Understory vegetation, resource availability, and litterfall responses to pine thinning and woody vegetation control in longleaf pine plantations

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Abstract: In six 8- to 11-year-old plantations of longleaf pine (*Pinus palustris* Mill.) near Aiken, S.C., responses of understory vegetation, light, and soil water availability and litterfall were studied in relation to pine thinning (May 1994), herbicidal treatment of nonpine woody vegetation (1995–1996), or the combined treatments (treatment responses described below are in absolute units). Treatment differences in fifth-year (1998) herbaceous species density were as follows: pine thinning > woody control = combined treatments > untreated (33, 30, 30, and 25 species per 40 m^2, respectively). Forb and grass covers were 13 and 8% greater, respectively, after pine thinning and 7 and 9% greater after woody control. Pine thinning stimulated a large increase in third-year gap fraction (0.26), short-term increases in soil water content (1%), and a reduction in pine litterfall by half (-120 g·m^{-2} per year). Woody control had no effect on gap fraction, decreased litterfall of nonpine woody vegetation (-32 g·m^{-2} per year), and stimulated season-long increases in soil water content (1–2%). The ranking of factors affecting herbaceous vegetation responses was as follows: light > soil water > herbicides > litterfall. Herbaceous species density and cover can be promoted in longleaf pine plantations by intensive thinning of pines and herbicidal control of non-pine woody vegetation.

Résumé : Dans six plantations de pin des marais (*Pinus palustris* Mill.) âgées de 8 à 11 ans et situées près de Aiken en Caroline du Sud, aux États-Unis, la réaction de la végétation de sous-bois, la disponibilité de la lumière et de l'eau du sol, de même que la chute de litière ont été étudiées en fonction de l'éclaircie (mai 1994), de la répression des autres espèces ligneuses à l'aide d'herbicides (1995-1996) et des traitements combinés (les réactions aux traitements sont présentées en unités absolues). Les différences de densité des espèces herbacées attribuables aux traitements après 5 ans étaient : éclaircie des pins > répression des espèces ligneuses = traitements combinés > témoin (respectivement 33, 30, 30 et 25 espèces par 40 m^2). La couverture des graminées et celle des autres espèces herbacées étaient respectivement supérieures de 8 et 13% après l'éclaircie et de 9 et 7% après la répression des espèces ligneuses. L'éclaircie a stimulé une forte augmentation de la proportion de trouées à la troisième année (0,26), des augmentations à court terme du contenu en eau du sol (1%) et une réduction de moitié de la chute de litière de pin (-120 g·m^{-2} par année). La répression des espèces ligneuses n'a pas eu d'effet sur la proportion de trouées, a réduit la chute de litière des autres espèces ligneuses (-32 g·m^{-2} par année), et a provoqué des augmentations saisonnières du contenu en eau du sol (1–2%). La classification des facteurs influençant la réaction de la végétation herbacée était : lumière > eau du sol > herbicides > chute de litière. La densité et la couverture des espèces herbacées peuvent être augmentées dans les plantations de pin des marais par une éclaircie intensive des pins et la répression des autres espèces ligneuses à l'aide d'herbicides.

[Traduit par la Rédaction]

Introduction

Extensive pine forests interspersed with open savannahs once occupied much of the Upper Coastal Plain of South Carolina (Oosting 1956). Longleaf pine (*Pinus palustris* Mill.) was probably the dominant canopy tree species because of its longevity (Platt et al. 1988) and ability to tolerate fire (Boyer 1990a). Today, only about 3% of the original longleaf pine forest remains because centuries of commercial exploitation for naval stores (i.e., pitch, tar, and rosin for ship building), livestock production, agriculture, and timber were followed by decades of misdirected efforts at restoring pine regeneration through vigorous suppression of wildfires (Frost 1993).

Although remnant stands may still contain a component of mature longleaf pine, fire suppression has shifted their structure from a patchy distribution of widely spaced, open-grown pines to a closed-canopy, stratified forest of overstory pines, midstory hardwoods, and understory woody and herbaceous vegetation. Forest floor conditions in these stands, such as dense shade and deep accumulations of litter, may prevent establishment and maintenance of herbaceous species integral to native longleaf pine communities, such as wiregrass (*Aristida stricta* Michx.) (Clewell 1989). A critical trait affecting performance of understory herbs is their ability to penetrate upward through the litter layer (Sydes and Grime 1981). In experimental seedbeds, Shelton (1995)

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demonstrated that forbs were excluded more rapidly than grasses in response to increasing rates of pine or hardwood litter.

Stands of longleaf pine can be established successfully with conventional methods of site preparation and planting (Pait et al. 1991). As such forest plantations develop, their merging canopies of systematically spaced conifers and resprouting woody vegetation compete strongly for light and soil water and exclude much of the herbaceous layer (Oliver and Larson 1996). For example, herbaceous biomass has been shown to decline 73 $kg \cdot ha^{-1}$ for every 1 $m^2 \cdot ha^{-1}$ increase in basal area of longleaf pine plantations as they developed from age 9 to 18 years (Wolters 1973).

Considerable research has focused on restoring and maintaining native understory communities in longleaf pine forests (Duever 1989). However, if such restoration efforts are to be successful and cost effective, an improved understanding is needed regarding effects of competition and litterfall from pine and nonpine woody vegetation on understory vegetation. Previous research in longleaf pine plantations underbumed at 3- to 5-year intervals indicated that herbaceous biomass will increase in proportion to thinning intensity (Grelen and Enghardt 1973).

In the present study, it was hypothesized that herbaceous species density (i.e., number of species per area sampled, a measure of species richness; Magurran 1988) and abundance could be increased if the canopy structure of dense plantations of longleaf pine was manipulated to increase resource availability and reduce litterfall in the understory by reducing abundance of pine and nonpine woody vegetation. The objective of this research was to determine the relative importance of light and soil water availability and litterfall in limiting herbaceous species density and abundance in longleaf pine plantations. Combinations of pine thinning and herbicidal control of nonpine woody vegetation after prescribed fire were used to stimulate development of various stand structures including (*i*) a closed-canopy, stratified structure of overstory pines, midstory hardwoods, and understory shrubs, vines, and herbs (untreated stands); (*ii*) widely spaced pines with a vigorous midstory and understory (tbinned stands); (*iii*) a closed-canopy stand of overstory pines and understory herbs (woody control); and (*iv*) widely spaced pines with a vigorous understory of herbs (pine thinning + woody control).

Methods

Study sites and treatments

The study was conducted in the Sandhills physiographic region of South Carolina, U.S.A. (Miller and Robinson 1995). Six 8- to 11-year-old plantations of longleaf pine were located during winter 1993-1994 at the Savannah River Site (SRS), a National Environmental Research Park near Aiken (Table 1). Study sites were selected to have fully stocked stands of longleaf pine (21200 stems/ha) and hardwoods (2600 stems/ha). Total area per site ranged from 17.4 to 20.6 ha. Each plantation had been established by machine planting 1-year-old, bare-root seedlings at a 1.8 x 3 m spacing within clearcut harvested areas in which woody debris had been windrowed or piled, and then bumed. Prior to harvest, the sites supported mature stands of old-field longleaf and loblolly (*Pinus taeda* L.) pines. Following site preparation and planting, volunteer trees ≥2.5 cm DBH (diameter at breast height, 1.37 m

Table 1. Characteristics of the study sites.

				Pine average size and stand density				Hardwood average size and stand density			
Site[a]	Soil series[b]	Method of site preparation	Planting year	DBH (cm)	Height[c] (m)	Stems/ha	Basal area ($m^2 \cdot ha^{-1}$)	DBH (cm)	Height (m)	Stems/ha	Basal area ($m^2 \cdot ha^{-1}$)
23-40	Blanton, Lakeland, and Troup	Windrow and burn	1983	8.9	7.1	1709	11.2	4.6	4.4	1326	2.1
28-26	Blanton, Lakeland, and Troup	Windrow and burn	1985	8.2	6.4	1351	7.9	3.7	4.2	688	0.8
56-02N	Lakeland	Pile and burn	1986	7.9	5.4	1341	6.8	2.8	3.4	617	0.4
56-02S	Lakeland	Pile and burn	1986	7.3	5.2	1297	5.5	3.4	3.7	953	0.9
79-05/07	Blanton and Troup	Windrow and burn	1984	9.6	7.7	1717	12.6	4.6	5.5	768	1.5
36-10	Blanton	Pile and burn	1984	10.4	7.8	1343	11.6	4.3	5.0	710	1.0

[a] Timber compartment and stand numbers are from the Savannah River Natural Resource Management and Research Institute.

[b] Rogers (1990).

[c] Pine and hardwood height measurements were taken in 1994; all other tree measurements were taken in 1993.

aboveground) originating from stump sprouts or seedlings were predominantly sand post oak (Quercus Ashe; mean 158 stems/ha), loblolly pine (115 stems/ha), water oak ***(Quercus nigra*** L.; 84 stems/ha), hickory (*Carya* spp.; 82 stems/ha), turkey oak ***(Quercus** laevis* Walter; 67 stems/ha), or bluejack oak ***(Quercus** incana* Bartram; 63 stems/ha). The long-term (1964-1985) average value for growing-season (March-September) rainfall at the SRS is 781 mm (Rogers 1990). The study sites represent a range of soil moisture classifications from xeric to moderately mesic (Van Lear and Jones 1987). Soils include loamy sands of the Blanton (Grossarenic Paleudults), Lakeland (thermic, coated Typic Quartzipsamments), or Troup series (loamy, siliceous, thermic Grossarenic Paleudults), which are well drained to excessively well drained, resulting in low to very low available water capacities (Rogers 1990). Field capacity and permanent wilting points of the surface soils occur at approximately 12 and 6% volumetric water contents, respectively, for soils of comparable texture (Baver et al. 1972).

A prescribed fire of moderate to high intensity was applied to each site in February 1994, topkilling all shrubs and most hardwoods 15 cm DBH. A second prescribed fire of similar intensity was applied to each site in February 1998. Each of the six sites were divided into four treatment plots of similar size (3-7 ha), and one of the following treatments was randomly assigned to each.

(i) Untreated: No other treatments were applied except the prescribed burns.

(ii) Pine thinning: In May 1994, longleaf pines were thinned to leave a uniform spacing of trees at approximately half of the original stem density, resulting in 635 and 1440 pines/ha for thinned and unthinned plots, respectively. Trees were cut with brushsaws and left on the ground to decay, resulting in minimal disturbance to the litter layer and soil.

(iii) Woody control: The objective of this treatment was to virtually eliminate all nonpine woody vegetation (vines, shrubs, and all sizes of hardwoods) with herbicides. Therefore, to promote herbicide uptake and activity, application was delayed until 1995 to allow woody vegetation to recover from the prescribed fire. In April 1995, undiluted Velpar® L (hexazinone, a soil-active herbicide) was applied at a rate of 1.7 kg active ingredient/ha with a spotgun to gridpoints on an approximate 1-m spacing. In March 1996, surviving stems of oak, hickory, black cherry (***Prunus** serotina* Ehrh.), sparkleberry ***(Vaccinium arboreum*** Marshall), and other woody species received a basal spray of Garlon® 4 (triclopyr ester, a non-soil-active herbicide) at 7% concentration in oil. In late June 1996, surviving target vegetation within 8 m of each sample point (described below) received a directed foliar spray of Arsenal®' AC (imazapyr, a soil-active herbicide), Accord® (glyphosate, a non-soil-active herbicide), and X-77® surfactant mixed in water at 0.5, 5, and 0.5% concentrations, respectively. All herbicides were applied with backpack sprayers, and vegetation deadened by the treatments was left standing.

(iv) Combined treatments: Pine thinning was combined with woody control.

The experimental design is a randomized complete block with six replications (sites) of the four treatments arranged as a 2 × 2 factorial. Within each of the 24 treatment plots, 10 sample points spaced on a 40-m grid were permanently marked for repeat measurements.

Measurements

In winter 1993-1994, pretreatment basal areas ($\mathrm{m^2 \cdot ha^{-1}}$) of pines and hardwoods were quantified at about half of the sample points with measurements of DBH (cm) of each tree 22.5 cm rooted within 3.59 m of a given sample point. In winter 1994-1995, DBH was measured on each tree rooted within 6 m of a given sample point, and 20% of the stems were selected randomly for measurement of their heights (m). Pretreatment basal areas averaged 9.3 $\mathrm{m^2 \cdot ha^{-1}}$ and 1.1 $\mathrm{m^2 \cdot ha^{-1}}$ for pines and hardwoods, respectively. At the end of the first year (1994), pine basal area in thinned stands (4.7 $\mathrm{m^2 \cdot ha^{-1}}$) was 45% of unthinned stands (10.5 $\mathrm{m^2 \cdot ha^{-1}}$).

Each understory species (forbs, grasses, vines, shrubs, and tree seedlings of DBH <2.5 cm) rooted within 3.59 m of a given sample point was recorded in August 1994-1996. Species nomenclature follows Radford et al. (1968). The combined forb and grass data were used to calculate herbaceous species density (number of species per 40 $\mathrm{m^2}$). Also in August 1994-1996, ground coverage of each understory species and of woody debris was estimated at each sample point with the line-intercept method (Mueller-Dombois and Ellenberg 1974). A 3.59-m transect starting at each sample point was permanently located along a randomly selected azimuth, and the length of each intersection (cm) of a species' crown or of individual woody debris was recorded, including vegetation with overlapping canopies. Cover (%) of a given species or of woody debris was calculated as the total length of its intersections divided by transect length × 100. The understory plant cover data were grouped into categories of forbs, grasses, vines, shrubs, or tree seedlings according to the descriptions of Radford et al. (1968).

In October 1998, sampling protocols developed for the North Carolina Vegetation Survey (Peet et al. 1996) were adopted to provide more comprehensive estimates of herbaceous species density and understory cover. At each of the odd-numbered sample points (120 total), nested square subplots of area 0.01, 0.1, 1, 10, and 100 $\mathrm{m^2}$ were located with their diagonal overlaid onto the original vegetation transect, and a list of understory species rooted within each subplot was compiled. Species' cover (%) was assessed visually within the 10-$\mathrm{m^2}$ subplot using the following cover classes and values were assigned as class midpoints: trace (class midpoint 0.1%), 0-1, 1–2, 2–5, 5-10, 10–25, 25–50, 50-75, 75-95, and 95–100%. Woody debris cover was not measured in 1998.

Canopy gap fraction (proportion of open sky) was measured in August 1994-1996 at each sample point with paired LAI-2000® plant canopy analyzers (LI-COR, Inc., Lincoln, Neb.), one located above a given sample point and one located within a nearby large opening (unobstructed sky at 15° or greater angle above the horizon). To standardize light conditions, all readings were taken at 1.37 m aboveground facing south during dawn, dusk, or overcast sky conditions. Readings of the paired sensors were merged by the nearest time interval and gap fraction was calculated with LI-COR software.

At half of the sample points within each treatment plot, volumetric soil water content (%) was measured within 0- to 15- and 0- to 45-cm depths at 3-week intervals from March to September 1995-1996 with a Trase® time-domain reflectometry sensor (SoilMoisture Equipment Corp., Santa Barbara, Calif.). Soil water content at 15–45 cm depth was derived by subtracting values of the two readings weighted by depth. Daily rainfall data for 1994-1998 were obtained from the Williston Barricade monitoring station located on the eastern boundary of the SRS, less than 30 km from each of the study sites.

At each sample point, litterfall ($\mathrm{g \cdot m^{-2}}$; foliage only) was collected monthly for 2 years (March 1995 to February 1997) from a randomly located 0.48-$\mathrm{m^2}$ circular trap constructed of PVC tubing and fiberglass window screen. After drying at 70°C to a constant weight, each sample was separated into either pine needles or leaves of nonpine woody vegetation and weighed (g). Cumulative annual values of litterfall ($\mathrm{g \cdot m^{-2}}$ per year) of pine and of nonpine woody vegetation were calculated for each sample point.

Statistical analysis

All statistical analyses were conducted with SAS (SAS Institute Inc.1989). Treatment plot means for understory vegetation, gap

Table 2. Mean values of herbaceous species density and understory cover in longleaf pine plantations that were untreated versus those in which pines were thinned in May 1994, nonpine woody vegetation was controlled in 1995-1996, or the combined treatments were applied.

Variable	Year[a]	Untreated	Pine thinning	Woody control	Combination	Main effects”
Species density	1994	22.8	22.6	23.0	22.3	
(No. of species/40 m^2)	1995	20.5	25.4	20.5	20.1	
	1996	22.1	27.6	17.6	22.3	P(+),W(–)
	1998	24.9*c*	32.8*a*	29.5*b*	30.0*b*	I
Forb cover (%)	1994	12.5	13.2	18.1	14.9	
	1995	10.0*a*	16.2*a*	13.2*a*	7.5*a*	1
	1996	8.4	15.7	5.3	10.0	P(+),W(–)
	1998	8.5	19.5	14.1	28.4	P(+),W(+)
Grass cover (%)	1994	12.1	13.1	13.3	14.2	
	1995	10.8	15.5	12.9	7.1	
	1996	9.7	17.5	8.4	14.6	P(+)
	1998	7.1	16.0	16.2	24.1	P(+),W(+)
Vine cover (%)	1994	5.1	6.3	4.0	5.1	
	1995	3.3*b*	6.7*a*	2.4*b*	1.8*b*	1
	1996	5.5*a*	8.8*a*	1.0*b*	0.6*b*	1
	1998	4.3	8.2	1.8	2.8	W(–)
Shrub cover (%)	1994	7.9	10.6	10.9	11.2	
	1995	9.4*ab*	15.0*a*	9.7*ab*	4.6*b*	1
	1996	9.3*ab*	17.9*a*	3.4*bc*	2.1*c*	1
	1998	5.6	10.8	2.4	2.6	W(–)
Tree cover (%)	1994	5.5	3.3	7.6	2.6	P(–)
	1995	8.7	4.8	5.3	1.2	P(–),W(–)
	1996	11.7	7.8	1.2	0.1	W(–)
	1998	10.1	5.9	2.2	0.9	W(–)
Debris cover[c] (%)	1994	0.8	6.0	0.8	2.8	P(+)
	1995	1.1	5.1	1.1	2.6	P(+)
	1996	0.2	3.0	0.2	1.5	P(+)

“1994-1996 and 1998 measurements were taken in August and October, respectively.

[b] Letters indicate significant ($p \leq 0.05$) main effects of pine thinning (P), woody control (W), or their interaction (I); signs in parentheses indicate direction of response. For a significant interaction, means followed by the same letter do not differ significantly.

“Woody debris cover was not measured in 1998.

fraction, and litterfall variables were calculated for each year and subjected to analysis of variance (ANOVA) of a randomized complete block design with a factorial arrangement of treatments for testing the main effects of pine thinning, woody control, or their interaction. Woody control main effects were included in the ANOVA for 1994 data to test for potential pretreatment differences. Treatment plot means for binomially distributed variables (i.e., understory cover and frequency, gap fraction, and soil water content) were normalized with an arcsine, square-root transformation prior to ANOVA (Snedccor and Cochran 1980).

The soil water data were separated by depth (O-15 or 15–45 cm), and for each, treatment plot means were calculated per measurement date and subjected to ANOVA. For each depth of soil water measurement, the maximum value observed in the combined 1995 and 1996 data was identified per sample point. Treatment plot means of the maximum values were calculated for each depth and used as a covariate in ANOVA to adjust soil water responses for microsite differences in field capacity.

Residuals from each ANOVA were plotted against predicted values to confirm they had a normal distribution. When the treatment interaction F test in a given ANOVA was significant ($p \leq 0.05$), the data were reanalyzed with a nonfactorial design (i.e., four treatments), and multiple comparisons among treatment means were conducted with Tukey's test (Snedecor and Cochran 1980). In the absence of a significant treatment interaction, main effects of pine thinning or woody control are reported in the original units of each variable, not as percentage change.

Treatment effects on the 1998 relationship of number of herbaceous species to area sampled were tested using the extra sums-of-squares approach in linear regression (Neter et al. 1989). The relationship was linearized by transforming the dependent and independent variables to natural logarithms. Indicator variables were specified for the effects of blocking, pine thinning, woody control, and the interaction of main effects. The full regression model included interccpt and slope variables for each of the four treatments, and F tests were applied to compare the full model to those with a common intercept, a common slope, or both. Block effects were retained in the final model to enable predictions of 1998 herbaceous species density for each site and treatment, given the sample area used in 1994-1996 (40 m^2). The predicted values were subjected to ANOVA to test the main effects of pine thinning, woody control, or their interaction. Understory cover data from 1998 were subjected to ANOVA using the same approach as described for the 1994-1996 data.

Results

Understory vegetation

A total of 326 species of understory vegetation were detected from 1994–1998, including 197 forbs, 59 grasses, 22

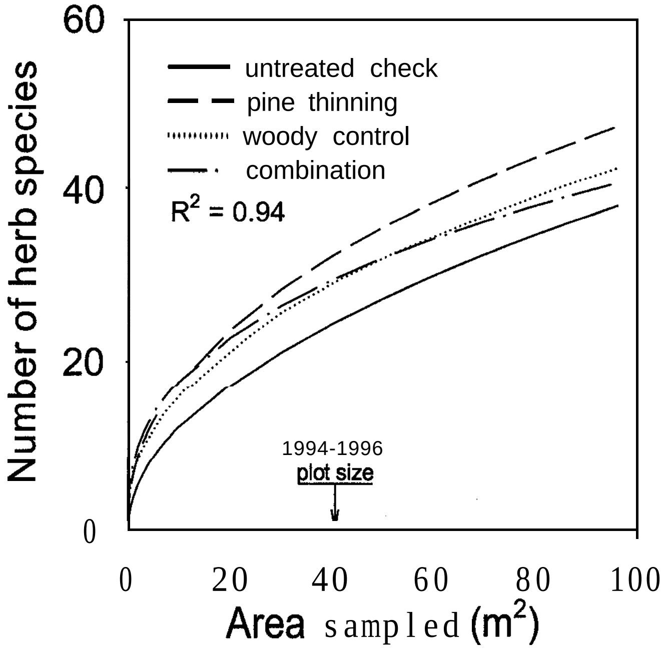

Fig. 1. Regression relationships of number of herbaceous species to area sampled developed from October 1998 measurements in longleaf pine plantations that were untreated versus those in which pines were thinned in May 1994, nonpine woody vegetation was controlled in 1995-1996, or the combined treatments were applied.

vines, 24 shrubs, and 24 trees. In 1998, 27% of the species detected in that year were found on each of the six sites, accounting for 73% of the overall average cover.

Although vegetation data were not collected prior to study initiation, the 1994 data provide information that predates the woody control treatment. Absence of significant treatment effects in 1994 for herbaceous species density and for cover of forbs, grasses, vines, or shrubs ($p \geq 0.141$) indicates that treatment effects observed in subsequent years probably are not attributable to differences that existed prior to treatment.

Herbaceous species density varied little among treatments in 1994 and 1995 ($p \geq 0.111$), averaging 22 species per 40 m^2 (Table 2). In 1996, herbaceous species density was five species greater in response to thinning main effects ($p = 0.004$), while it was five species less in response to woody control main effects ($p = 0.006$). In 1998, a significant interaction was detected for herbaceous species density ($p < 0.001$), and multiple comparisons of treatment means resulted in the following ranking: pine thinning (33 species) > combined treatments (30 species) = woody control (30 species) > untreated (25 species).

In the year of the hexazinone treatment (1995), a significant interaction was detected for forb cover ($p \leq 0.038$); however, multiple comparisons of means failed to distinguish among the treatments (Table 2). Grass cover did not vary significantly among treatments in 1995, although treatment means were of similar value and ranking as those of forbs. In 1996, forb and grass covers were 6-7% greater in response to thinning main effects ($p \leq 0.009$), while forb cover was 4% less in response to woody control main effects ($p = 0.041$). Two years later (1998), positive responses in forb and grass covers were observed for each of the main effects of pine thinning ($p \leq 0.001$) and woody control ($p \leq 0.025$), yielding increases in their covers of 7-13%.

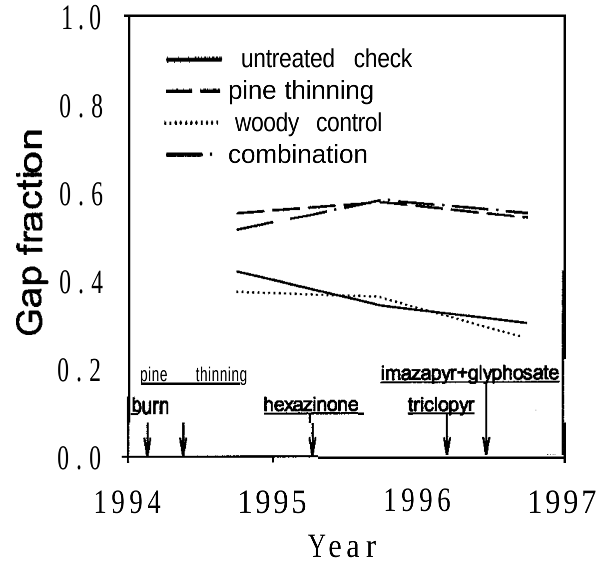

Fig. 2. Mean values of gap fraction (proportion of open sky) for longleaf pine plantations that were untreated versus those in which pines were thinned in May 1994, nonpine woody vegetation was controlled in 1995-1996, or the combined treatments were applied. Main effects of pine thinning were significant ($p \leq 0.002$) in each year.

A significant interaction was detected for vine and shrub covers in 1995 and 1996 ($p \leq 0.031$) (Table 2). Multiple comparisons of treatment means revealed that vine and shrub covers in the pine thinning treatment exceeded those in the combined treatments by 5–16%. In 1998, covers of vines and shrubs were 4–6% less in response to woody control main effects ($p \leq 0.006$). Shrub cover decreased strongly from 1996 to 1998 in most of the treatments, probably as a result of the prescribed fire of February 1998.

Almost all of the tree seedlings detected in the cover measurements were hardwood species; very few pine seedlings were found. Cover of tree seedlings in 1994 and 1995 was 4% less in response to thinning main effects ($p \leq 0.019$), while in 1995 and 1996 it was 3 and 9% less, respectively, in response to woody control main effects ($p \leq 0.035$) (Table 2). The negative effects of pine thinning on cover of tree seedlings perhaps resulted from smothering of this vegetation by woody debris, while the negative effects of woody control can be attributed directly to herbicide phytotoxicity.

In 1994, 1995, and 1996, cover of woody debris was 4, 3, and 2% greater, respectively, in response to pine thinning main effects ($p \leq 0.001$). From 1994 to 1996, mean cover of woody debris in thinned plots declined from 4 to 2%.

The 1998 relationship of number of herbaceous species to area sampled varied significantly among treatments (Fig. 1). The relationship was plotted after averaging the individual site regression intercepts. The slope parameter for the combination treatment did not differ significantly from that of the untreated check ($p = 0.111$), and therefore, it was dropped from the final model. The final model ($R^2 = 0.94$;

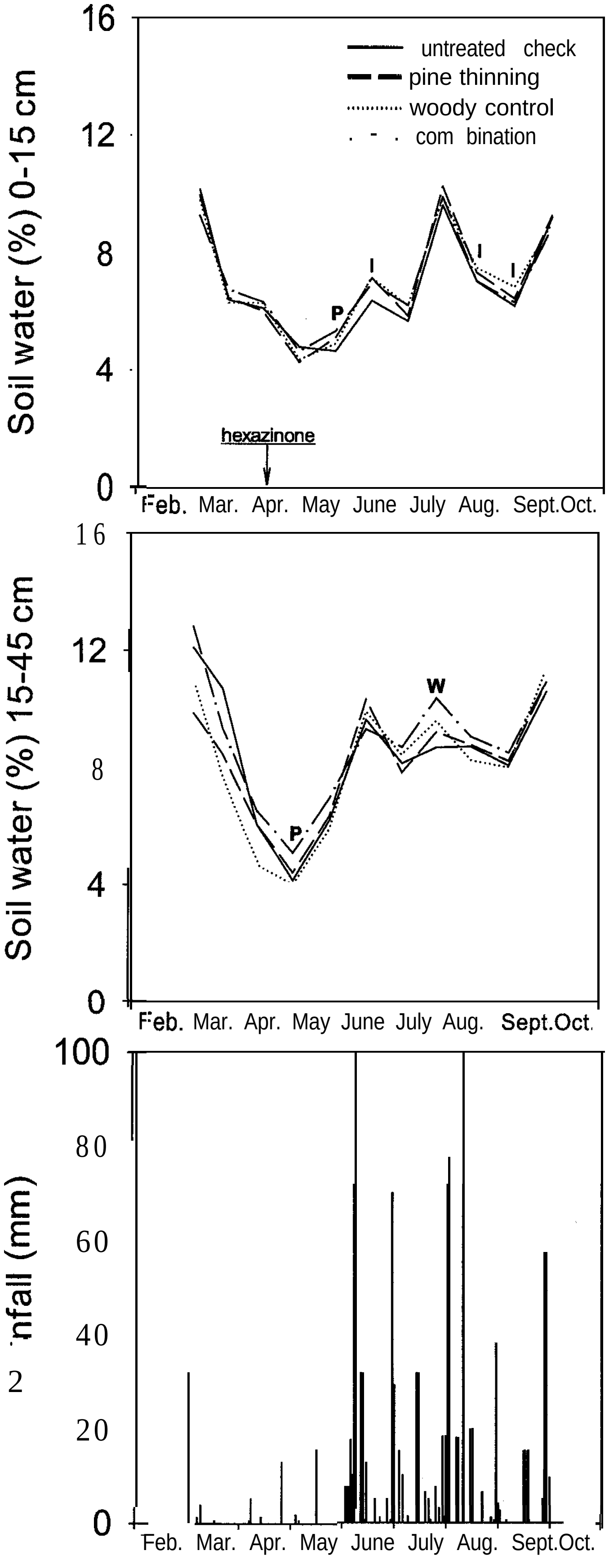

Fig. 3. Mean values of soil water content and daily rainfall during the 1995 growing season for longleaf pine plantations that were untreated versus those in which pines were thinned in May 1994, nonpine woody vegetation was controlled in 19951996, or the combined treatments were applied. Letters indicate when main effects of pine thinning (P) or woody control (W) resulted in significant ($p \leq 0.05$) increases in soil water content or when the interaction (1) was significant.

$s_{y\cdot x}$ = 0.355) contained separate regression intercepts for each treatment, plus regression slopes for the untreated check, pine thinning treatment, and woody control treatment. At the point of greatest departure among treatments (i.e., area sampled 100 m^2), the regression relationship predicts that herbaceous species density in the pine thinning, woody control, and combination treatments exceeds that of the untreated check by 9, 4, and 3 species per 100 m^2, respectively.

Light and soil water availability

In 1994, 1995, and 1996, gap fraction was 0.14, 0.22, and 0.26 greater ($p \leq 0.001$), respectively, in response to pine thinning main effects; however, it did not vary significantly in response to woody control main effects ($p \geq 0.268$) (Fig. 2). From 1994 to 1996, gap fraction of unthinned stands declined from 0.39 to 0.29 as crown closure of the pine plantations intensified.

Growing season (March to September) rainfall was above average for the duration of the study, with values of 846, 977,794, 819, and 811 mm for 1994, 1995, 1996, 1997, and 1998, respectively. Nevertheless, assuming that the permanent wilting point of soils on the study sites occurs near 6% water content (see soils information in Methods), soil water measurements indicate that several significant spring and summer droughts occurred during 1995 and 1996. Following the April 1995 hexazinone treatment, very little rain fell until June (Fig. 3). Because this herbicide is activated by rainfall, the limited number of spring showers may have reduced the efficacy of the treatment.

A significant treatment interaction was detected for measurements of soil water content at 0-15 cm depth during June, August, and September 1995 ($p \leq 0.044$) (Fig. 3). Multiple comparisons of treatment means for these dates indicated that soil water content was up to 1% greater in the woody control treatment than in the untreated check for June and September. Soil water content at 15-45 cm depth declined rapidly during the spring drought of 1995. During May 1995, at the height of the drought, soil water content at 15-45 cm depth was 1% greater in response to pine thinning main effects ($p = 0.022$). During a dry period in late July 1995, soil water content at 15-45 cm depth was 1% greater in response to woody control main effects ($p = 0.015$).

Throughout the 1996 growing season, soil water content at 0-15 cm depth did not vary significantly as a result of the experimental effects ($p \geq 0.22$), except for a marginally significant increase due to woody control main effects in July ($p = 0.086$) (Fig. 4). In early May 1996, soil water content at 15115 cm was 1% greater in response to pine thinning main effects ($p = 0.010$). From late May through September 1996, soil water content at 15-45 cm depth was 1–2% greater in response to woody control main effects ($p \leq 0.007$).

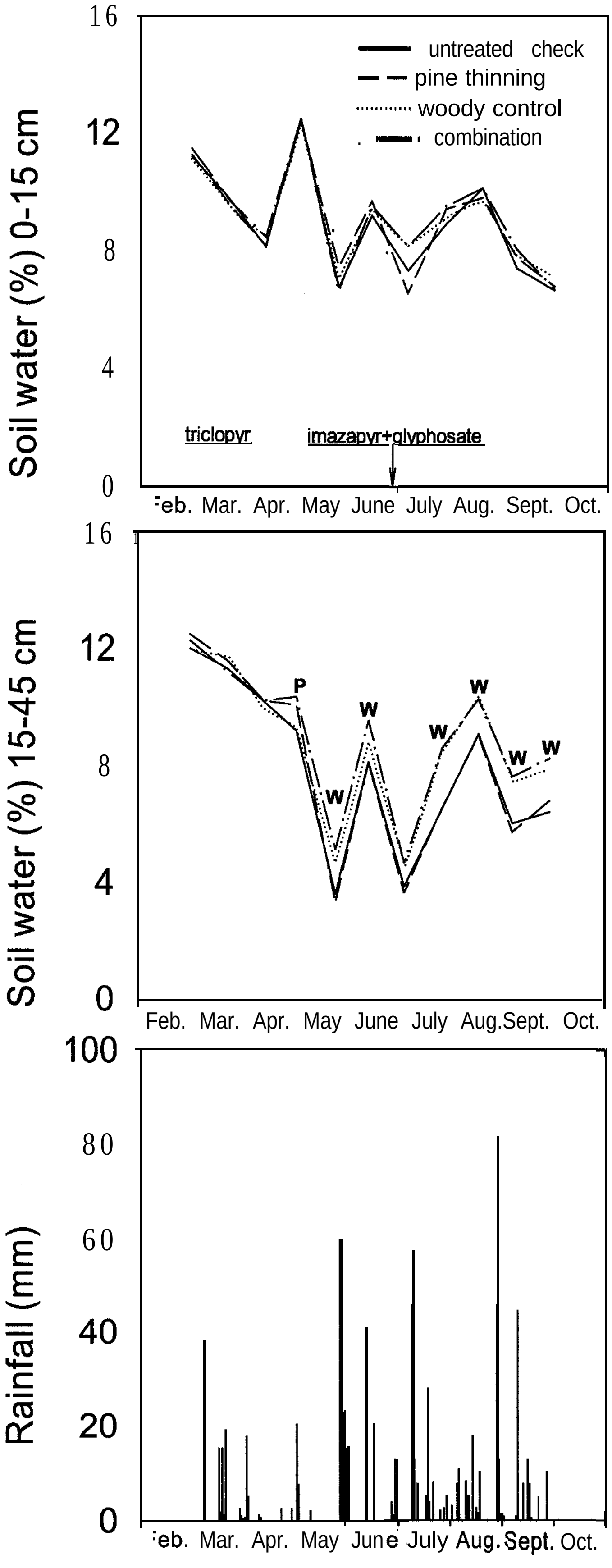

Fig. 4. Mean values of soil water content and daily rainfall during the 1996 growing season for longleaf pine plantations that were untreated versus those in which pines were thinned in May 1994, nonpine woody vegetation was controlled in 1995-1996, or the combined treatments were applied. Letters indicate when main effects of pine thinning (P) or woody control (W) resulted in significant ($p \leq 0.05$) increases in soil water content or when the interaction (1) was significant.

Litterfall

In the untreated check, annual litterfall of pines was six to seven times that of nonpine woody vegetation in 1995 and 1996 (Table 3). Pine litterfall was 100 and 120 $g \cdot m^{-2}$ less in response to pine thinning main effects in 1995 and 1996, respectively ($p < 0.001$), but it did not vary significantly as a result of woody control main effects ($p \geq 0.216$). In 1995, annual litterfall of nonpine woody vegetation did not vary significantly as a result of the experimental effects ($p \geq 0.356$); however, in 1996, it was 32 $g \cdot m^{-2}$ less in response to woody control main effects ($p = 0.018$). The responses of total litterfall to the main effects mirrored those found for pine and nonpine woody vegetation.

Discussion

Thinning of pines and control of nonpine woody vegetation stimulated substantial increases in herbaceous species density and abundance in plantations of longleaf pine. By the fifth year of the study (1998), herbaceous species density differed among treatments by up to 8 species per 40 m^2, while herbaceous cover increased 21 and 16% in response to main effects of pine thinning and woody control, respectively. Because the treatments caused a variety of simultaneous changes in growing conditions of the understory (i.e., changes in light and soil water availability, litterfall, and woody debris cover), it is difficult to identify the specific causes of the responses observed for herbaceous vegetation. However, by comparing the proportionate responses of understory vegetation, resource availability, and litterfall to the experimental effects, a relative ranking of importance among factors can be inferred.

The large and sustained increases in gap fraction that occurred as a result of pine thinning suggest that light availability was the dominant factor affecting herbaceous responses, given the magnitude of increases in species density and cover observed for this vegetation. Responses of herbaceous vegetation to woody control cannot be attributed to increases in light availability since gap fraction did not vary significantly as a result of this treatment. However, since gap fraction measurements were taken at 1.37 m aboveground, they may not fully quantify light availability at the forest floor.

Because gap fraction declined steadily in unthinned stands because of crown closure, while it remained essentially unchanged in thinned stands, differences in light availability attributable to thinning increased throughout the duration of the study. These results suggest that understory responses to thinning at a comparable intensity are likely to last well beyond the five years of this study. When viewed in terms of consequences to herbaceous vegetation, a potentially

Table 3. Mean annual foliar litterfall values of pine and nonpine woody vegetation for longleaf pine plantations that were untreated versus those in which pines were thinned in May 1994, nonpine woody vegetation was controlled in 1995-1996, or the combined treatments were applied.

Source of litterfall	Year	Untreated	Pine thinning	Woody control	Combination	Main effects[a]
Pines ($g \cdot m^{-2}$ per year)	1995	215	121	203	97	P(–)
	1996	242	133	243	112	P(–)
Nonpine woody vegetation ($g \cdot m^{-2}$ per year)	1995	30	45	42	47	
	1996	43	48	17	9	W(–)
Total ($g \cdot m^{-2}$ per year)	1995	245	166	245	144	P(–)
	1996	285	181	260	121	P(–),W(–)

[a] Letters indicate significant ($p \leq 0.05$) experimental effects of pine thinning (P) and woody control (W); signs in parentheses indicate direction of response.

negative effect of thinning was to stimulate large increases in abundance of vines and shrubs, which almost doubled their cover prior to the 1998 prescribed fire. Such vegetation ultimately will reduce light availability to the forest floor and ultimately exclude herbaceous vegetation.

Because the woody control treatment did not affect gap fraction, but it did result in significant increases in herbaceous species density and cover by 1998, inferences can be made that competition for soil water, and perhaps nutrients, from nonpine woody vegetation was an important factor limiting responses of herbaceous vegetation. Since the magnitude of herbaceous responses resulting from pine thinning was greater than that from woody control, and the primary effect of each of pine thinning and woody control was to increase light and soil water availability, respectively, soil water is ranked second in importance among factors limiting the herbaceous community in longleaf pine plantations. Note that the 1998 prescribed fire probably stimulated some of the herbaceous responses to woody control by liberating nutrients from living and dead vegetation for uptake by surviving plants.

Increases in soil water availability from pine thinning (May 1995–1996), woody control (summer 1996), or their interaction (summer 1995) may have stimulated some increases in herbaceous species density and abundance. Given the coarse texture of surface soils on the study sites, the observed changes in soil water content from woody control indicate that this treatment reduced the severity and duration of water stress for understory vegetation. However, since the strongest and most prolonged increases in soil water were associated with the herbicide applications of the woody control treatment, only those plant species able to avoid (from lack of exposure) or tolerate the phytotoxic effects of this treatment could have benefitted from improvements in soil water availability that occurred in 1995 and 1996.

It appears that the observed increases in soil water content from pine thinning resulted from the reduced crown interception of rainfall by thinned stands, which allowed more water to reach the soil, because each of the May 1995 and 1996 soil water measurements were immediately preceded by significant rainfall. However, differences in soil water between thinned and unthinned plots were no longer apparent by June, indicating that the additional water had been consumed by evaporation and transpiration.

Herbicide phytotoxicity was ranked as third in importance among factors affecting the herbaceous vegetation because of significant, although temporary, reductions in species density and forb abundance in 1996. Competition from other vegetation does not account for these herbaceous vegetation responses since the herbicide applications reduced the abundance of grasses (although not significantly) and nonpine woody vegetation, increased soil water availability, and had no detectable effect on light availability.

To virtually eliminate all nonpine woody vegetation, several herbicide treatments were required, including the application of two chemicals that are soil active (hexazinone and imazapyr). Efficacy of the hexazinone treatment may have been limited by the dry spring conditions in 1995. Cumulative effects of the three herbicide treatments resulted in only 6% cover of nonpine woody vegetation by 1998, at which time the herbaceous community occupied 16% more cover in the presence versus absence of woody control.

In a 1-year-old clearcut in the Florida sandhills, Wilkins et al. (1993) observed 62 and 70% decreases in herbaceous species richness and cover, respectively, 1 year following application of hexazinone at 1.7 kg active ingredient/ha, applied as Velpar® ULW (i.e., a granular product). However, treatment effects were no longer significant in the second year because of recovery of the herbaceous community. Others have reported similar recovery of the herbaceous community following single applications of herbicides in recently clearcut areas (Blake et al. 1987; Zutter et al. 1987; Boyd et al. 1995). Although the hexazinone rate used in our study was identical to that of Wilkins et al. (1993), significant treatment effects in the year of hexazinone application (1995) were observed only for forb cover and not herbaceous species density. Apparently the cumulative effects of 2 years of herbicide treatments, combined with variation in herbicide mode of activity, caused the reductions in herbaceous species density observed in 1996.

For each of forbs, grasses, vines, shrubs, and tree seedlings, there was evidence of an interaction between pine thinning and woody control. Reductions in abundance of this vegetation from woody control were greater in thinned versus unthinned plots perhaps because increases in resource availability from thinning stimulated the physiological activity of understory vegetation, resulting in greater uptake, translocation, and subsequent phytotoxicity of the herbicides.

Litterfall was ranked fourth among factors affecting herbaceous species density and abundance. The certainty of this conclusion is limited by the ability to make inferences regarding the relative effects of decreased litterfall versus increased availability of light (and soil water, to a limited extent) because of confounding that exists among these factors. The absolute reduction in 1996 total litterfall from the main effects of pine thinning (120 $g \cdot m^{-2}$) was almost four times that from the main effects of woody control (32 $g \cdot m^{-2}$). However, equations by Shelton (1995) predict increases of only 25 and 12% in the biomass of forb and grass seedlings, respectively, that germinated and grew through forest floors of weight varying from 285 to 121 $g \cdot m^{-2}$, the range of litterfall treatment means observed in the present study.

In a comparison of herbaceous species responses to variable amounts and types of hardwood leaf litter, surface area and persistence of the litter were the primary characteristics limiting biomass development of test plants (Sydes and Grime 1981). Therefore, given the persistence of longleaf pine litter, its accumulation in the understory in the absence of prescribed burning is likely to cause some limitations in the abundance of herbaceous vegetation. Like litterfall, woody debris and pine needles from the thinning treatment may have diminished the responses of the herbaceous community to the main effects of pine thinning and woody control. Apparently this negative effect of thinning debris was short term, because in the first 3 years of the study its cover had declined by half.

Silvicultural implications

Thinning of dense plantations of longleaf pine at an intensity comparable with this study will provide increases in light availability and decreases in litterfall sufficient to promote herbaceous species density and abundance for 5 years or more. However, in the absence of further manipulations of stand structure, encroaching nonpine woody vegetation will compete for the above- and below-ground resources necessary for sustaining a diverse and productive herbaceous community. Prescribed fire, by itself, would take years to eliminate nonpine woody vegetation in dense, stratified stands such as those in the present study. Over an 18-year period, Boyer (1993) found that hardwood basal area increased from 0.8 to 2.2 $m^2 \cdot ha^{-1}$ following winter biennial burns, while it decreased from 0.9 to 0.3 $m^2 \cdot ha^{-1}$ following spring biennial burns. Summer burns, although effective at controlling small hardwoods (Glitzenstein et al. 1995), are not advisable because of unacceptably high rates of mortality for longleaf pines of all size classes (Boyer 1990*b*). In addition, low-intensity fires are not effective at controlling hardwoods greater than 5 cm in DBH (USDA Forest Service 1989). Thus, by accelerating the removal of nonpine woody vegetation and by making such stands easier and safer to burn with subsequent applications of prescribed fire, herbicides provide an effective tool for rehabilitating the stand structure of longleaf pine plantations, particularly when average hardwood DBH exceeds 5 cm.

To avoid the temporary reductions in herbaceous species density and abundance like those observed in this study, herbicide exposure to this vegetation must be minimized. One approach is to use a backpack sprayer to apply herbicides as foliar or basal-stem sprays directed specifically at nonpine woody vegetation. Soil-active herbicides applied in this manner should be used sparingly and with considerable care. Alternatively, herbicides can be injected into individual woody stems to prevent exposure to herbaceous vegetation.

For a number of reasons, it may be best to apply herbicides first, prescribed fire second, and thinning last when rehabilitating the structure of longleaf pine plantations. First, evidence from this research indicates that herbicide phytotoxicity to both herbaceous and woody vegetation was less when the treatment was applied in unthinned versus thinned stands. Second, the feasibility of locating and applying herbicides to target vegetation is greater in unthinned stands because of the absence of thinning debris. Third, uninjured plants will have greater herbicide uptake than those that have been trampled by vehicle or foot traffic during the thinning operation because their physiology has not been impaired. Fourth, treatments that combine herbicides and prescribed fire provide greater control of woody vegetation than those that rely on herbicides alone (Harrington et al. 1998). Finally, stands that have had a woody control treatment can be thinned with greater uniformity and care because crop trees are easier to identify in the absence of midstory hardwoods and understory shrubs and vines.

Once the structure of a longleaf pine stand has been rehabilitated with thinning and herbicide treatments, prescribed fire plus thinning should be applied on a regular basis to maintain the open stand conditions that support a vigorous herbaceous community. The repeated applications of herbicides in the present study were used to virtually eliminate all nonpine woody vegetation as an experimental factor. In an operational setting, such an intensive treatment regime probably is not necessary to stimulate increases in herbaceous species density and abundance. Also, an operational thinning would stimulate a different pattern of recruitment of herbaceous vegetation from that observed in this study, since it would remove much of the woody debris and disturb the litter and soil layers.

As an alternative approach for restoring longleaf pine communities, herbicides could be applied manually during site preparation, and then followed by a prescribed fire. This approach would increase recruitment of herbaceous species, as well as the survival and early growth of planted longleaf pine seedlings. When the new stand is safe to burn, applications of prescribed fire in the spring every 2 or 3 years could be used to maintain abundance of nonpine woody vegetation at a low level. Interplanting or artificial seeding of selected herbaceous species could be applied early in stand development to re-introduce or enrich populations of native species.

Several features of the understory communities present on the study sites indicate they are still recovering from disturbances associated with stand establishment (i.e., clearcutting and mechanical site preparation) and the treatments of this research. These include relatively low values of herbaceous species density and abundance and the presence of species typically found during old-field succession (e.g., ***Andropogon virginicus*** L., ***Eupatorium compositifolium*** Walter, ***Senecio vulgaris*** L., and ***Erigeron canadensis*** L.) (Oosting 1942). Although the communities differ strikingly in abundance and species composition from those reported for relatively undisturbed, natural stands of longleaf pine (Peet and Allard 1993), they share features of stand structure that, perhaps, can be exploited to accelerate community restoration efforts, including a two-layered canopy (overstory trees over understory herbs), an understory of high pyrogenicity (Platt et al. 1988), and an overstory of widely spaced, vigorous pines. Thus, conventional silvicultura1 treatments, such as thinning, herbicides, and prescribed fire have the potential to play a critical role in the restoration of longleaf pine ecosystems.

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