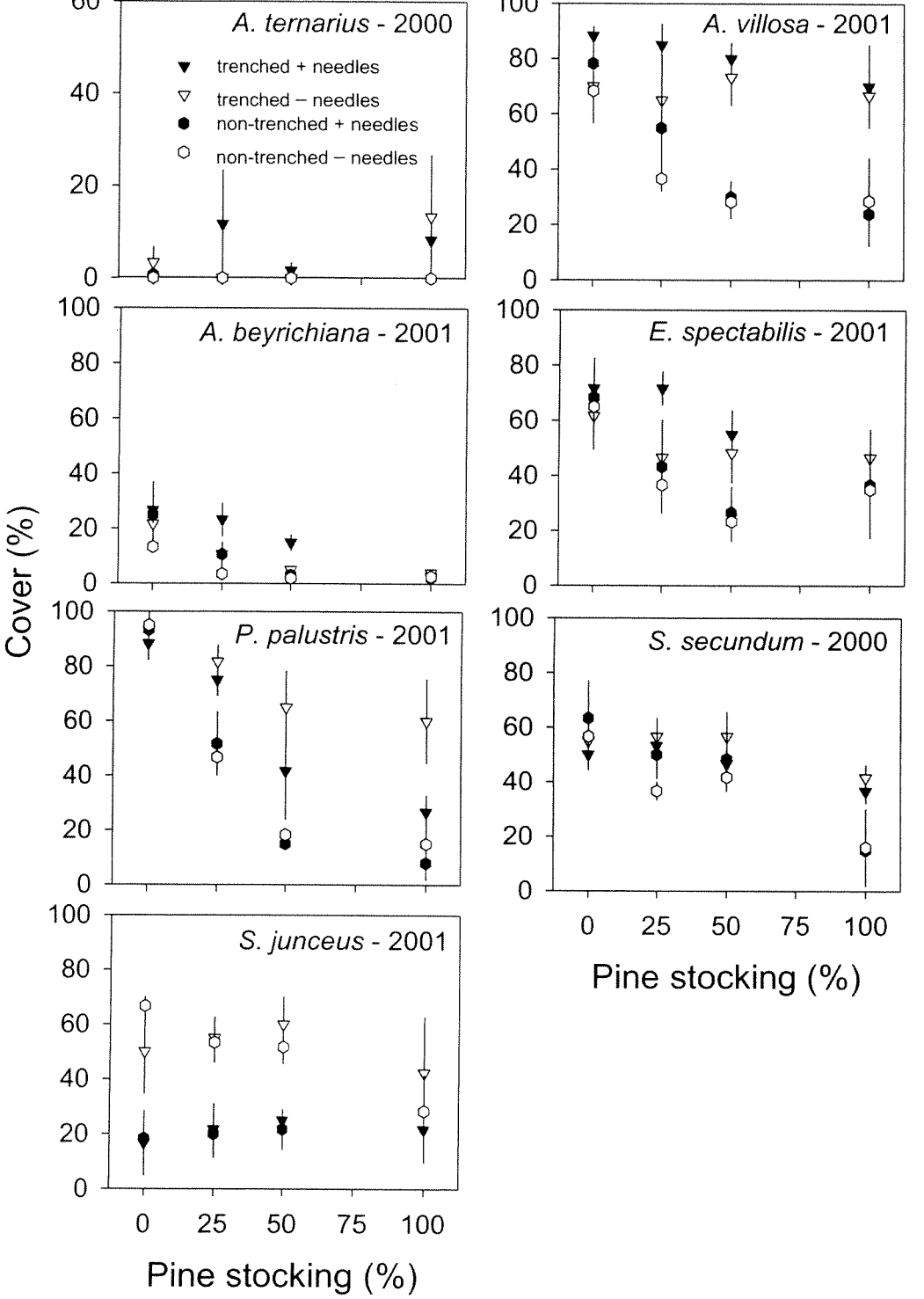

Figure 5. Average cover of grass species and longleaf pine seedlings (± standard error) in 1 m^2 quadrats planted 1 to 3 yr after a 1998 thinning of three longleaf pine plantations to four levels of stocking with or without trenching or needlefall. Data plotted are for October of the year shown for each species.

trenching interaction (Table 2). In the absence of trenching, cover of species with this "interactive" response declined with increasing stocking, while in the presence of trenching, cover reductions with increasing stocking were either absent or they occurred at higher stockings (Figures 5 and 6). Other significant interactions were detected. For *P. palustris*, significant negative effects of needlefall were detected only in the presence of trenching, while for *S. secundum*, significant positive effects of trenching were detected only in the absence of needlefall. For *L. elegans*, differences among levels of trenching and needlefall were detected only at 50% stocking, while for *A. beyrichiana*, significant positive effects of needlefall were only detected at 25% stocking.

An "additive" response pattern (i.e., stocking effects were independent of trenching or needlefall effects) was observed

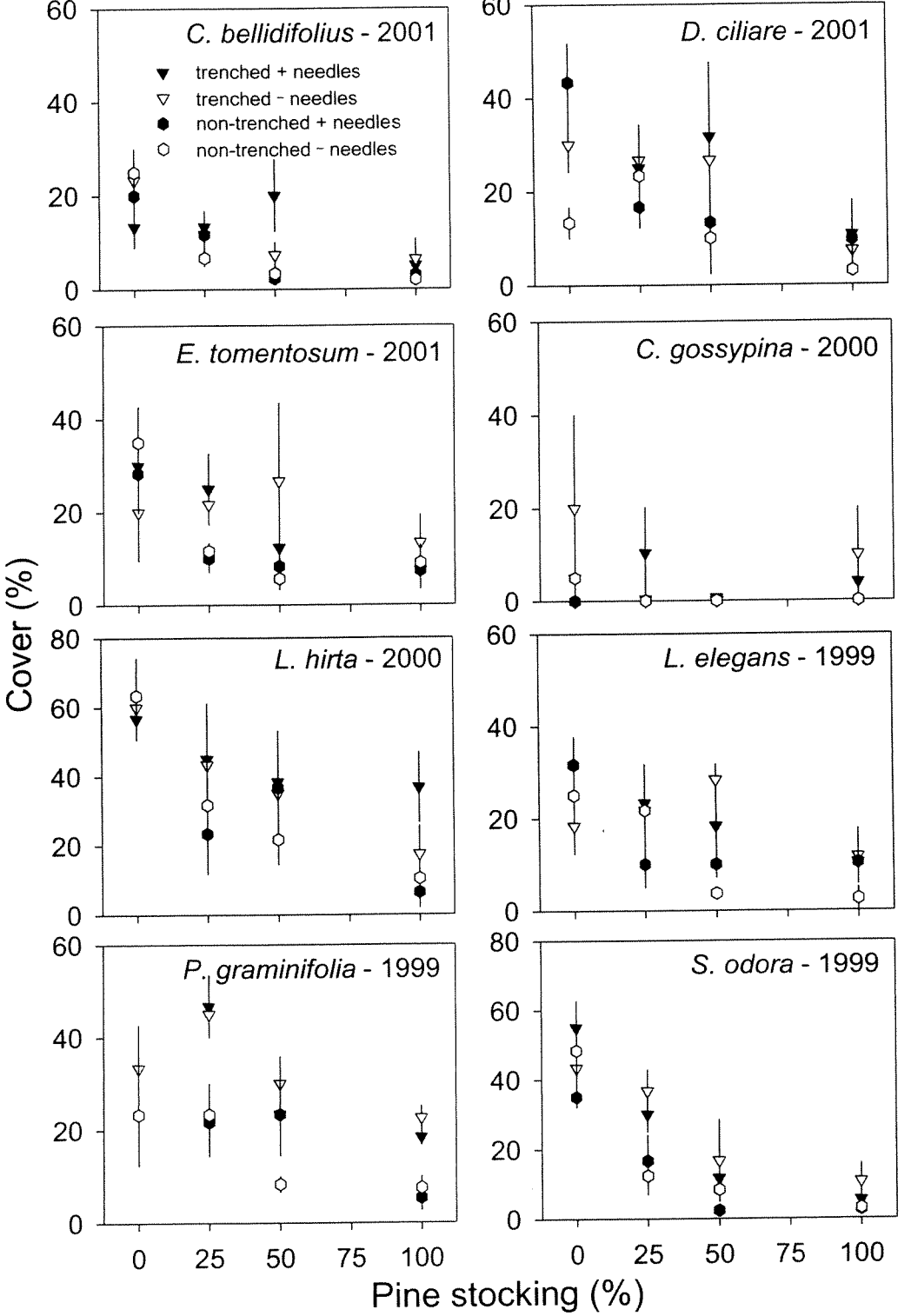

Figure 6. Average cover of broadleaf herbaceous species (± standard error) in 1 m^2 quadrats planted 1 to 3 yr after a 1998 thinning of three longleaf pine plantations to four levels of stocking with or without trenching or needlefall. Data plotted are for October of the year shown for each species.

for *L. hirta*, *S. odora*, and *E. spectabilis*. For these species, cover declined with increasing pine stocking, and the response was independent of other responses from trenching or needlefall (Table 2). Stocking was the only experimental factor that significantly influenced cover of *C. bellidifolius*. *S. junceus*, *Pityopsis graminifolia* (Michx.) Nutt., and *Desmodium ciliare* (Muhl. Ex Willd.) DC each had a "shade tolerant" response pattern. Cover of these species did not vary significantly with pine stocking (Table 2), but it did vary with either or both of trenching or needlefall. *S. junceus* was the only species that exhibited strongly negative responses to needlefall even at 0% stocking (Figure 5). Two species, *Andropogon ternarius* (Michx.) and *Chrysopsis gossypina* (Michx.) Ell., could not be grouped into either of the three

response patterns because of their poor survival and limited cover development in 2000 and the fact that they were not replanted in 2001.

Because the treatments used in this study were effective at separating effects of above- and belowground competition and needlefall, the following approach can be used to assess the relative importance of each factor on plant cover responses. The importance of aboveground competition for a given level of needlefall can be quantified as the change in plant cover per unit change in pine stocking for trenched plots. Likewise, combined above- and belowground competition effects for a given level of needlefall can be assessed as the change in plant cover per unit change in pine stocking for nontrenched plots. Finally, the importance of belowground competition can be quantified by subtracting aboveground effects from combined above- and belowground effects.

Depending on the species, the importance of belowground competition was found to increase (e.g., *A. villosa*, *P. palustris*, and *S. secundum*), stay relatively constant (e.g., *S. odora* and *P. graminifolia*), or decrease (e.g., *A. beyrichiana*, *E. spectabilis*, *D. ciliare*, and *E. tomentosum*) with increasing pine stocking (Figures 5 and 6). The declining importance of belowground competition with increasing pine stocking observed for some species may have resulted from the diminishing effects of trenching on soil water during 2001. For a given level of trenching, changes in the importance of needlefall with increasing pine stocking can be quantified similarly. For most species, including *S. junceus*, the importance of needlefall decreased with increasing pine stocking.

Based on the approach described above, the relative importances of above- and belowground competition were calculated for each species in needlefall-absent split-plots. Aboveground competition effects were calculated as the absolute difference in cover between the 0 and 100% pine stockings for trenched split-plots, and belowground competition effects were calculated as the mean absolute difference in cover between trenched and nontrenched split-plots for stockings of 25, 50, and 100%. Results indicate that mean reductions in plant cover from the effects of above- and belowground competition were of similar magnitude, averaging 16.5 and 14.1%, respectively.

Biomass.—Responses of mean plant biomass were relatively similar to those observed for cover (Table 2). In general, needlefall effects were less detectable for biomass than they were for cover. For example, biomass of *E. spectabilis* did not vary significantly in the presence versus absence of needlefall, although its cover was significantly greater in the presence of needlefall.

Foliar Nitrogen.—In 2000, nitrogen concentration of *S. junceus* foliage was somewhat greater ($P = 0.06$) in the presence (1.0%) versus absence (0.9%) of needlefall. However, in 2001, foliar nitrogen concentration of *A. villosa* (1.2%) did not vary significantly among levels of pine stocking, trenching, or needlefall. Foliar nitrogen content for *S. junceus* was less in the 100% pine stocking (7.4 kg ha^{-1}) than in the other stockings (17.0–31.6 kg ha^{-1}). For *A. villosa*, foliar nitrogen content was greater in the presence (19.8 kg ha^{-1}) versus absence (6.6 kg ha^{-1}) of trenching, and it was greater in the 0% pine stocking (30.7 kg ha^{-1}) than in the other stockings (6.4–9.8 kg ha^{-1}).

Discussion and Conclusions

Environmental Conditions

For the duration of the study, pine basal area and crown closure varied discretely as a result of the thinning treatments. However, vigorous stand growth caused crown closure in the 25 and 50% pine stockings to approach values observed at study initiation for the 50 and 100% stockings, respectively. This suggests that, in order to maximize duration of increased light availability in the understory, thinning must occur at a high intensity (e.g., leaving 10–15% stockings); it must occur at several times during the life of the stand; or discrete gaps 0.1 ha or larger must be created in the overstory.

The soil water responses indicate that trenching was effective at eliminating belowground competition from split-plots receiving this treatment for 1999, 2000, and the first half of 2001. The supplemental applications of needlefall also were effective at holding this variable independent of pine stocking level. Therefore, these treatments successfully separated the effects of above- and belowground competition and needlefall on performance of planted species.

Diminishing effects of trenching in 2001 may indicate that roots of overstory pines are beginning to exploit the additional water present at 0–0.45 m. An alternative explanation is that cumulative evaporation from the various episodes of summer drought has eliminated the surplus water once present from trenching or differential stocking of pine. Responses of species planted in 2001 may have been affected by these diminishing effects of trenching, resulting in a lessened ability to independently quantify the relative importance of above- versus belowground competition.

This study demonstrated that longleaf pine depleted soil water in proportion to its stand basal area. Trees were able to extract water at 3% volumetric water content—considerably below the assumed wilting point of 6%. The presence of needlefall had only a limited effect of preserving soil water via a "mulching" effect. Additional water made available through elimination of belowground competition went entirely to the development of understory vegetation, because soil water rarely varied among treatments for quadrats planted with *S. junceus*, the species used to test effects of presence versus absence of quadrat vegetation.

Soil surface temperatures were moderated by the presence of overstory longleaf pines. Presumably, such moderating effects by the canopy could slow rates of evaporation from the soil surface. However, in trenched plots, soil water never varied among stocking levels, indicating that effects of overstory shade on soil water were negligible to nonexistent. Despite the higher surface temperatures at 0% stocking, plant performance in trenched plots generally exceeded that of other stocking levels, suggesting that there was no beneficial effect from partial shade. The

presence of understory vegetation (*S. junceus*) also acted to reduce temperature extremes at the soil surface.

Needlefall provided a significant source of nitrogen to the soil, with inputs of 15–20 kg ha^{-1} yr^{-1}. Available soil nitrogen exhibited different responses in 2000 versus 2001 that may be attributable to the observed soil water and needlefall responses. In 2000, responses of available soil nitrogen were similar to those of soil water; i.e., nitrogen concentrations were higher in the presence versus absence of trenching—presumably a result of uptake by pine roots. In 2001, when the trenching treatment possibly was less effective at partitioning above- and belowground competition, nitrogen concentrations were higher in the presence versus absence of needlefall. Probably it took a year or more for nitrogen inputs from the needlefall treatment to be mineralized into detectable concentrations of nitrate and ammonium.

Plant Responses

Although responses to competition and needlefall were species-specific, the research has provided a framework for understanding and classifying these responses. First and foremost, initial establishment of planted species depended critically on adequate soil moisture at the time of planting or soon thereafter. Although the 1999 growing season was substantially drier than the long-term average, survival was severely affected only in 2000 because of the lack of rainfall in April and May despite near-average growing season rainfall. Dry soil conditions also existed at the time of planting in 2001, but rains followed soon thereafter. In addition to vigorous vegetative growth, most of the species flowered by the end of their first growing season. Rates of flowering, seed production, and seed viability varied among the treatments and are the subject of an ongoing study (T.B. Harrington, unpublished data). Previous research has demonstrated that burning or clipping can be used to stimulate flowering of species common to longleaf pine communities (Streng et al. 1993, Outcalt 1994, Brewer and Platt 1994).

Second, in the presence of belowground competition, plant performance generally increased at an accelerating rate with decreasing pine stocking. The general response observed for most of the species was a similarity of performances for the 50 and 100% stockings, while a marked improvement in performance occurred as stocking decreased to 25 and then 0%. This finding indicates that the additional soil water made available by reducing pine stocking to 50% is not sufficient to increase understory plant performance; pine stocking must be reduced further in order to limit effects of belowground competition.

Third, species' response patterns were classified as either interactive, additive, or shade tolerant. Species with the interactive response pattern responded more discretely to specific combinations of above- and belowground competition and needlefall than those having the other response patterns. In general, their performance will be maximized under full sunlight and in the absence of belowground competition and needlefall. Species with the additive response pattern will perform incrementally better with decreased above- and belowground competition and needlefall; these individual factors can be manipulated independently to improve plant performance. Species with the shade tolerant response pattern can be established successfully in the understory of moderately stocked pine stands, and their performance will increase with reductions in belowground competition and needlefall.

Finally, the research provides a method for ranking the relative importance of above- and belowground competition and needlefall. On the average, limitations in performance of the 15 species tested were of similar magnitude for above- versus belowground competition effects. However, at high pine stockings, aboveground competition had an overriding influence that shrouded the effects of belowground competition and needlefall. Note that crown closure did not exceed 81% for the duration of the study, suggesting that aboveground competition effects were not at their potential maximum. At low pine stockings, belowground competition generally had a stronger effect than needlefall in modifying plant performance. As described previously, performance of certain species increased in the presence of needlefall, more likely a result of nitrogen addition ("fertilizer" effect) than from a mulching effect that conserves soil water.

Regarding the four primary hypotheses of the research, it is clear that competition had a much stronger effect than needlefall in limiting plant performance (Hypothesis #1). With the exception of the survival responses of *A. villosa* and *S. odora*, there was little evidence of intensified reductions in plant performance when needlefall was combined with high levels of overstory competition (Hypothesis #2). Limitations in plant performance were of similar magnitude for above- and belowground competition (Hypothesis #3). Although 25% stocking did moderate soil surface temperatures, evaporation was not reduced, and availabilities of light and soil water clearly were limited by competition from overstory trees. Thus, plant performance at 25% stocking was, at best, similar but more often less than that observed at 0% stocking (Hypothesis #4).

Implications for Understory Restoration

This study has increased our understanding of the complexity by which overstory pines affect understory vegetation through resource competition and needlefall. In general, aboveground competition imposed similar limitations on understory plant performance as belowground competition. However, performance of most species was increased when availability of belowground resources was elevated, regardless of availability of light. In addition, effects of trenching interacted with pine stocking for certain species, indicating that limiting effects of aboveground competition can be either moderated or intensified by variation in availability of belowground resources. The three response patterns—interactive, additive, and shade tolerant—provide meaningful categories for classifying herbaceous species according to their potential performance in longleaf pine community restoration, given specific overstory and understory conditions.

It is important to emphasize that results from this study are based on virtual absence of competition from nonpine veg-

etation: therefore, they represent competitive effects from longleaf pine only. Competitive effects from associated hardwood, shrub, and herbaceous vegetation are likely to shroud increases in availability of light and soil water that occur following thinning of overstory pines (Harrington and Edwards 1999, McGuire et al. 2001); therefore, abundance and size of this competing vegetation should be reduced if understory restoration efforts are to be successful.

In order to apply study results to other stand conditions, particularly those associated with mature longleaf pine, stocking levels must be adjusted appropriately by calibrating the relationship of crown closure to stand basal area. Because of the wider spacing among mature trees, belowground competition may not be as severe as in the plantations studied here, but the zone of influence around individual trees is likely to be of greater area. Mature longleaf pines can exert a competitive influence on longleaf pine seedlings located up to 16 m away in an adjacent canopy gap (Brockway and Outcalt 1998, McGuire et al. 2001).

One practical application of these results lies in the development of silvicultural regimes that fit within the context of longleaf pine community restoration and provide high resource availability for planted species. Methodology developed in this research provides some insight into possible approaches. Discrete canopy gaps of 0.1 ha or larger (i.e., a "patchy" forest stand structure) may be a useful setting for understory restoration in young plantations (≤15 yr old) because they provide conditions of full sun (i.e., if surrounding tree height ≤ gap radius; Runkle 1985) and reduced belowground competition. In stands of mature longleaf pine, larger gaps (0.15–0.20 ha or larger) may be required if understory species are to be established greater than 16 m from neighboring trees, and therefore, outside of the zone of their competitive influence (Palik et al. 1997, Brockway and Outcalt 1998, McGuire et al. 2001). Silvicultural systems that retain a clumped distribution of overstory trees will provide a higher percentage of area in these larger gaps than those that retain trees evenly dispersed across a given area of land (Palik et al. 1997). The shape and orientation of individual gaps also can be modified to change duration of sunlight and intensity of belowground competition.

To maximize performance of reintroduced species, non-soil-active herbicides can be used to suppress competing vegetation prior to planting. Alternatively, disking or other tillage treatments can be used to temporarily reduce abundance and size of competing vegetation. Application of nutrients may further stimulate improved performance of planted species, particularly if the fertilizer is incorporated into the soil during planting. However, broadcast application of nitrogen fertilizer may, in fact, reduce performance of certain herbaceous species because it stimulates more rapid rates of crown closure and associated competition from species first to colonize the site (Goldberg and Miller 1990). Containerized seedlings, although expensive, provide an effective method for rapid establishment, growth, and flowering, assuming that soils are fully hydrated at the time of planting or that soaking rains are expected soon thereafter.

Endnotes

[1] This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate state or federal agencies, or both, before they can be recommended. CAUTION: Pesticides can be injurious to humans, domestic and wild animals, and desirable plants if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

[2] Regression equations were developed for each month from data collected from the same study sites (Harrington and Edwards 1999) to predict needlefall of an individual plot from its stand basal area. The difference between twice the predicted monthly value for a nonthinned stand of 20 m^2 ha^{-1} basal area and that predicted for a given plot equaled the amount to be applied that month as stand-produced plus supplemented needlefall. Predicted monthly needlefall supplements were revised at the beginning of each year using the most recent measurements of stand basal area per plot.

[3] *S. junceus* quadrats were selected for monitoring the effects of a planted species on soil surface temperature and soil water content because of the uniformity of the species' vegetative cover.

[4] Species from the 1999 cohort retained in 2000 and 2001 (Table 1) were selected based on the uniformity of their first-year survival and cover development.

[5] Almost all of the clipped plants, including longleaf pine seedlings, resprouted from the root system resulting in only a small effect on readings of cover taken in October.

[6] These species were selected for nitrogen analyses either to relate to corresponding measurements of surface temperature and soil water (*S. junceus*) or because of consistent cover responses to trenching (*A. villosa*).

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