Overstory and understory relationships in longleaf pine plantations 14 years after thinning and woody control

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Abstract: To develop silvicultural strategies for restoring longleaf pine (*Pinus palustris* Mill.) savannas, mortality and growth of overstory pines and midstory hardwoods and abundance and species richness of herbs were studied for 14 years after pine thinning and nonpine woody control. Pine cover in thinned stands was about half of that in nonthinned stands through year 5, but it lagged by only 8% and 3% in years 9 and 14, respectively, because of vigorous crown responses. Despite a cumulative mortality of 64% of hardwood stems from prescribed fires in years 0, 4, and 9, hardwood basal area in thinned stands (2.1 $m^2 \cdot ha^{-1}$) was three times that in nonthinned stands (0.7 $m^2 \cdot ha^{-1}$) in year 14. Thinning was associated with 13%–22% more cover and six to eight more species of herbs in years 3–8 but only 6% more cover and two more species in year 14 because of accelerated growth of pine cover and hardwood basal area. However, similar increases in cover and richness of herb species in the woody control treatment were retained through year 14 because it had sustained reductions in hardwood and shrub abundance. Silvicultural strategies that substantially delay encroachment by pines, hardwoods, and shrubs will be those most effective at retaining herb species in longleaf pine savannas, including planting pines at wide spacing, periodic thinning and woody control, and frequent burning.

Résumé : Pour mettre au point des stratégies sylvicoles visant à restaurer les savanes de pin des marais (*Pinus palustris* Mill.), la mortalité et la croissance des pins de l'étage dominant et des feuillus de l'étage intermédiaire de même que l'abondance et la richesse en espèces des plantes herbacées ont été étudiées pendant les 14 années qui ont suivi une éclaircie du pin et la maîtrise de la végétation ligneuse autre que le pin. Le couvert de pin des peuplements éclaircis était environ la moitié de celui des peuplements non éclaircis après 5 ans, mais l'écart était seulement de 8 % après 9 ans et de 3 % après 14 ans à cause d'une réaction vigoureuse des cimes. Malgré une mortalité cumulative de 64 % des tiges feuillues à la suite de brûlages dirigés appliqués aux années 0, 4 et 9, la surface terrière en feuillus des peuplements éclaircis (2,1 $m^2 \cdot ha^{-1}$) était trois fois supérieure à celle des peuplements non éclaircis (0,7 $m^2 \cdot ha^{-1}$) après 14 ans. L'éclaircie était associée à des hausses de 13 % à 22 % du couvert herbacé et à six à huit espèces herbacées de plus pendant les années 3 à 8, mais ces valeurs sont passées à seulement 6 % du couvert herbacé et deux espèces de plus après 14 ans à cause d'une accélération de la croissance du couvert de pin et de la surface terrière en feuillus. Cependant, des augmentations similaires en couvert et richesse en espèces herbacées ont été observées dans le traitement de maîtrise de la végétation ligneuse à l'année 14 parce que ce traitement a réduit l'abondance des feuillus et des arbustes. Les stratégies sylvicoles qui retardent substantiellement l'établissement des pins, des feuillus et des arbustes seront les plus efficaces à retenir les espèces herbacées dans les savanes de pin des marais. De tels traitements incluent la plantation de pins à grand espacement, des éclaircies et des traitements périodiques de maîtrise de la végétation, et de fréquents brûlages dirigés.

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Introduction

Invasion of woody species and their subsequent interference with herbaceous species, commonly referred to as "woody encroachment", are primary factors leading to degradation of savanna ecosystems worldwide (Price and Morgan 2008). By definition, a savanna is an open, grassland community interspersed with trees or shrubs having nonoverlapping canopies (Scholes and Archer 1997). Because of this open-canopy structure, savannas are prone to invasion by woody plant species attributable to fire suppression, overgrazing, and soil disturbance (Asner et al. 2004; Mitchell et al. 2006). Treatments for reducing woody encroachment in savanna communities include applications of prescribed fire, thinning, and herbicides (Provencher et al. 2001; Freeman and Jose 2009).

During the past decade, restoration of longleaf pine (*Pinus palustris* Mill.) savannas has become a common management objective on public lands and retired agricultural lands in the southeastern United States. Forces stimulating this movement include government tree planting programs, wildlife habitat considerations, and efforts to restore native plant communities. For example, the 2006 Longleaf Pine Initiative of the Conservation Reserve Program provided cost-share assistance

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Table 1. Characteristics of the longleaf pine (*Pinus palustris*) study sites.

Site[a]	Soil series[b]	Site index (m)[c]	Site preparation	Planting year
23-40	Blanton, Lakeland, Troup	16.3	Inject hardwoods[d]; shear, windrow, and burn (1982)	1983
28-26	Blanton, Lakeland, Troup	14.9	Shear, windrow, and burn (1984)	1985
56-02N	Lakeland	12.8	Apply herbicide[e] and burn (1985)	1986
56-02S	Lakeland	12.2	Apply herbicide and burn (1985)	1986
79-05/07	Blanton, Troup	17.5	Inject hardwoods; shear, windrow, and burn (1983)	1984
36-10	Blanton	18.2	Inject hardwoods; shear, windrow, and burn (1984)	1985

[a]Timber compartment and stand numbers from the US Forest Service Savannah River.
[b]After Rogers (1990).
[c]Predicted site index for a base age of 25 years (Boyer 1980).
[d]Hardwoods were injected with Tordon 101R (picloram) herbicide.
[e]Pronone (hexazinone) herbicide was applied as a broadcast treatment at 1.5 kg active ingredient·ha^{-1}.

to support increases in longleaf pine forests of over 100 000 ha in the southeastern United States (USDA Farm Service Agency 2006). Additionally, the Conservation Reserve Program of the 2008 Farm Bill authorized additional support for planting of native plant species in longleaf pine forests (USDA Farm Service Agency 2008).

Savanna restoration involves establishing the overstory canopy structure as well as component understory species. Typical overstory densities of longleaf pine savannas are intermediate between closed-canopy forest and tropical savannas (McGuire et al. 2001). A previous land use history of traditional tillage farming, repeated forest harvesting, and fire exclusion in longleaf pine savannas has left many of these communities lacking in native species and over populated with nonnative species (Brudvig and Damschen 2011). Only 3% of the original extent of longleaf pine communities exists today (Frost 1993). In remnant old-growth stands of longleaf pine, infrequent burning has lead to development of dense layers of shrubs and hardwoods (Gilliam and Platt 1999). In second-growth forests, natural restoration processes are slowed by the combined effects of excessively high densities of overstory pines and infrequent burning (Platt et al. 2006).

Plantation forestry has been proposed as a suitable means for wide-scale restoration of longleaf pine savannas, particularly those that have not already been degraded of benchmark herb species by past land use practices (Hedman et al. 2000). In practice, these stands are often machine planted at high densities (>1000 seedlings·ha^{-1}) to ensure adequate stocking given expected losses in survival from competition and wildlife damage and to allow for future income from thinning, as typically done for loblolly pine (*Pinus taeda* L.) (Kilgo and Blake 2005). The resulting high density and uniformity of tree spacing in plantations greatly accelerates their site occupancy, possibly contributes to growth stagnation and an early onset of density-associated mortality (Oliver and Larson 1996), and creates severe competitive pressure for understory vegetation (Harrington and Edwards 1999). Combined effects of overstory shade, needle-fall, and shrub and hardwood competition for belowground resources can interact to limit abundance and richness of herb species (Harrington and Edwards 1999). In an overstory thinning and root-trenching study, Harrington et al. (2003) observed that negative effects of overstory shade and root competition on 2- to 3-year development of reintroduced herb species were of similar magnitude, whereas negative effects of needle-fall had lesser consequences. Dense stands of woody vegetation also can restrict production of fine fuels, resulting in reduced frequency and intensity of fire and further encroachment by shrubs and hardwoods (Mitchell et al. 2006).

Much of the efforts for longleaf pine savanna restoration have focused on reestablishing key understory species (Mulligan et al. 2002; Aschenbach et al. 2010). Less attention has been applied to management regimes for planted longleaf pine that maintain a vigorous herbaceous community by manipulating densities of overstory pines, midstory hardwoods, and understory shrubs (Kush et al. 1999). In this study, combinations of pine thinning and nonpine woody control were applied to 8- to 11-year-old longleaf pine plantations to quantify changes in abundance and richness of herb species and their relationships to stand development of pines and hardwoods. During the first 5 years of the study, forb and grass covers increased by 7%–13% and herb species richness increased by five to eight species per 40 m^2 sample area as a result of the treatments (Harrington and Edwards 1999). This report describes overstory and understory responses through year 14 and includes addressing the following research questions. Given periodic applications of prescribed fire, (*i*) how did pine thinning influence hardwood and shrub abundance, (*ii*) what was the magnitude and duration of reductions in hardwood and shrub abundance from the woody control, and (*iii*) how did these changes in stand dynamics indirectly influence abundance and richness of herb species?

Methods

Study sites and treatments

The study was conducted at the Savannah River Site, a National Environmental Research Park near Aiken, South Carolina. Study sites were selected to have fully stocked stands of longleaf pine (≥1200 stems·ha^{-1}) with midstory hardwoods (≥600 stems·ha^{-1}). Six 8- to 11-year-old plantations of longleaf pine were located during winter 1993–1994 (Table 1). Annual precipitation was monitored for the study duration at six Savannah River Site weather stations located near the study sites. Soils include loamy sands of the Blanton (Grossarenic Paleudults), Lakeland (thermic, coated Typic Quartzipsamments), and Troup (loamy, siliceous, thermic Grossarenic Paleudults) series with low to very low available water-holding capacities (Rogers 1990).

Each site was divided into four treatment plots, each 3–7 ha in area, and one of the following treatments was randomly assigned to each plot.

Nontreated. No other treatments were applied except prescribed burning (described below).

Pine thinning. In May 1994, longleaf pines were thinned to leave a uniform spacing of trees at approximately half of the original stem density. Every third row of trees was cut and additional trees were cut within the residual rows to achieve the target density. Trees were cut with brushsaws and left on the ground to decay, resulting in minimal disturbance to the litter layer and soil.

Woody control. The objective of this treatment was to virtually eliminate all nonpine woody vegetation (vines, shrubs, and 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 of early 1994 (described below). In April 1995, undiluted Velpar L (hexazinone, a soil-active herbicide) was applied at a rate of 1.7 kg active ingredient·ha^{-1} with a spotgun to gridpoints on an approximate 1 m spacing. In March 1996, surviving stems of oak (*Quercus* spp.), hickory (*Carya* spp.), black cherry (*Prunus serotina* Ehrh.), tree 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.

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 (i.e., presence versus absence of pine thinning and woody control). Within each of the 24 treatment plots, 10 sample points were permanently marked for sampling of trees and understory vegetation. The sample points were located at 40 m intervals along one to three transects spaced evenly throughout each plot to provide a systematic sample of overstory and understory conditions for each treatment plot. To reduce fuel accumulations and abundance of nonpine woody vegetation, dormant-season prescribed fires were applied to each site in early 1994, 1998, and 2003 corresponding to zero, four, and nine growing seasons after the thinning treatment. References to study year indicate the number of growing seasons after thinning.

Measurements

In winter 1993–1994, pretreatment densities of pines and hardwoods were quantified at about half of the sample points with measurements of diameter at breast height (DBH) (centimetres) of each tree ≥2.5 cm rooted within 3.6 m of a given sample point (i.e., a 0.004 ha subplot). In years 1, 2, 3, 5, and 9, each tree (≥2.5 cm DBH) rooted within 6 m of a sample point (i.e., a 0.011 ha subplot) was tagged and its species and DBH were recorded. No hardwood trees were tagged and measured in the woody control treatment because virtually all of these trees were eliminated by the treatment. Height (metres), crown height (height to base of continuous live crown, metres), and crown width (measurements along north–south and east–west directions, metres) also were measured on 20% of the trees in each subplot, which were randomly selected in year 1. Tree measurements in year 14 were identical to those in previous years except that ingrowth trees (≥ 2.5 cm DBH, not previously tagged) also were counted by species in each subplot.

In August of years 1, 2, and 3, understory cover by species was estimated at each sample point with the line-intercept method (Mueller-Dombois and Ellenberg 1974). A 3.6 m transect starting at each sample point was permanently located along a randomly selected azimuth, and the length of each intersection (centimetres) of a species' crown was recorded. Cover (percent) of a given species was calculated as the total length of its intersections divided by transect length and multiplied by 100. In August or September of years 5, 8, and 14, understory vegetation was sampled with protocols developed for the North Carolina Vegetation Survey (Peet et al.1996). At each of the odd-numbered sample points (120 total), nested square subplots of area 0.01, 0.1, 1, 10, and 100 m^2 sharing a common corner were located along the same randomly selected azimuth described previously, and a list of understory species occurring within each subplot was compiled. Cover (percent) by individual species was assessed visually within the 10 m^2 subplot. Species nomenclature follows the USDA Plants Database (USDA, NRCS 2011). Because the line-intercept method produces a positive bias in cover estimates for species of low foliage density (Mueller-Dombois and Ellenberg 1974), cover values estimated with this technique are likely to be somewhat higher than those estimated visually within fixed-area plots.

Statistical analysis

All statistical analyses were conducted with SAS (SAS Institute Inc. 2005) using a significance level of $\alpha = 0.05$. Tree growth data for each sample point were separated into pine and hardwood species groups. For each species group and measurement year, sample point means were calculated first and then treatment plot means were calculated from the sample point means. Tree response variables included DBH (expressed as quadratic mean diameter), height, crown height, crown length, and crown width (expressed as the geometric mean of the north–south and east–west dimensions). Stand response variables included tree mortality (expressed as a percentage of stems present in year 1), stand density index (SDI) (Reineke 1933), stem density (trees per hectare), basal area (square metres per hectare), volume (cubic metres per hectare), and crown cover (percent). SDI values for pine (in English units) were converted to a percentage of the species' maximum for longleaf pine developed by Kush et al. (2006): 971 trees·ha^{-1} having a quadratic mean diameter of 25.4 cm. Similarly, SDI values for hardwoods were converted to a percentage of the maximum value cited for upland hardwoods by Schnur (1937): 568 trees·ha^{-1} having a quadratic mean diameter of 25.4 cm. Basal area was calculated for each sample point as the total cross-sectional area of stems; the values were then averaged by treatment plot and divided by the total sample area. Crown cover was calculated for each sample point by multiplying mean crown area by stem density, dividing by 10 000 m^2·ha^{-1}, and multiplying by 100. If crown cover for a given sample point exceeded 100% because of overlap among adjacent trees, the value was set to 100%.

Crown cover per treatment plot was then calculated as the mean of sample point values.

Preliminary analyses of the data indicated that the relationship of height versus DBH for longleaf pine varied among sites and thinning levels. Therefore, to predict height of longleaf pine trees for which only DBH was measured, the following general equation (Curtis 1967) was fitted to pooled measurement-year data for each site and thinning level using nonlinear regression in Proc NLIN:

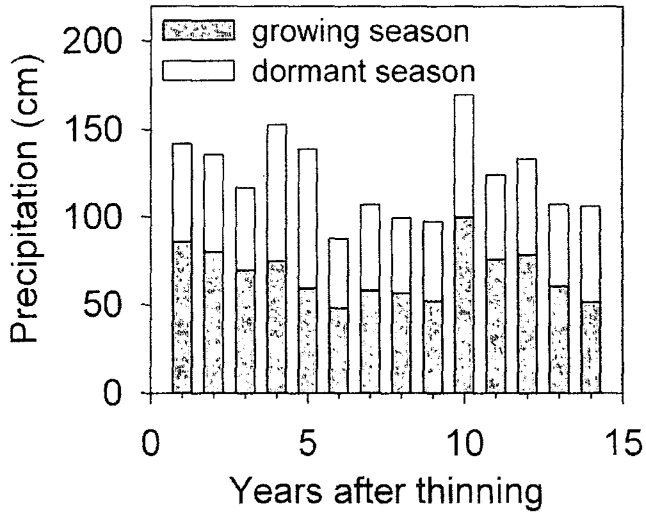
$$[1] \quad H = 1.37 + \exp[a_0 + a_1(D)^{a_2}]$$

where H is height (metres), D is DBH (centimetres), and a_0, a_1, and a_2 are regression coefficients to be estimated. The equation also was fitted for hardwoods and for loblolly pine by pooling the data for each species group across sites and fitting separate models for each thinning level. The variables DBH, height, and predicted height were applied to the equations of Clark and Saucier (1990) and Clark et al. (1986) to calculate stem volume per tree of pines and hardwoods, respectively. Total volume by species group was calculated for each sample point, and the values were then averaged by treatment plot and divided by the total sample area. Longleaf pine site index (base age 25 years) was predicted for each site by applying the methods of Boyer (1980) to the height and age data from nontreated plots.

Vegetation cover data were separated into herb and woody (vines, shrubs, and trees <2.5 cm DBH) species groups, and treatment plot means were calculated by measurement year for each. Vegetation frequency data were compiled by species, and treatment plot means were calculated for each measurement year. Treatment effects on the relationship of number of herb species versus area sampled (subplot area) 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 pine thinning and woody control. The full regression model included indicator variables for blocks and intercept and slope variables for each of the four treatments. F tests were applied to compare the full model with reduced models having a common intercept, a common slope, or both.

Treatment plot means for each of the tree, stand, and understory response variables were subjected to repeated-measures analysis of variance (ANOVA) in PROC Mixed to test for effects of pine thinning, woody control, years since treatment, and their interactions. Because woody control virtually eliminated all hardwoods present at study initiation, only the effects of pine thinning, years since treatment, and their interaction were tested in the ANOVAs for hardwood variables. Each model accounted for random effects of blocks and plots within blocks. The pretreatment (winter 1993–1994) variable having the greatest significance in each ANOVA ($P \leq 0.05$) was included as a covariate (i.e., DBH, stem density, or stand basal area). An angular transformation was applied to variables having a binomial distribution (i.e., cover, mortality, SDI, and species' frequency) and a logarithmic transformation was applied to the remaining tree and stand variables to homogenize their residual variances (Sokal and Rohlf 1981). Residuals for each response variable were

Fig. 1. Average growing season (May–October) and dormant season (November–April) precipitation during 14 years after thinning and woody control in longleaf pine (*Pinus palustris*) plantations (1994–2007). Means are based on data from six weather stations located near the study sites.



plotted against predicted values to check for nonhomogeneous variance. If a significant treatment-by-year interaction was detected, multiple comparisons were performed with Bonferroni-adjusted probabilities to identify individual years in which differences existed due to treatment (Sokal and Rohlf 1981). Plot means for hardwood in-growth in year 14 were subjected to ANOVA using a mixed-model approach in PROC Mixed to test for significant effects of pine thinning, woody control, and their interaction. Blocking was assigned as a random effect in this ANOVA. To quantify relationships of understory vegetation to overstory density, stepwise linear regression in PROC Reg was used to identify the stand variables (i.e., pine, hardwood, and total values for stem density, basal area, and crown cover) having the strongest relationships with herb cover and species richness based on the coefficient of determination (R^2) and standard error of estimate ($s_{y.x}$). The overstory–understory regression analyses were conducted separately on data for 5 and 14 years after thinning to assess how the relationships changed with time. Differences in the regression slopes and intercepts due to presence or absence of pine thinning and woody control were tested using the extra sums-of-squares approach (Neter et al. 1989). Piecewise linear regression in PROC Nlin was used to estimate the stand density value associated with the observed competition threshold response for herb cover.

Results

Annual precipitation

Annual precipitation near the study sites averaged 123 cm during the 14-year study period, with 68 cm falling during the growing season (May–October). Rogers (1990) observed a slightly smaller average of 62 cm of growing season precipitation during the period of 1964–1985. Growing season precipitation varied twofold between the driest year (48 cm in 1999, year 6) and wettest year (100 cm in 2003, year 10) (Fig. 1). The three growing seasons that followed year 6 also

Table 2. ANOVA results for effects of pine thinning and woody control on tree size variables for pines and hardwoods in longleaf pine (*Pinus palustris*) plantations.

		df[b]		Probability > *F* for tree size variable:[a]				
Species group	Source of variation	N	D	Ht	CL	CH	CW	DBH
Pines	Thinning (T)	1	14	0.136	0.004	<0.001	<0.001	0.013
	Woody control (W)	1	14	0.268	0.872	0.018	0.271	0.490
	T × W	1	14	0.286	0.803	0.038	0.669	0.412
	Year (Y)	5	100	<0.001	<0.001	<0.001	<0.001	<0.001
	T × Y	5	100	0.106	<0.001	0.006	<0.001	<0.001
	W × Y	5	100	0.150	0.678	0.786	0.016	0.104
	T × W × Y	5	100	0.654	0.781	0.850	0.343	0.534
	Covariate[c]	1	100	<0.001	0.002	<0.001	<0.001	<0.001
Hardwoods	T	1	4	0.280	0.118	0.328	0.527	0.028
	Y	5	44	<0.001	<0.001	<0.001	<0.001	<0.001
	T × Y	5	44	0.264	0.090	0.070	0.247	0.383
	Covariate[d]	1	44					0.032

[a]Variables are height (Ht), crown length (CL), crown height (CH), crown width (CW), and stem diameter at breast height (DBH).

[b]df is degrees of freedom for the numerator (N) and denominator (D) of the *F* test.

[c]Pretreatment (winter 1993–1994) pine stand basal area (for Ht and CH) and DBH (for CL, CW, and DBH).

[d]Pretreatment hardwood stem density.

Table 3. ANOVA results for effects of pine thinning and woody control on stand variables for pines and hardwoods in longleaf pine (*Pinus palustris*) plantations.

		df[b]		Probability > *F* for stand variable:[a]					
Species group	Source of variation	N	D	COV	BA	VOL	DENS	MORT	SDI
Pines	Thinning (T)	1	14	<0.001	<0.001	<0.001	<0.001	0.161	<0.001
	Woody control (W)	1	14	0.947	0.938	0.952	0.906	0.171	0.852
	T × W	1	14	0.837	0.549	0.342	0.536	0.451	0.963
	Year (Y)	5	100	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	T × Y	5	100	0.001	<0.001	<0.001	0.017	0.002	0.206
	W × Y	5	100	0.622	0.865	0.773	0.927	0.750	0.842
	T × W × Y	5	100	0.940	0.820	0.791	0.979	0.852	0.952
	Covariate[c]	1	100	<0.001	<0.001	0.001	0.014		<0.001
Hardwoods	T	1	4	0.126	0.180	0.144	0.768	0.507	0.042
	Y	5	49	0.004	0.225	0.209	<0.001	<0.001	0.090
	T × Y	5	49	0.139	0.005	0.026	0.016	0.066	0.028
	Covariate[d]	1	49	<0.001	0.007	0.042	0.004		<0.001

[a]Variables are crown cover (COV), basal area (BA), volume (VOL), stem density (DENS), mortality (MORT), and the Reineke (1933) stand density index (SDI).

[b]df is degrees of freedom for the numerator (N) and denominator (D) of the *F* test.

[c]Pretreatment (winter 1993–1994) pine stand basal area.

[d]Pretreatment hardwood DBH (for COV, BA, and DENS) and stem density (for VOL and SDI).

had below-average precipitation: 58, 57, and 52 cm, respectively. The years that included the last three measurements of understory vegetation (years 5, 8, and 14) varied considerably in annual precipitation (139, 100, and 106 cm, respectively) but not in growing season precipitation (59, 57, and 52 cm, respectively).

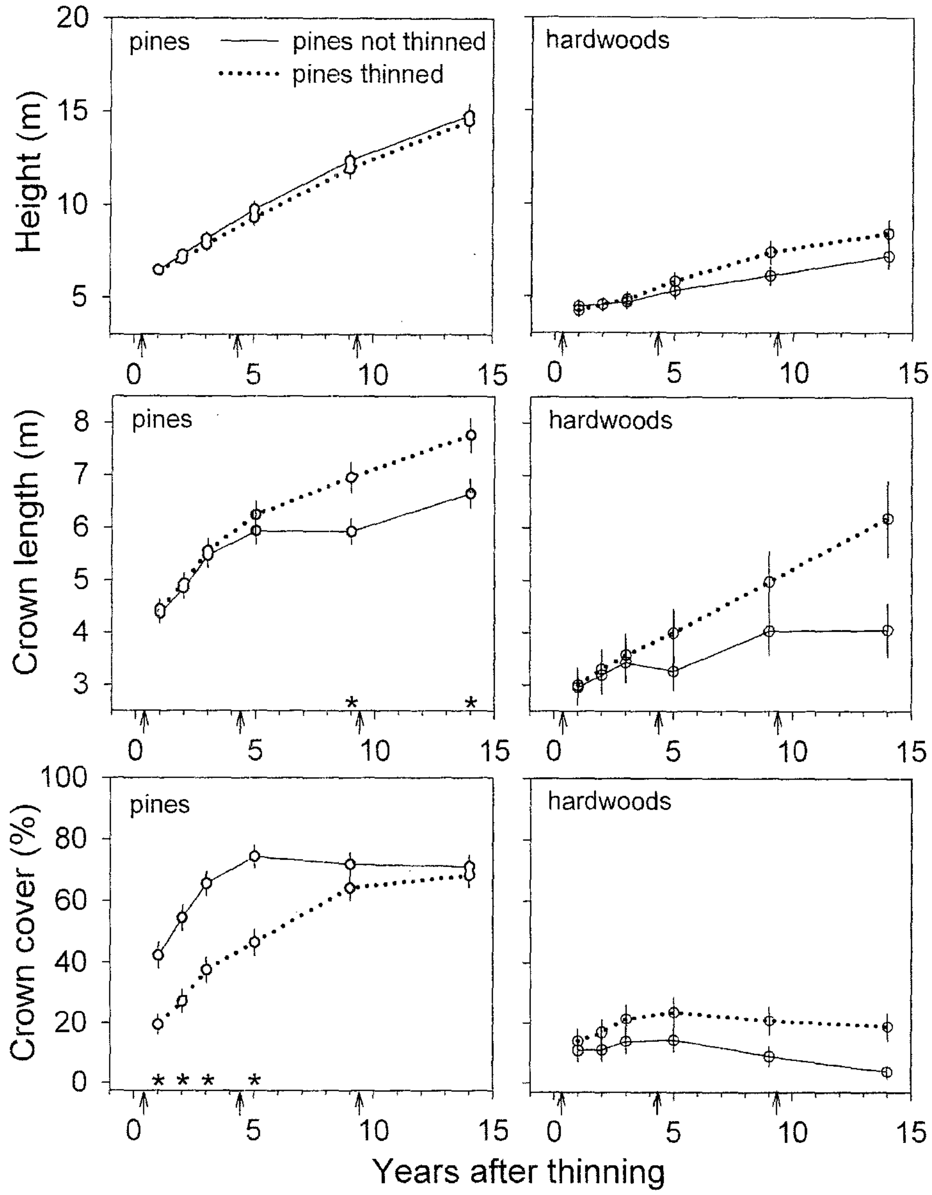
Tree responses

Site index of longleaf pine ranged from 12.2 to 18.2 m among the six study sites (Table 1). Sites of lower productivity had soils of the Lakeland series, whereas those of higher productivity had soils of the Blanton and Troup series. Although the sites spanned a broad range of productivity levels, they would be considered in the middle of the observed range for longleaf pine (Boyer 1980).

Tree and stand responses of longleaf pine to the treatments were primarily attributable to the interaction of pine thinning and measurement year (Tables 2 and 3). The interaction of woody control and measurement year was significant for only one variable (pine crown width, described below), and the three-way interaction of thinning, woody control, and measurement year was not significant for any of the response variables.

Pine height did not differ significantly between thinning levels in any of the measurement years ($P = 0.106$) (Table 2; Fig. 2), and in year 14, it averaged 14.6 m. At 9 and 14 years after thinning, crown length of pines in thinned stands averaged 1.0 and 1.1 m greater, respectively, than in nonthinned stands ($P < 0.001$). Crown cover of pines was significantly less in thinned stands than in nonthinned stands in each year

Fig. 2. Effects of pine thinning on height, crown length, and crown cover (±SE) of pines and hardwoods during 14 years after thinning and woody control in longleaf pine (*Pinus palustris*) plantations. Asterisks indicate years in which means differed significantly ($P \leq 0.05$) between thinning levels; arrows indicate the timing of prescribed fires.



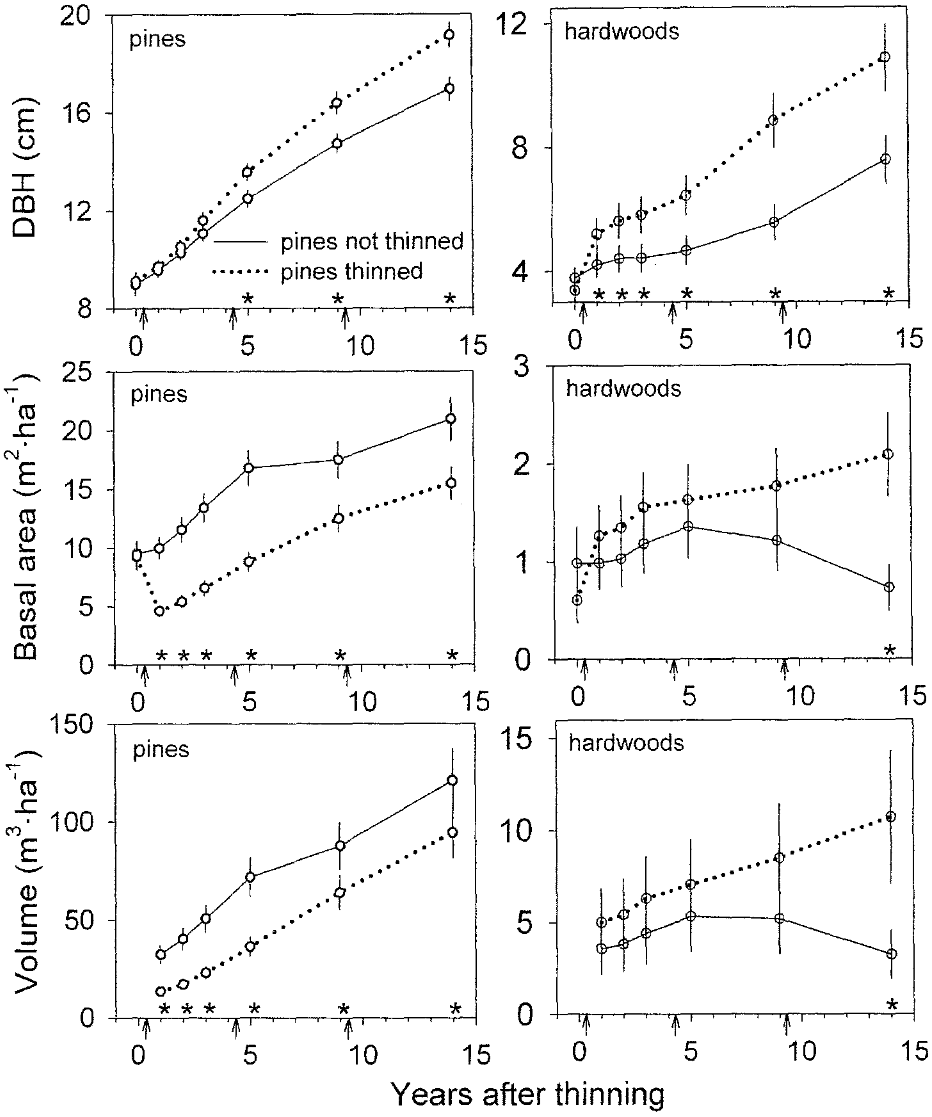
except years 9 and 14 when values differed by less than 8% ($P = 0.001$) (Table 3).

In year 14, the cumulative effects of thinning were associated with a 2.1 cm increase in pine DBH, a 0.9 m increase in pine crown width, and a 1.5 m decrease in pine crown height relative to trees in nonthinned plots ($P \leq 0.006$) (Table 2). Increases in crown width from thinning were statistically significant beginning in year 3, whereas those for DBH were significant beginning in year 5 (Fig. 3). Woody control was associated with increases in crown width of 0.2 and 0.3 m in years 5 and 14, respectively ($P = 0.016$).

The five most abundant hardwood species were, in decreasing order of average density, *Quercus margarettae* (Ashe) Small (124 stems·ha^{-1}), *Quercus incana* Bartram (92 stems·ha^{-1}), *Quercus laevis* Walter (87 stems·ha^{-1}), *Quercus nigra* L. (68 stems·ha^{-1}), and *P. serotina* (49 stems·ha^{-1}). The main effects of pine thinning or its interaction with measurement year were not significant for hardwood height, crown width, crown length, or crown height ($P \geq 0.070$), although as observed for the pines, crown length of hardwoods in thinned stands diverged from that in nonthinned stands during the last three measurements (Table 2; Fig. 2). In year 14, hardwood height averaged 7.8 m. Hardwood crown cover did not differ between thinning levels in any measurement year ($P = 0.139$) (Table 3), averaging 11% in year 14. The main effects of thinning were significant for hardwood DBH because the treatment was associated with a 1 to 3 cm increase throughout the 14-year study period ($P = 0.028$) (Table 2; Fig. 3).

Development of pine basal area and volume followed approximately parallel trajectories for thinned and nonthinned stands throughout the 14-year study period (Fig. 3). In each

Fig. 3. Effects of pine thinning on DBH, basal area, and volume (±SE) of pines and hardwoods during 14 years after thinning and woody control in longleaf pine (*Pinus palustris*) plantations. Asterisks indicate years in which means differed significantly ($P \leq 0.05$) between thinning levels; arrows indicate the timing of prescribed fires. Note the differences in the *y*-axis scales.



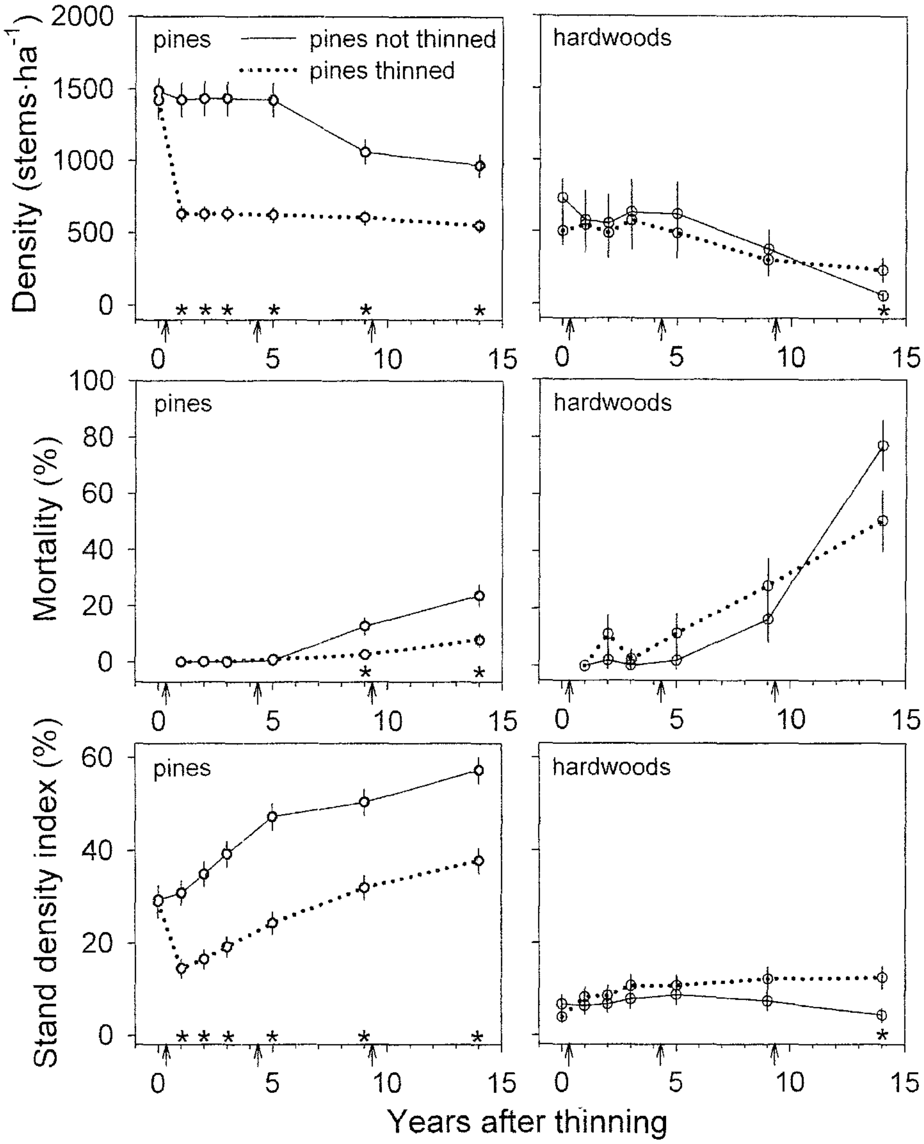
year, basal area, volume, and stem density of pines were significantly less in thinned stands than in nonthinned stands ($P \leq 0.017$) (Table 3; Figs. 3 and 4). In year 14, stem density of pines in thinned stands was 57% of that in nonthinned stands, whereas basal area and volume in thinned stands were 74% and 78%, respectively, of those in nonthinned stands.

Pine mortality was greater in nonthinned stands than in thinned stands in years 9 and 14 when values differed by 10% and 16% of the initial stem density, respectively ($P = 0.002$) (Table 3; Fig. 4). The primary source of mortality was an outbreak of southern pine beetle (SPB) (*Dendroctonus frontalis* Zimmermann) in year 9 (2002) in nonthinned stands at the site of lowest productivity, 56-02S (site index = 12.2 m) (Table 1). Cumulative pine mortality of the SPB-infested stands at site 56-02S averaged 77% in year 14. To determine whether the SPB infestation influenced overall results of the study, statistical analyses were conducted that excluded all data from site 56-02S. Only mortality and stand density variables were affected by exclusion of these data; all other overstory and understory responses remained essentially unchanged. Even with exclusion of data from the SPB-infested stands, pine mortality in year 14 differed significantly between thinned and nonthinned stands (7% and 15%, respectively, $P = 0.019$).

SDI of longleaf pine developed at a rapid rate, reaching 24% and 47% of the species' maximum by year 5 in thinned and nonthinned stands, respectively, and 38% and 57% of the maximum by year 14 (Fig. 4). The interaction of thinning and measurement year was not significant for pine SDI ($P = 0.206$), although presence of thinning main effects indicated a consistent response from year to year ($P < 0.001$) (Table 3). Excluding the data from site 56-02S, pine SDI averaged 41% and 66% of the species' maximum in year 14 for thinned and nonthinned stands, respectively.

In year 14, basal area, volume, and stem density of hardwoods in thinned stands were greater than in nonthinned stands, but significant differences were not detected for years

Fig. 4. Effects of pine thinning on stem density, mortality, and Reineke (1933) stand density index (percentage of species' maximum) (±SE) of pines and hardwoods during 14 years after thinning and woody control in longleaf pine (*Pinus palustris*) plantations. Asterisks indicate years in which means differed significantly ($P \leq 0.05$) between thinning levels; arrows indicate the timing of prescribed fires.



1–9 ($P \leq 0.026$) (Table 3; Figs. 3 and 4). Cumulative mortality of hardwood stems accelerated from year 5 (7%) to year 14 (64%), attributable, in part, to the prescribed fires in years 4 and 9; however, it did not differ significantly between thinning levels in any measurement year ($P = 0.066$). In year 14, SDI of hardwoods was greater in thinned stands than in nonthinned stands (12% and 4% of the species' maximum, respectively) because of declining values in nonthinned stands ($P = 0.028$). Hardwood in-growth in year 14 did not differ significantly between presence and absence of pine thinning (41 and 14 trees·ha^{-1}, respectively) or woody control (13 and 45 trees·ha^{-1}, respectively) ($P \geq 0.132$) (ANOVA results not shown).

Understory responses

The pine thinning and woody control treatments were associated with similar increases in herb species cover and richness that peaked in year 5 but declined thereafter. Responses of herb cover were attributable to a treatment-by-year interaction (Table 4). Herb cover was greater in thinned stands than in nonthinned stands for years 3–8, with the greatest difference (22%) occurring in year 5 ($P = 0.001$) (Fig. 5). Similarly, herb cover was greater with than without woody control for years 5–14, with the greatest difference (17%) also occurring in year 5 ($P < 0.001$). The main effects of thinning or its interaction with measurement year were not significant for woody cover ($P \geq 0.348$). For years 2–14, woody cover was 12%–28% less with than without woody control ($P < 0.001$).

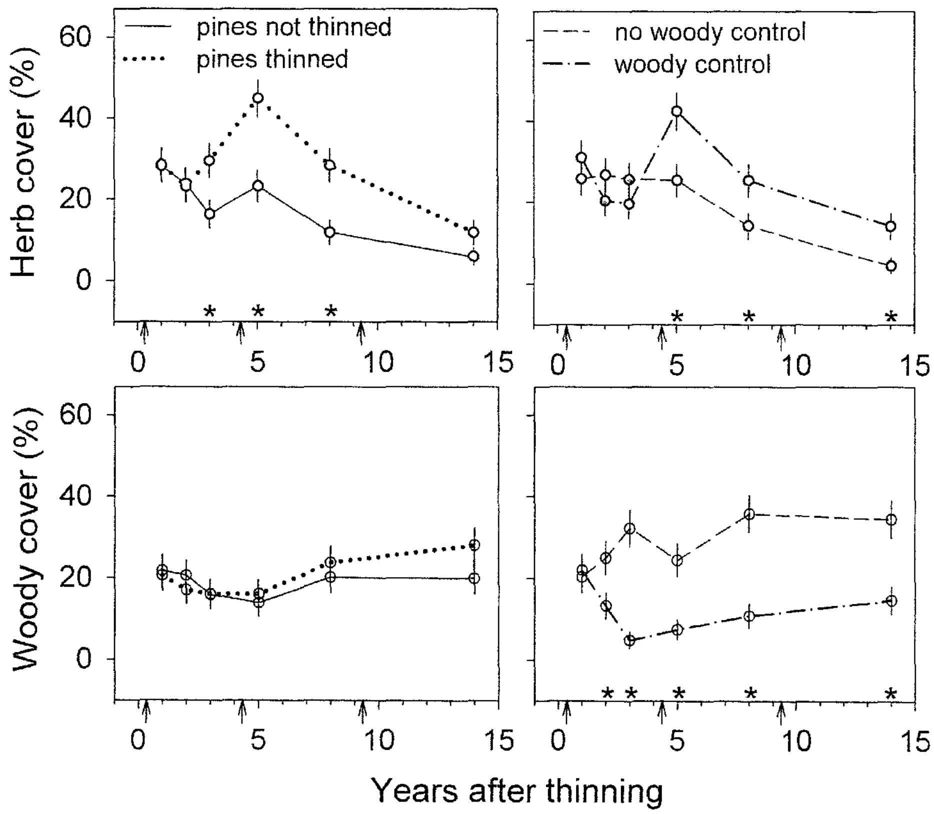
Regression models for predicting herb species richness from area sampled indicated a loss of approximately half of the species from year 5 to 14 (Fig. 6). Models for each measurement year ($R^2 = 0.92$ to 0.97) had a common slope parameter but separate intercepts for pine thinning and woody

Table 4. ANOVA results for effects of pine thinning and woody control on cover of herbaceous and woody vegetation in longleaf pine (*Pinus palustris*) plantations.

	df[a]		Probability > *F* for cover variable:	
Source of variation	N	D	Herbs	Woody
Thinning (T)	1	15	0.002	0.580
Woody control (W)	1	15	0.042	<0.001
T × W	1	15	0.340	0.164
Year (Y)	5	100	<0.001	<0.001
T × Y	5	100	0.001	0.348
W × Y	5	100	<0.001	<0.001
T × W × Y	5	100	0.187	0.426

[a]df is degrees of freedom for the numerator (N) and denominator (D) of the *F* test.

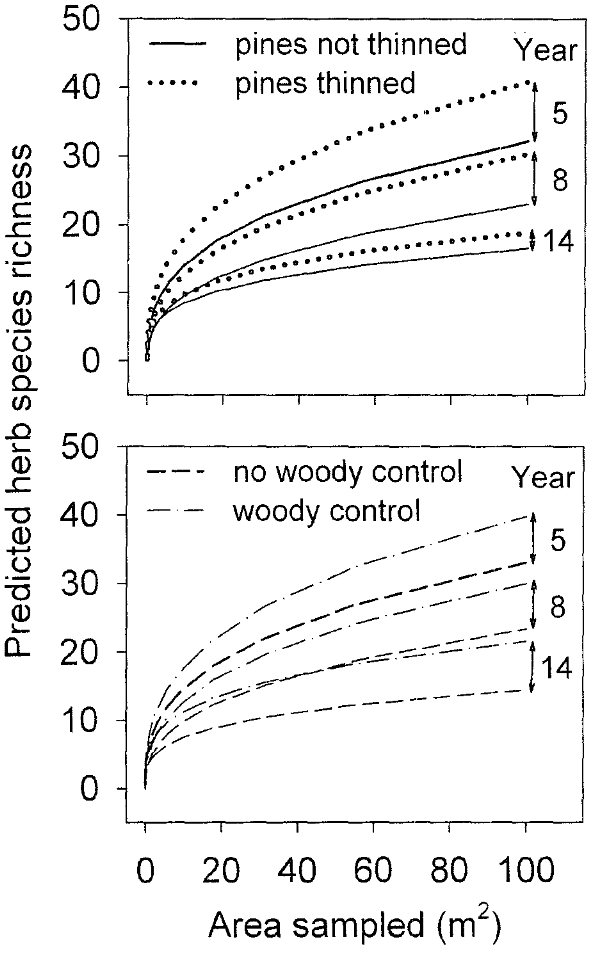
Fig. 5. Effects of pine thinning and woody control on cover of herb and woody understory species (±SE) during 14 years after thinning and woody control in longleaf pine (*Pinus palustris*) plantations. Asterisks indicate years in which means differed significantly ($P \leq 0.05$) between levels of thinning and woody control; arrows indicate the timing of prescribed fires.



control, indicating significant main effects of each treatment (Table 5). The interaction of thinning and woody control was not significant in any of the regression models ($P \geq 0.091$). The regression slope (i.e., the coefficient for area sampled) changed little from year 5 to 8, but a decline in year 14 signaled a reduction in species richness across all treatments. The regression intercept decreased from year 5 to 8, indicating an overall reduction in species richness independent of area sampled and treatment. From year 5 to 8, regression coefficients for thinning and woody control were of similar magnitude and changed little with time. However, from year 8 to 14, the regression coefficient for thinning decreased by 53%, while that for woody control increased by 56%. Assuming an area sampled of 100 m^2, regression models for years 5 and 8 predicted increases in species richness of six to eight species from either treatment. In contrast, the regression model for year 14 predicted increases in species richness of two species from thinning and seven species from the woody control.

A total of 265 herb and woody species were identified in the understory of the study sites. Eighty-one herb species had an average frequency of 10% or more. Significant treatment effects on frequency were detected for 18 of the 81 herb species, including one fern, two grasses, and 15 broadleaf herbs (Table 6). Species having increased frequencies due to the presence versus absence of pine thinning or woody control included 11 perennials and four annuals, and only one species was classified as nonnative (*Rumex acetosella* L.) (USDA, NRCS 2011). The main effects of pine thinning and woody control were associated with increased frequen-

Fig. 6. Regression predictions of the effects of pine thinning and woody control on relationships of herb species richness to area sampled in longleaf pine (*Pinus palustris*) plantations. Arrows indicate the magnitude of the response for each year. See Table 5 for details about the regression models.



cies of three and five species, respectively, indicating sustained effects of the treatments. Species that responded to a treatment-by-year interaction generally had increased frequencies in years 5 and 8 and no change in year 14, indicating a short-term response. Frequencies of three species decreased in response to woody control: *Eupatorium mohrii* Greene, *Hieracium gronovii* L., and *Lactuca canadensis* Michx.

Overstory and understory relationships

The regression analysis identified a negative linear relationship between herb cover and total stem density of pines and hardwoods that was significant in year 5 ($P < 0.001$, $R^2 = 0.55$) but not in year 14 ($P = 0.071$, $R^2 = 0.14$) (Fig. 7). The regression slope and intercept did not differ between levels of pine thinning or woody control. A distinct break in the relationship for year 5 was detected at a density of approximately 2000 stems·ha^{-1}. In the fitted piecewise regression model, herb cover declined linearly with increasing total stem density up to an estimated threshold of 1928 stems·ha^{-1}. For every additional 100 stems·ha^{-1}, herb cover declined approximately 3%. At stem densities above the threshold, herb cover remained constant at approximately 17%. The piecewise regression model accounted for an additional 7% of the variation in herb cover over that explained by simple linear regression.

Herb species richness had a negative linear relationship with total stem density of pines and hardwoods that was significant in year 14 ($P = 0.002$, $R^2 = 0.35$) but not in year 5 ($P < 0.206$, $R^2 = 0.07$). The regression slope and intercept did not differ between levels of pine thinning or woody control. The model for year 14 predicts a loss of approximately one herb species for each additional 100 stems·ha^{-1} (Fig. 7). Relationships of herb species cover and richness with the other variables of overstory density (i.e., pine, hardwood, and total values for basal area and crown cover) were not as strong as those with total stem density. Note that negative linear relationships were detected in year 5 between herb species richness and either pine stem density ($P = 0.032$, $R^2 = 0.19$) or pine basal area ($P = 0.028$, $R^2 = 0.20$), indicating that loss of herb species was weakly related to pine density during early stages of the study.

Discussion

In the 14-year study period, tree and stand characteristics of the longleaf pine and hardwoods have undergone considerable change. As expected from thinning, crown length, crown width, and DBH of pines have increased and upward crown recession has slowed. However, crown responses of longleaf pine to thinning were much less than those observed in previous research on loblolly pine. Six years after a thinning of similar intensity, Peterson et al. (1997) observed 1.5 and 2.3 m increases in crown length and crown width of loblolly pine, respectively, from thinning, whereas increases in the present study after 14 years were only 1.1 and 0.9 m, respectively.

In the absence of thinning, longleaf pine exceeded 50% of its maximum biological density between years 5 and 9, rendering the stands vulnerable to density-associated mortality (Kush et al. 2006). As a result, by year 14, cumulative mortality of pines in nonthinned stands was 24% compared with 8% in thinned stands. Although longleaf pine is considered to have low susceptibility to attack by SPB (Boyer 1990), four consecutive years of growing season drought (i.e., years 6–9) probably reduced the vigor of trees in this study, particularly those in nonthinned stands on the site of lowest productivity (56-02S). The year of SPB attack (2002) was noted to be among the top five years of greatest damage from this pest in the adjacent state of Georgia for the period of 1972–2007 (Georgia Forestry Commission 2010).

Woody control had little effect on growth of longleaf pine. The only pine responses observed from woody control were increases in crown width of 0.2 and 0.3 m in years 5 and 14, respectively. Although sustained reductions in woody cover resulted from this treatment for the 14-year period of the study, herb species filled the void by increasing their cover by 10%–17% during years 5–14. In previous research, loblolly pine and slash pine (*Pinus elliottii* Engelm.) of similar age demonstrated significant increases in growth after controlling understory vegetation (Oppenheimer et al. 1989; Fortson et al. 1996). However, the plantations in those studies were specifically selected to have a high abundance of understory vegetation, primarily shrubs, and repeated applications

Table 5. Regression coefficients[a] (standard errors shown in parentheses) for models predicting effects of pine thinning and woody control on herb species richness in during 14 years after thinning in longleaf pine (*Pinus palustris*) plantations.

	Regression coefficient						
Years after thinning	Intercept	Pine thinning	Woody control	Area sampled (m^2)	$s_{y.x}$	R^2	n
5	1.860 (0.062)	0.232 (0.037)	0.181 (0.037)	0.337 (0.006)	0.203	0.97	120
8	1.445 (0.079)	0.263 (0.047)	0.241 (0.047)	0.351 (0.007)	0.257	0.95	120
14	1.470 (0.079)	0.123 (0.047)	0.376 (0.047)	0.263 (0.007)	0.258	0.92	120

Note: See Fig. 6 for a graphical depiction of the models.

[a]Equations have the form $\log_e(R + 1) = B_0 + B_1(T) + B_2(W) + B_3(\log_e (A))$, where R is herb species richness, B_{0-3} are regression coefficients, T and W are indicator variables for presence or absence of pine thinning and woody control, respectively, and A is area sampled.

of herbicides were used to maintain complete control of all competing vegetation for 8–10 years.

By year 9, pine crown cover in thinned stands (64%) was similar to that in nonthinned stands (72%), yet pine crown length in thinned stands exceeded that in nonthinned stands by 1 m or more. In the absence of woody control, a second canopy layer of hardwoods has developed averaging 7.8 m in height below a pine canopy averaging 14.6 m in height. These changes in canopy structure since study initiation indicate that both thinned and nonthinned stands have developed deep and relatively continuous canopies with the potential to competitively exclude herb species. Although hardwood cover and crown length did not differ significantly between thinning levels, they contributed additional shade and root competition to what was already a highly competitive understory environment. Despite the fact that application of prescribed fires in years 0, 4, and 9 killed or top-killed 64% of hardwood stems, surviving stems were able to increase their DBH each year in response to pine thinning, resulting in a threefold difference in hardwood basal area in year 14 between thinned and nonthinned stands.

Pine thinning and woody control each stimulated increases in herb cover of similar magnitude that peaked in year 5 and declined thereafter. Although short-term reductions in herb cover from the woody control were observed in analyses of data from the first five years of the study (Harrington and Edwards 1999), these differences were not detected when data from years 8 and 14 were included. By year 14, increases in herb cover and species richness from thinning were negligible, probably because pine cover was approximately the same in thinned and nonthinned stands and because thinning stimulated increases in pine crown length and hardwood basal area, both indicators of a highly competitive understory environment. In contrast, by sustaining reductions in abundance of hardwoods and shrubs, the woody control treatment preserved more cover and species richness of herbs than the pine thinning treatment.

The timing of peak levels of herb species abundance and richness in year 5 and the dramatic decline in these variables from year 5 to 14 may have been associated with variation in annual precipitation. Years 1–5 were noticeably wetter than years 6–9, and the extended drought may have intensified competition from pines and hardwoods, resulting in reduced abundance and loss of herb species.

The observed increases in species' frequency indicate that pine thinning and woody control stimulated establishment of new populations of herb species that persisted at least through year 8. Species that had sustained increases in frequency likely are more tolerant to shade and root competition than those that had short-term increases. The short-term increases in herb species richness that resulted from the treatments provided absolute values of richness of up to 8 herb species·m^{-2}, as predicted from the regression model for year 5. This species richness value for longleaf pine plantations is considerably below those reported for undisturbed savannas of longleaf pine (40–50 species·m^{-2}: Walker and Peet 1984; Peet and Allard 1993).

Variation in fifth-year cover of herb species was described by a competition threshold model that indicated linear declines with increasing stem density of pines and hardwoods up to an estimated threshold density of 1928 stems·ha^{-1}. Above this threshold density, a shade-tolerant cohort of herb species survived, averaging 17% in cover. By year 14, herb cover declined to 12% and 6% in thinned and nonthinned stands, respectively, and the relationship between herb cover and stem density was no longer significant because a high level of pine cover (about 70%) had developed in each of the treatments regardless of stem density. The presence of a weak negative relationship between herb species richness and pine stem density in year 5 ($P = 0.028$, $R^2 = 0.20$) indicated that the pine canopy had begun to play a role in competitively excluding herb species. In year 14, herb species richness had a relatively strong negative relationship with total stem density ($P = 0.002$, $R^2 = 0.35$), indicating that both pine and hardwood canopies had become associated with the loss of herb species.

Results of this research suggest that a pine thinning of moderate intensity (i.e., removal of about half of the original planting density) will provide increases in herb species cover and richness in longleaf pine plantations for up to 8 years, whereas woody control will provide a somewhat longer duration of increases. Any significant reduction in tree density below about 1900 stems·ha^{-1} resulting from thinning, prescribed fire, or mortality is likely to increase cover of herbs; therefore, increases in herb cover and the duration of such increases will be proportionate to thinning intensity. This model is supported by previous research in which cover and biomass of understory species, including longleaf pine seedlings, were greater in gaps than in forest stands of various densities and uniformities of spacing (McGuire et al. 2001; Harrington et al. 2003). Likewise, retention of herb species, although not necessarily in a vigorous state of growth and reproduction (Harrington 2006), is likely to be enhanced by any significant reduction in stem density of pines and hardwoods.

These research findings imply two possible strategies for managing longleaf pine plantations to facilitate savanna restoration. In the first strategy, pines and hardwoods are precom-

Table 6. Relative change (+, increase; –, decrease; 0, no change) in frequency of herb species due to the presence versus absence of pine thinning or woody control in longleaf pine (*Pinus palustris*) plantations through 14 years after thinning.

				Pine thinning		Woody control	
Species	Life-form[a]	Nativity[b]	Duration[c]	Main effects	Treatment × year[d]	Main effects	Treatment × year[d]
Aristida purpurascens Poir.	G	N	P				0, 0, +
Asplenium platyneuron (L.) Britton, Sterns & Poggenb.	F	N	P			+	
Bulbostylis capillaris (L.) Kunth ex C.B. Clarke	G	N	A/P		0, +, 0		+, +, 0
Chrysopsis gossypina (Michx.) Elliott	H	N	P	+			
Conyza canadensis (L.) Cronquist	H	N	A/B	+			+, +, 0
Croptilon divaricatum (Nutt.) Raf.	H	N	A		+, +, 0		
Diodia teres Walter	H	N	A/P		+, +, 0		0, +, 0
Eupatorium capillifolium (Lam.) Small	H	N	P			+	
Eupatorium compositifolium Walter	H	N	P			+	
Eupatorium mohrii Greene	H	N	P			–	
Hieracium gronovii L.	H	N	P				–, 0, 0
Hypericum gentianoides (L.) Britton, Sterns & Poggenb.	H	N	A		+, +, 0	+	
Lactuca canadensis L.	H	N	A/B				–, –, 0
Lactuca graminifolia Michx.	H	N	B/P	+			
Lespedeza hirta (L.) Hornem.	H	N	P		+, +, 0		
Pseudognaphalium obtusifolium (L.) Hilliard & B.L. Burtt	H	N	A/B		+, +, 0		+, +, 0
Rumex acetosella L.	H	I	P			+	
Stipulicida setacea Michx.	H	N	P				+, +, 0

Note: Only those species having an average frequency of 10% or greater and significant ($P \leq 0.05$) treatment effects are listed.

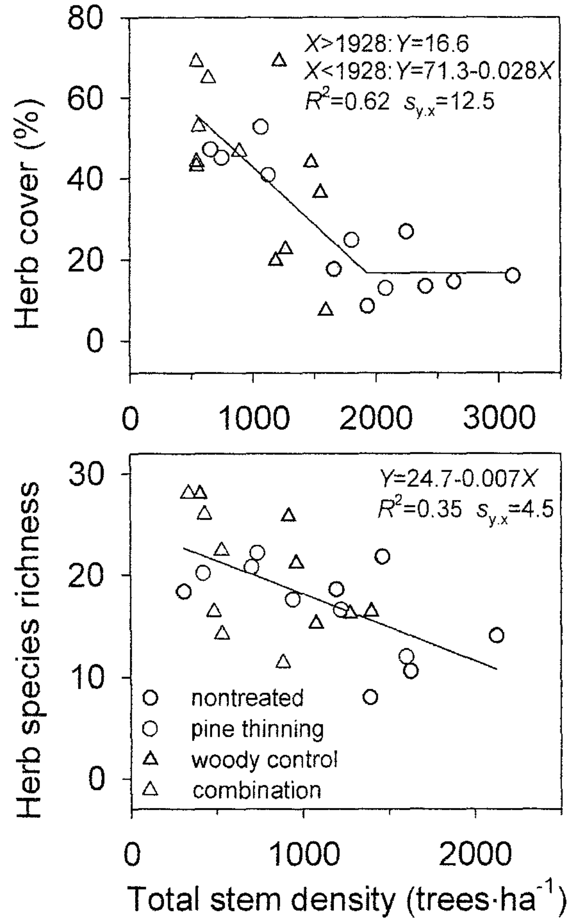
[a]Fern (F), graminoid (G), or broadleaf herb (H).

[b]Native (N) or introduced (I).

[c]Annual (A), biennial (B), or perennial (P).

[d]Relative change in frequency due to treatment in years 5, 8, and 14, respectively.

Fig. 7. Regression relationships of herb cover and herb species richness (species·100 m^{-2}) to total stem density of pines and hardwoods after thinning and woody control in longleaf pine (*Pinus palustris*) plantations. Data for the top and bottom graphs are from 5 and 14 years after thinning, respectively. Note the change in the *x*-axis scales.



mercially thinned early in stand development (age 8–11 years, depending on site quality) and then later when crown cover of pines exceeds 50%. Such an approach may provide a reasonable compromise between pine stand production and savanna restoration. An alternative approach would result in drastically lower initial densities of pines and hardwoods, either by establishing fewer trees at planting or by applying a higher intensity of precommercial thinning. In this latter approach, savanna community restoration would be encouraged by the prolonged absence of closed overstory canopy conditions and lower levels of root competition, assuming that hardwood and shrub abundance is kept low via prescribed fire and woody control. Regardless of the management regime, the dynamic canopy development of young pine and hardwood stands is likely to necessitate repeated treatments of pine thinning, woody control, and prescribed fire to fully restore and maintain a vigorous herbaceous community.

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