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Effect of initial seedling size, understory competition, and overstory density on the survival and growth of *Pinus echinata* seedlings underplanted in hardwood forests for restoration

John M. Kabrick[1] · Benjamin O. Knapp[2] · Daniel C. Dey[1] · David R. Larsen[2]

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Abstract There is interest in restoring shortleaf pine (*Pinus echinata*) in pine–oak woodlands where it once was abundant. Because of its shade intolerance and slow initial growth rate, shortleaf pine restoration has remained a challenge because competition from hardwoods exhibits greater initial growth following canopy removal but greater shade tolerance with canopy retention. The study objective was to examine the survival and growth of underplanted shortleaf pine seedlings relative to competing hardwoods as a function of initial seedling size, overstory density, and understory competition. In the Ozark Highlands of southeastern Missouri, USA, 48, 0.4-ha experimental units were each harvested from below to a uniform stocking level from 0 to 90 % and 30, 1–0 improved shortleaf pine seedlings were planted on a 3.7 × 7.3 m spacing. Linear or logistic regression was used to determine how shortleaf pine seedling (1) survival, (2) basal diameter growth, and (3) shoot growth were related to initial seedling size, overstory stocking, and understory competitor height during the first 5 years after underplanting. After five growing seasons, the survival rate of shortleaf pine seedlings was 50 % and was positively related to the initial basal diameter but was not related to overstory stocking or competitor height. Increasing overstory stocking decreased the basal diameter and height growth of shortleaf pine seedlings, explaining >51 % of the variation in basal diameter and 54 % of the variation in seedling height. Although competing hardwood seedlings were consistently taller than the shortleaf pine seedlings throughout the study, shortleaf pine seedlings maintained similar growth rates as competitors from the second to the fifth growing season. The eventual release of shortleaf pine is essential for recruitment, but releases can be delayed for several years after underplanting.

✉ John M. Kabrick
jkabrick@fs.fed.us

[1] USDA Forest Service, Northern Research Station, University of Missouri, 202 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA

[2] Forestry Department, University of Missouri, 203 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA

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Introduction

Restoring pine (*Pinus*) and pine–oak (*Pinus–Quercus*) forests has remained an important management objective throughout North America (Fulé and Covington 1994; Fulé et al. 2005; Zald et al. 2008; Rodriquez-Trejo and Myers 2010) particularly on public forestland in the USA (USDA Forest Service 2012). Although these efforts are commonly focused on restoring the native composition and structure of forest communities, inherent is also restoring ecological resistance and resilience so that these ecosystems are better positioned to withstand emerging threats to forest health, changes in disturbances associated with management, and a changing climate (Walker et al. 2004; Churchill et al. 2013; Lake 2013).

In the south-central USA, there is considerable interest in restoring shortleaf pine (*Pinus echinata*) throughout much of its natural range (Kabrick et al. 2007; Zhang et al. 2012). This shade-intolerant conifer species is widely distributed, ranging from Texas to New Jersey and southern New York (Lawson 1990). Shortleaf pine occurs with other pines in the Coastal Plain and with oaks (*Quercus*) and other hardwoods in the Interior Highlands (Guldin 2007) and southern Appalachians (Lawson 1990). In the Missouri Ozarks, mixtures of shortleaf pine and oaks were once dominant on about 1.7 million hectares and were prominent on an additional 1.0 million hectares (Liming 1946). They were most abundant on rolling to steep terrain on soils derived from sandstone or cherty dolomite that were well drained and acidic (Fletcher and McDermott 1957). Today, shortleaf pine in its native range often accounts for less than 15 % of stand stocking (Kabrick et al. 2004b), having been displaced by *Quercus* species and other hardwoods following extensive timber harvesting, subsequent land clearing, and frequent burning during the early 1900s (Cunningham 2007).

There are several motivating factors for restoring shortleaf pine ecosystems. In addition to interest in restoring the native plant and animal communities of this ecoregion, restoring shortleaf pine on former pine and oak–pine sites is viewed as a long-term strategy for mitigating chronic oak decline (Law et al. 2004). Two oak species, *Q. velutina* and *Q. coccinea*, that have largely replaced shortleaf pine throughout the Missouri Ozarks are particularly susceptible to oak decline as they mature (Shifley et al. 2006; Kabrick et al. 2008). Few management options (e.g., stand improvement or sanitation harvests, shortened rotations) have been successful in reducing accelerated mortality associated with decline in oak-dominated stands (Kabrick et al. 2004a; Dwyer et al. 2007), other than by shifting species composition to more heterogeneous mixes that contain fewer red oak group species (*Quercus* section *Lobatae*). In natural stands on well-drained soils of the Ozark Highlands, shortleaf pine is long-lived and is susceptible to few insect pests and diseases (Brinkman and Smith 1968). Restoring a mixture of shortleaf pines along with oaks of the white oak group (*Quercus* section *Quercus*), which are less susceptible to decline than are red oak group species, is likely to reduce the extent of oak decline and produce forests and woodlands that are less susceptible to insect and disease problems than are those comprising oaks alone (Kabrick et al. 2008). Restoring shortleaf pine is also considered a strategy for positioning forest and woodland ecosystems of the Ozark Highlands to be resistant to projected changes in climate.

Shortleaf pine is adapted to excessively drained, nutrient-deficient soils (Fletcher and McDermott 1957; Kabrick et al. 2008). It is also drought-tolerant, windfirm, and adapted to frequent but low-severity surface fires (Brinkman and Smith 1968; Lawson 1990; Brandt et al. 2014). Under various projected climate change scenarios for North America, the incidence or severity of disturbances such as drought, windstorms, and wildfire are anticipated to increase (IPCC 2012). Despite the uncertainty and wide range of conditions that are predicted using available climate models, shortleaf pine is forecasted to increase in abundance and native range under a number of climate change scenarios (Iverson et al. 2008).

Restoring shortleaf pine has remained a challenge because of intense competition from hardwood regeneration (Jensen et al. 2007). Previous research has yielded recommendations for optimizing the growth and yield of timber crops (Brinkman and Rogers 1967; Brinkman and Smith 1968) rather than for maintaining biodiversity or ecological resistance and resilience. Consequently, guidelines for establishing shortleaf pine recommend complete overstory removal and the control of competing hardwoods with herbicides so that shortleaf pine growth is maximized (Brinkman and Smith 1968). Contemporary restoration efforts are not intended to maximize timber production. Rather, they are intended to restore the native plant composition, structure, and functionality of shortleaf pine and pine–oak ecosystems. Retaining standing live trees or a partial overstory is often an important restoration objective, because these trees provide habitat for wildlife and are the desirable "legacy" trees needed for meeting other restoration goals (Franklin et al. 2007; Kabrick et al. 2014).

When examined across multiple biomes, including temperate deciduous, temperate coastal, boreal, and tropical forests, the survival and growth of underplanted trees of various species were optimized where a partial overstory was retained due to reduced understory competition and protection from wind, frost, predation, and other stressors (Paquette et al. 2006). However, the species commonly used for underplanting have been moderately tolerant of shade (Paquette et al. 2006), and it is uncertain if underplanting is a viable approach for shade-intolerant species such as shortleaf pine. Past research indicates that retaining a residual overstory, particularly of hardwoods, will disproportionately reduce the survival and growth of shortleaf pine seedlings because of their shade tolerance (Shelton and Cain 2000). In contrast, Knapp et al. (2013) reported that the survival of underplanted *Pinus palustris*, a shade-intolerant conifer, was increased by leaving a partial overstory compared to clearcutting, although seedling growth was reduced by canopy retention. Because of discrepancies in the literature and the interest in underplanting intolerant conifers such as shortleaf pine for restoration, we developed this study to quantify the survival and growth of shortleaf pine seedlings relative to competing hardwood seedlings as a function of initial shortleaf pine seedling size, understory competition, and overstory stocking. Specific hypotheses were underplanted shortleaf pine seedling survival and growth would (1) increase with decreasing overstory density; (2) increase with increasing initial stem diameter; (3) decrease with increasing height of competing hardwoods in the reproduction cohort; and (4) decrease more with increasing overstory density than that of competing hardwoods. Findings from this study will be used to guide strategies for restoring shade-intolerant conifers by underplanting where retaining a partial overstory is an important management objective.

Materials and methods

Study area

This study was initiated in 2006 at the Sinkin Experimental Forest in southeastern Missouri (37.5 lat, −91.27 long), on sites suited for managing shortleaf pine or *Pinus–Quercus* mixes. Sites are located within the Ozark Highlands Ecological Section (Bailey 2009) on summit and shoulder slope positions on soils derived from sandstones (Roubidoux formation) or cherty dolomites (Gasconade formation) that were deep (>1.5 m), moderately well to excessively well drained, that had a low available water holding capacity (<9 cm) and a low pH (<5.2) and base cation supply. Soil series included Nixa (Loamy-skeletal, siliceous, active, mesic, Glossic Fragiudults) and Coulstone and Clarksville (each Loamy-skeletal, siliceous, semiactive, mesic, Typic Paleudults). The site index (*Q. velutina* equivalent, age 50) was approximately 17 m. Long-term weather data collected on the Sinkin Experimental Forest indicated that the average annual precipitation is 1118 mm and falls mostly as rain, with occasional freezing rain, sleet, and snow during the winter months. The average daily temperature in winter is 1 °C and the average daily temperature in summer is 24 °C.

Experimental units and treatments

The study used a completely randomized design comprising 48 0.4-ha square experimental units that each were uniform in forest type, soil properties, slope, and aspect. In the center of each experimental unit, one 0.08-ha circular plot was established for the inventory of all trees ≥5 cm dbh and one nested circular 0.0004-ha plot was established for the inventory of all trees <5 cm dbh. Inventories in 2005, prior to initiating the study, indicated that forests were mature and fully stocked comprising (by percent basal area) *Q. velutina* (34 %), *Q. alba*, (27 %), shortleaf pine (17 %), *Q. coccinea* (6 %), *Q. stellata* (5 %), *Carya* spp. (5 %), and other hardwoods (6 %).

During the fall and winter 2006–2007, the overstory density of each of the 48 experimental units was adjusted approximately to a single stocking level (Gingrich 1967; Rogers 1983). The stocking level was approximated by converting to a basal area range so that it could be readily implemented by marking trees for retention using a 2.3-basal-area-factor prism. Four basal area range classes were designated to ensure a range of stocking among experimental units including <2, 4–9, 10–14, and >14 m^2 ha^{-1}. Twelve replicates of each of the basal area ranges were randomly assigned. Experimental units were harvested "from below" to create structure resembling a shelterwood with reserves, as would commonly be applied during pine woodland restoration in the study region (Tuttle and Houf 2007). Preferred trees to retain were >25 cm d.b.h. and were in this order shortleaf pine, *Q. alba*, *Q. stellata*, *Q. rubra*, *Q. coccinea*, *Q. velutina*, and *Carya* spp. In the winter of 2007–2008, harvesting and follow-up operations were completed, including cutting trees <5 cm diameter at breast height (dbh) to meet the stocking goal assigned to each treatment unit. On May 8, 2009, a major windstorm passed over the study area and resulted in widespread blowdown of canopy trees, resulting in drastic reduction of overstory density on many of the plots. Of the 36 plots with canopy trees present in 2008, only four had an increase in density from 2008 to 2009. The reduction in stand stocking ranged from 2 to 43 %, with a mean of 18 % reduction across all plots with canopy trees. Following the wind event, trees per hectare (tph) ranged from 0 to 296, stand basal areas ranged from 0 to

22 m^2 ha^{-1}, and stocking ranged from 0 to 73 % stocked across the 48 study plots ("Appendix").

Shortleaf pine seedlings

Shortleaf pine seedlings used in this study were 1–0 bareroot seedlings produced by the George O. White State Tree Nursery in Licking, MO. The seed used to establish the seedlings originated from the shortleaf pine seed orchard located on the Womble Ranger District on the Ouachita National Forest in Mound Ida, AR, USA. The seed orchard was established in the early 1960s by grafting to local rootstock scions collected from superior shortleaf pine trees growing in the Mark Twain National Forest in Missouri. Information about the establishment of the seed orchard and the shortleaf pine tree improvement program was reported on by Studyvin and Gwaze (2007).

Shortleaf pine seedling establishment and measurement

In the 0.08-ha circular vegetation plots, thirty shortleaf pine seedlings were hand planted at 3.7 × 7.3 m spacing during the first week of April 2008. Planting within the 0.08-ha plot ensured a buffer of at least 24 m (>height of mature trees) between the experimental unit boundary and the nearest planted seedling. After planting, a numbered metal tag attached to a wire was placed next to each seedling so that they each could be relocated for subsequent determination of survival and growth. The initial basal diameter (measured one cm above the root collar) and height (shoot length) of each seedling were recorded after planting. The 1440 seedlings that were planted initially had an average basal diameter of 3 mm (range 1–7 mm) and an average shoot length of 22 cm (range 4–45 cm). We also noted the presence of browse or other forms of animal and insect damage. Seedlings were reinventoried during the dormant season in 2009, 2010, 2011, and 2013.

Quantifying competing vegetation

To quantify competing vegetation in the regeneration cohort, the tallest competing hardwood seedling growing within a 1.37-m-radius of each planted shortleaf pine seedling was tagged, and the species, basal diameter, and height were recorded during the dormant season in 2010 and 2013. This radius length was selected because it corresponds to the land area theoretically required for a dominant or codominant hardwood sapling having an 11 cm dbh. In theory, only one dominant or codominant tree of this size is expected to persist within this growing space (see Sander et al. 1984). Consequently, the tallest hardwood tree occurring within the 1.37-m-radius of each planted shortleaf pine seedling was considered to be present or a future competitor with each planted seedling.

Data analyses

The probability of individual shortleaf pine seedling survival in relation to overstory density and initial basal diameter was determined using logistic regression for each growing season that data were collected. We used a generalized linear mixed model with a binary distribution, a logit link function, and a random intercept that used the experimental unit as the subject, using PROC GLIMMIX in SAS 9.3 software (SAS Institute, Inc., Cary, NC).

We used linear regression to determine relationships between the independent variable of overstory stocking and several dependent variables: plot-level means of shortleaf pine seedling size (basal diameter and height), the plot-level percentage of total shortleaf pine seedling survival, and the plot-level means of competitor size (basal area and height). Linear regression models were run for data collected in 2008, 2009, 2010, 2011, and 2013 for shortleaf pine seedlings and for data collected in 2010 and 2013 for competitors. Plot-level metrics were calculated and analyzed for all competing species collectively and for the species groups including white oaks (*Quercus alba*, *Q. stellata*), red oaks (*Q. coccinea*, *Q. falcata*, *Q. velutina*), *Carya* spp., *Nyssa* spp., *Acer* spp., *Prunus* spp., and 'other' species (*Fraxinus* spp., *Juglans* spp., *Sassafras* spp.). After determining no relationship between overstory stocking and total seedling survival in any year, we used repeated measures Analysis of Variance with an autoregressive order 1 covariance structure to determine year effects on total seedling survival across all plots. Pair-wise comparisons were evaluated using Tukey's Honestly Significant Difference adjustment.

To describe the composition of the tallest competitors in the reproduction cohort for underplanted shortleaf pine seedlings, we calculated the frequency of occurrence of each species group at the plot-level (n = 30 shortleaf pine seedlings/plot). We created the following five categorical stand stocking classes to cover the entire range of stocking levels encountered in the study: 0 % stocking (n = 13 plots), 0–20 % stocking (n = 7 plots), 20–40 % stocking (n = 11 plots), 40–60 % stocking (n = 12 plots), and >60 % stocking (n = 5 plots). We used Analysis of Variance to test for effects of stand stocking on the

Table 1 Results of logistic regression modeling of individual seedling survival at each measurement period by stocking and initial basal diameter and by initial basal diameter only (as shown in Fig. 3)

Year	Parameter	Num DF	Den DF	Estimate	Standard error	F value	*p* value
Year 1	Intercept	1	46	−0.328	0.284	1.32	0.25
	Initial basal diameter	1	1388	0.333	0.069	23.43	<0.01
	2009 stocking (%)	1	46	0.002	0.005	0.14	0.71
	Intercept	1	47	−0.275	0.243	1.28	0.26
	Initial basal diameter	1	1388	0.333	0.069	23.43	<0.01
Year 2	Intercept	1	46	−0.474	0.277	2.92	0.09
	Initial basal diameter	1	1389	0.257	0.065	15.47	<0.01
	2009 stocking (%)	1	46	0.002	0.005	0.09	0.76
	Intercept	1	47	−0.431	0.236	3.31	0.07
	Initial basal diameter	1	1389	0.257	0.065	15.48	<0.01
Year 3	Intercept	1	46	−0.483	0.262	3.42	0.07
	Initial basal diameter	1	1387	0.234	0.064	13.33	<0.01
	2013 stocking (%)	1	46	−0.001	0.005	0.03	0.87
	Intercept	1	47	−0.505	0.228	4.93	<0.01
	Initial basal diameter	1	1387	0.234	0.064	13.35	<0.01
Year 5	Intercept	1	46	−0.757	0.266	8.12	<0.01
	Initial basal diameter	1	1385	0.232	0.064	12.98	<0.01
	2013 stocking (%)	1	46	0.001	0.005	0.02	0.90
	Intercept	1	47	−0.740	0.231	10.24	0.02
	Initial basal diameter	1	1385	0.232	0.064	12.98	<0.01

frequency of each of the competitor species groups. To determine size differences between underplanted shortleaf pine seedlings and the dominant competitors in 2010 and 2013, we used Analysis of Covariance with plot-level means of basal diameter and height (dependent variables), competitor species group as the independent variable, and overstory stocking as the covariate. In addition, we used each seedling pair (shortleaf pine and the dominant competitor) to calculate the difference in height in the year 2013 ($HTDIFF_{2013}$), as well as the difference in the annual height growth increment between 2010 and 2013 (AHGDIFF). We used Analysis of Covariance to determine the effects of competitor species group and overstory stocking on $HTDIFF_{2013}$, and AHGDIFF, with overstory stocking as the covariate.

We used the plot-level longitudinal data of shortleaf pine size (basal diameter and height) to project seedling growth into the future (thirteen years after planting) using two exponential model forms ($y = y_0 + a(e^{(bx)})$ and $y = a(e^{(bx)})$). Because overstory stocking affected the growth rate of shortleaf pine seedlings, separate models were fit for each of the five categorical stand stocking classes described above.

Results

Shortleaf pine seedling survival

Logistic models of seedling survival at the end of each year included the basal diameter at the time of planting as a significant variable, but overstory stocking was not significant in any of the models (Table 1). After the first growing season, seedlings >5 mm basal diameter had at least 80 % probability of survival; after five growing seasons, seedlings had at least 50 % probability of survival with initial planting diameter of around 3.5 mm (Fig. 1). The percentage of total seedling survival at the end of each year was not

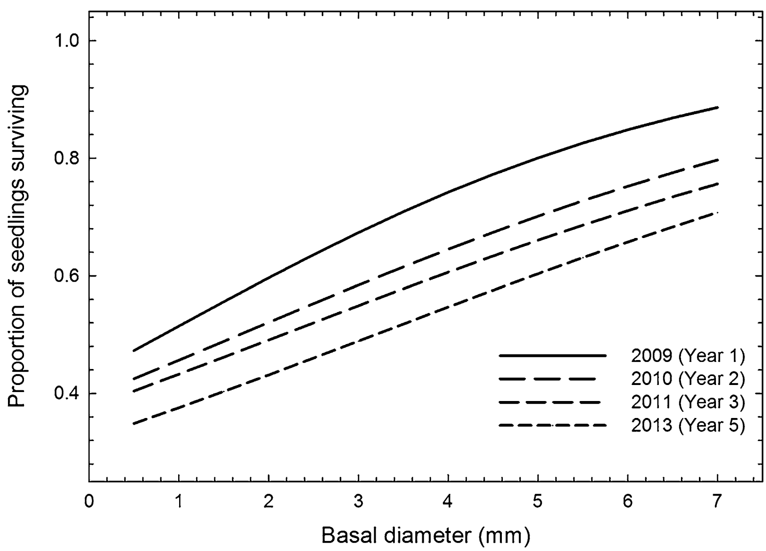

Fig. 1 Probability of seedling survival at the end of each year based on basal diameter at time of planting

significantly related to overstory stocking. Shortleaf pine seedling survival was 67.1, 58.8, 55.6, and 50.2 % following the first, second, third, and fifth growing seasons, respectively, although survival did not significantly decrease after the second growing season.

Shortleaf pine seedling growth

At the time of planting, plot-level means for basal diameter ranged from 2.67 to 3.75 mm, with a mean of 3.18 mm and standard error of 0.03 mm. There was no relationship between the overstory stocking and the basal diameter at the time of planting (Table 2). At the time of planting (2008), the plot-level means for seedling height ranged from 16.03 to 28.13 cm, with a mean of 21.51 cm, a standard error of 0.36 cm, and no relationship between seedling height and overstory stocking.

There were significant, negative relationships between overstory stocking and seedling size (basal diameter and height) in each of the subsequent measurement periods (Table 2; Fig. 2). Overstory stocking explained 22 % of the variation in shortleaf pine basal diameter after the first growing season (2009) and accounted for 50, 43, and 51 % of the variation in basal diameter after the second, third, and fifth growing seasons, respectively. Seedling height was more closely related to overstory stocking after the first growing season than was basal diameter, with overstory stocking explaining 39, 47, 45, and 54 % of the variation in seedling height after the first, second, third, and fifth growing seasons, respectively. After five growing seasons (2013), basal diameters ranged from 4.47 mm at high stocking levels to 40.47 mm with no canopy cover and seedling heights ranged from 39.4 to 219.0 cm.

Shortleaf pine competitors

By the fifth growing season, overstory stocking had significant, negative relationships with the heights of all species groups of competitors except the 'other' group ($p = 0.51$)

Table 2 Results of simple linear regression relationships between overstory stocking (%) and shortleaf pine seedling basal diameter (mm) and height (cm)

Year	*m*	*b*	RMSE	F value	*p* value	R^2
Dependent variable—shortleaf pine basal diameter (mm)						
Planting	3.16	0.00	0.24	0.14	0.71	0.00
Year 1	4.57	−0.01	0.65	15.35	<0.01	0.25
Year 2	9.55	−0.07	1.54	45.69	<0.01	0.50
Year 3	14.18	−0.10	2.92	33.34	<0.01	0.43
Year 5	25.70	−0.25	5.98	47.94	<0.01	0.51
Dependent variable—shortleaf pine height (cm)						
Planting	22.36	−0.02	2.44	2.86	0.10	0.06
Year 1	32.44	−0.10	3.51	28.37	<0.01	0.38
Year 2	56.77	−0.36	8.86	41.14	<0.01	0.47
Year 3	88.79	−0.59	15.67	37.28	<0.01	0.45
Year 5	154.77	−1.31	28.83	54.95	<0.01	0.54

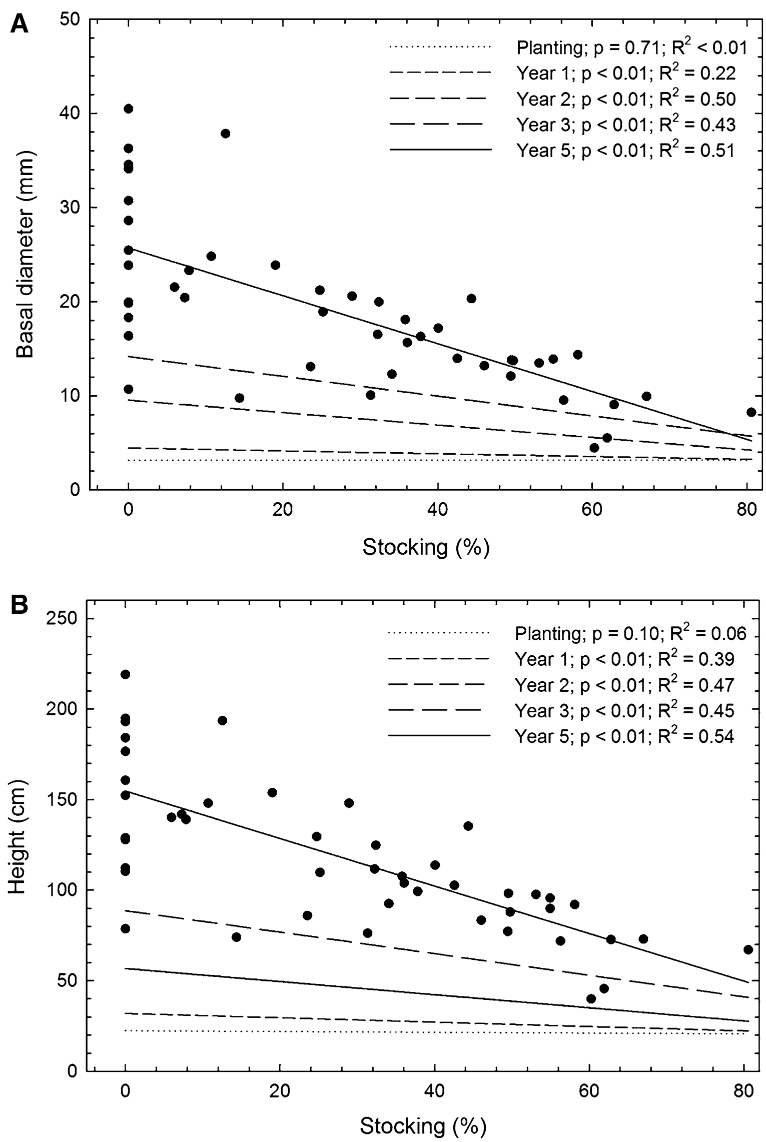

Fig. 2 Relationships between residual overstory stocking and underplanted shortleaf pine **a** basal diameter and **b** height for different years after underplanting (at planting and after 1, 2, 3, and 5 growing seasons). All relationships are of the form $y = m + bx$, and only data points from Year 5 are shown to improve clarity. Relationships from planting use stocking levels at the time of planting (2008), relationships from Years 1 and 2 use stocking levels from Year 1 (2009), and relationships from Years 3 and 5 use stocking levels from Year 5 (2013)

(Fig. 3). Hickories and the white oaks were the most affected by overstory stocking, with stocking explaining 45 and 44 % of the variation in height in those respective species groups. Besides the 'other' group, *Nyssa* and *Prunus* had the weakest relationships with overstory stocking, explaining 16 and 17 % of the variation in seedling height,

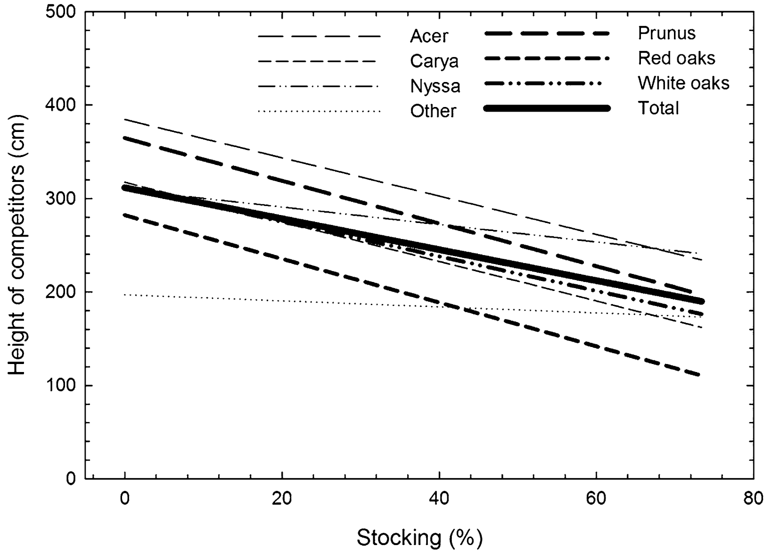

Fig. 3 Relationships between overstory stocking and heights of different species groups of competitors within 1.37 m of underplanted shortleaf pine seedlings in after five growing seasons (2013)

respectively. Seedlings in the *Acer* and *Prunus* species groups were the tallest, particularly when overstory stocking was <40 %.

Nyssa species were most frequently the tallest competitor of shortleaf pine seedlings (31 % of seedling competitors), followed by white oaks (20 % of competitors) and *Acer* species (13 % of competitors). Among the competing species groups, the proportional frequency significantly differed among overstory stocking classes for *Carya* species and for *Prunus* species. *Carya* species comprised <6 % of the competitors where overstory stocking was <20 % but 15 % for overstory stocking levels >60 %. In contrast, *Prunus* species comprised 15 % of the proportional frequency on the plots with 0 % stocking, but were 1 % at overstory stocking levels >60 %.

Table 3 Results of simple linear regression relationships between overstory stocking (%) and plot-level basal diameters and heights of underplanted shortleaf pine seedlings and the tallest competitors within 1.37 m of each seedling in 2010 (after two growing seasons) and in 2013 (after five growing seasons)

Variable	*m*	*b*	RMSE	F value	*p* value	R^2
Independent variable—stand stocking (%)						
Year 2 SLP basal diameter	9.55	−0.07	1.54	45.69	<0.01	0.50
Year 2 Comp basal diameter	25.03	−0.10	3.76	18.82	<0.01	0.29
Year 5 SLP basal diameter	25.70	−0.25	5.98	47.94	<0.01	0.51
Year 5 Comp basal diameter	41.08	−0.21	5.51	35.60	<0.01	0.44
Year 2 SLP height	56.77	−0.36	8.86	41.14	<0.01	0.47
Year 2 Comp height	213.54	−0.91	27.04	27.67	<0.01	0.38
Year 5 SLP height	154.77	−1.31	28.83	54.95	<0.01	0.54
Year 5 Comp height	310.40	−1.58	35.10	53.66	<0.01	0.54

SLP shortleaf pine, *Comp* competitors

Shortleaf pine growth relative to competitors

Underplanted shortleaf pine seedlings were shorter than the tallest competitor within 1.37 m after the second (2010) and fifth (2013) growing seasons. Results from ANCOVA showed the plot-level mean basal diameters of both shortleaf pine and their tallest competitors were significantly reduced by overstory stocking in 2010 ($p < 0.01$) and in 2013 ($p < 0.01$) (Table 3; Fig. 4a). Competitors had larger basal diameters than shortleaf pine

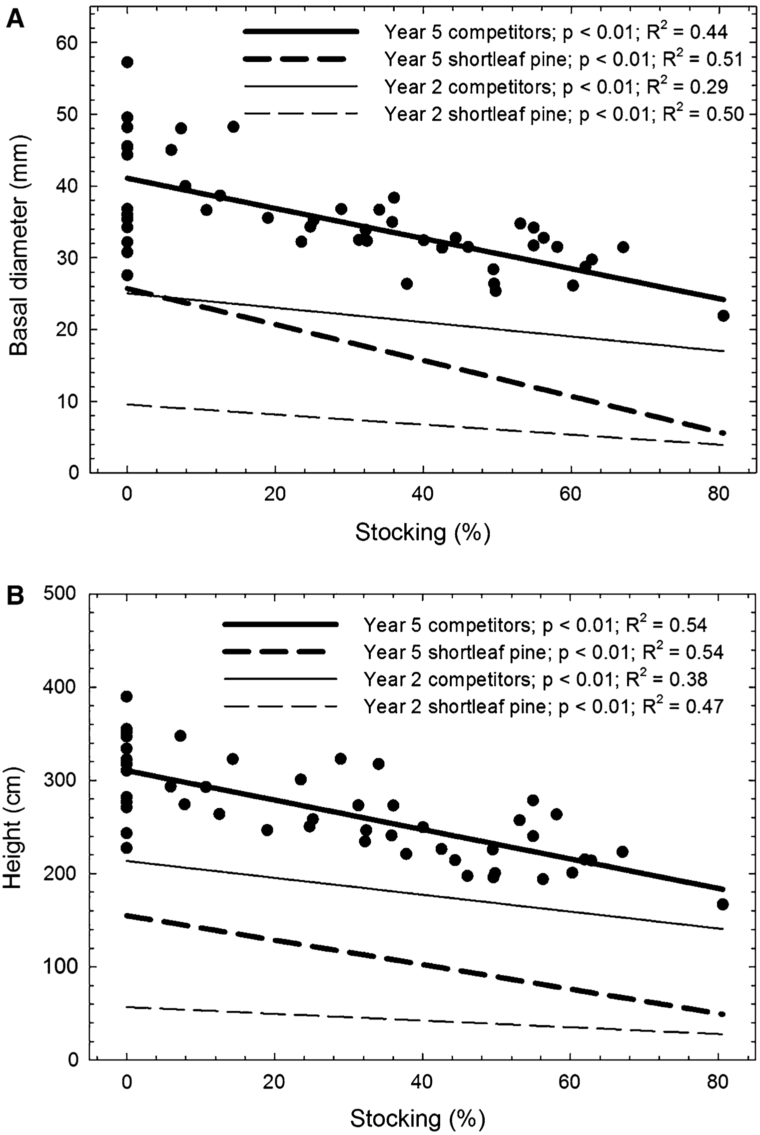

Fig. 4 Relationships between overstory stocking and **a** basal diameter and **b** height for plot-level means of underplanted shortleaf pine seedlings and competitors for 2 and 3 years after planting. *Scatter plots* are only shown for the competitors in Year 5 (2013) to improve clarity

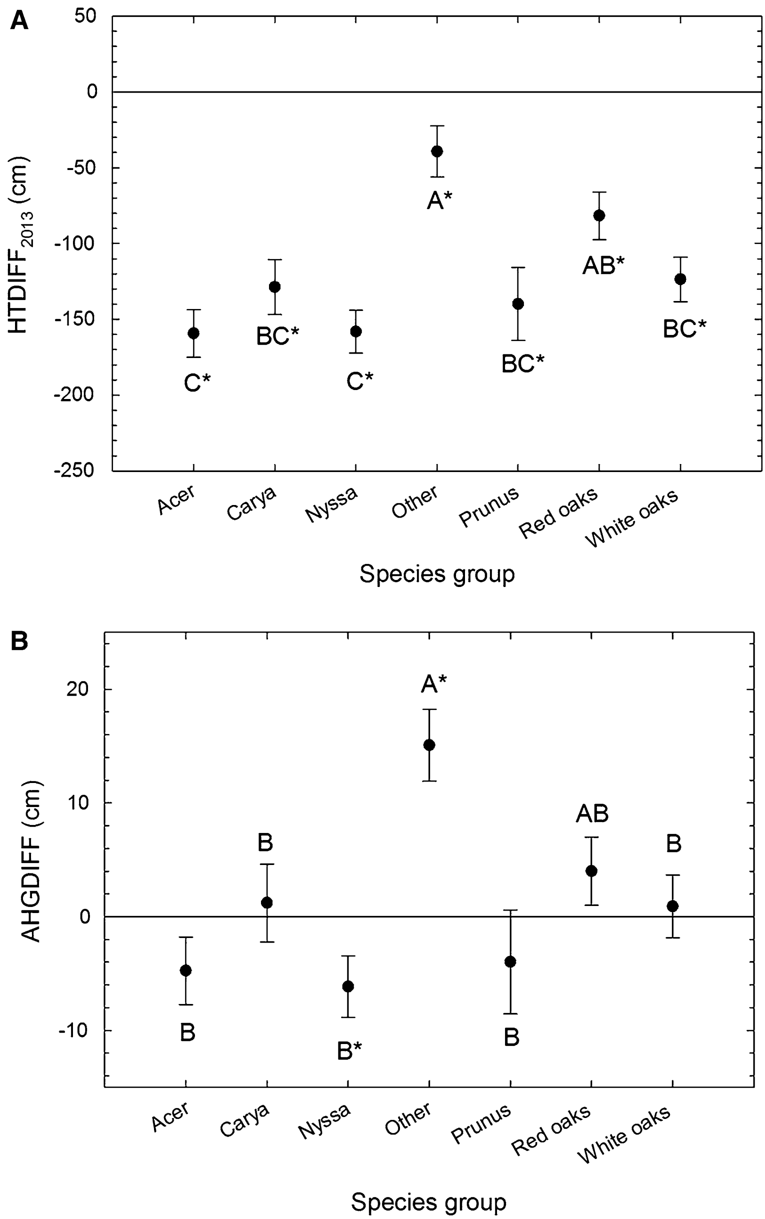

Fig. 5 Least square means (± 1 standard error) of the **a** height difference in the year 2013 ($HTDIFF_{2013}$) and in the **b** annual height growth difference (AHGDIFF) from the year 2010 to the year 2013 between shortleaf pine seedlings and the tallest competitor within 1.37 m for major species groups. The *zero line* represents no difference between shortleaf pine and competitors; positive values represent advantage to shortleaf pine seedlings

seedlings in 2010 ($p < 0.01$) and in 2013 ($p < 0.01$). The effect of overstory stocking on basal diameter did not differ for the two species groups in 2010 ($p = 0.15$) or in 2013 ($p = 0.40$).

Similarly, the plot-level mean heights of both shortleaf pine and their tallest competitors within 1.37 m were significantly reduced by overstory stocking after the second ($p < 0.01$) and fifth ($p < 0.01$) growing seasons (Table 3; Fig. 4b). Competitors were significantly taller than shortleaf pine seedlings at both measurement periods ($p < 0.01$). After the second growing season, the height of competitors was more strongly affected by overstory stocking than was the height of the shortleaf pine seedlings ($p = 0.01$), and the relationships of height to overstory stocking were not significantly different for the two species types after the fifth growing season ($p = 0.23$).

Overstory stocking did not affect the height difference between the shortleaf pine seedlings and competing hardwoods ($HTDIFF_{2013}$, $p = 0.51$) and there was no interaction between species group effect and stocking ($p = 0.14$). Shortleaf pine seedlings were significantly shorter than all other species groups (Fig. 5a). The average heights of seedlings within the 'other' species group were <50 cm greater than shortleaf pine, whereas the average heights of species in the *Acer* and *Nyssa* groups were >150 cm taller than shortleaf pine. The ANCOVA results indicated that the interaction between stocking and species group was not significant ($p = 0.23$) for the annual height growth difference between shortleaf pine seedlings and competing hardwoods (AHGDIFF). However, the 'other' species group and the *Nyssa* species group had annual height growth increments that differed from shortleaf pine from the second to the fifth growing season, with shortleaf pine growing 15 cm more per year than 'other' species and 6 cm less per year than *Nyssa* species during that time period (Fig. 5b). Stand stocking in 2013 significantly affected the difference in annual height growth between shortleaf pine and the nearest competitors ($p = 0.04$), with the mean relative annual height growth of 7.9 cm in clear cuts decreasing by 0.25 cm with each additional unit of stand stocking.

Projected shortleaf pine growth

We fit two exponential growth models to the basal diameter and height data and projected growth through 13 years. The model form $y = y_0 + a(e^{(bx)})$ (Model 1) resulted in slightly lower R^2 values than the model form $y = a(e^{(bx)})$ (Model 2), calculated as $(1 - SSE/SST)$ (Table 4). Previous research (Dey and Hartmann 2005) suggested that shortleaf pine has a 50 % probability of surviving fire when the basal diameter is 30 mm, a 75 % probability of survival at around 60 mm, and a 90 % probability of survival at around 100 mm. Using these thresholds, we projected with Model 1 (Fig. 6a) that the basal diameter of shortleaf pine seedlings would exceed 30 mm 5 years after planting at 0 % stocking and 10 years after planting at >60 % stocking. According to Model 1, seedling basal diameter is projected to exceed 100 mm 10 years after planting at 0 % stocking but would not reach that size threshold within our projection period at >60 % stocking. We projected with Model 2 (Fig. 6b) that the basal diameter of planted shortleaf pine seedlings would exceed 30 mm in 5 years after planting at 0 % stocking and 8 years after planting at >60 % stocking (Fig. 6). With Model 2 seedling basal diameter will exceed 100 mm 8 years after planting at 0 % stocking and 12 years after planting with >60 % stocking.

Table 4 Parameters and fit of models used for projecting seedling size through 13 growing seasons using two different models forms, where x = years after underplanting and individual models were fit for each stocking class

Response	Stocking	Parameter			R^2
		y_0	a	b	
Model 1: $y = y_0 + a(e^{(bx)})$	0	−12.68	15.23	0.19	0.76
	0–20	−11.37	13.91	0.18	0.78
	2–40	−9.21	11.81	0.17	0.68
	40–60	−16.39	19.10	0.09	0.75
	>60	−3.08	5.80	0.23	0.47
Model 2: $y = a(e^{(bx)})$	0		4.29	0.37	0.90
	0–20		3.99	0.35	0.91
	20–40		3.68	0.33	0.88
	40–60		3.51	0.27	0.93
	>60		3.15	0.31	0.77

Discussion

Shortleaf pine seedling survival

The hypothesis that shortleaf pine seedling survival will increase with decreasing overstory density was not supported. There was insufficient evidence that the survival of underplanted seedlings was reduced by the shading caused by the overstory canopy (Table 1). This was unexpected because shortleaf pine is considered to be shade intolerant and expected to exhibit poor survival when under a canopy (Lawson 1990). However, Shelton and Cain (2000) noted that shortleaf pine seedlings appear to exhibit some level of shade tolerance that allows them to persist for a few years under a partial overstory, particularly underneath the relatively open canopy created by pine crown architecture. Survival rates observed in our study were similar to those reported by Gwaze et al. (2007b), who examined the performance of open-grown, bare-root shortleaf pine seedlings from five different states in the central and eastern USA planted in provenance trials on the Sinkin Experimental Forest. Our findings suggest that the underplanting of shade-intolerant species such as shortleaf pine under a partial overstory of hardwoods will not adversely affect survival during the first five growing seasons.

There was evidence in support of the hypothesis that planting stock with a larger initial basal diameter would exhibit significantly greater survival than stock with a smaller initial basal diameter (Table 1; Fig. 1). Although we did not measure the root mass or volume prior to planting, larger basal diameters have been correlated to a greater root mass in hardwood seedlings (Knapp et al. 2006). Barnett and Brissette (2004) reported that container-grown shortleaf pine stock exhibited greater survival than bare-root stock, a result that they attributed to larger root systems of the container stock. Container-grown stock generally have a more balanced root:shoot ratio which reduces planting shock (Struve and Joly 1992). We also observed that the beneficial effect of having a larger basal diameter at the time of planting was persistent throughout the study and confirmed by the observation that the initial basal diameter remained a significant effect in survival models after five growing seasons (Table 1; Fig. 1).

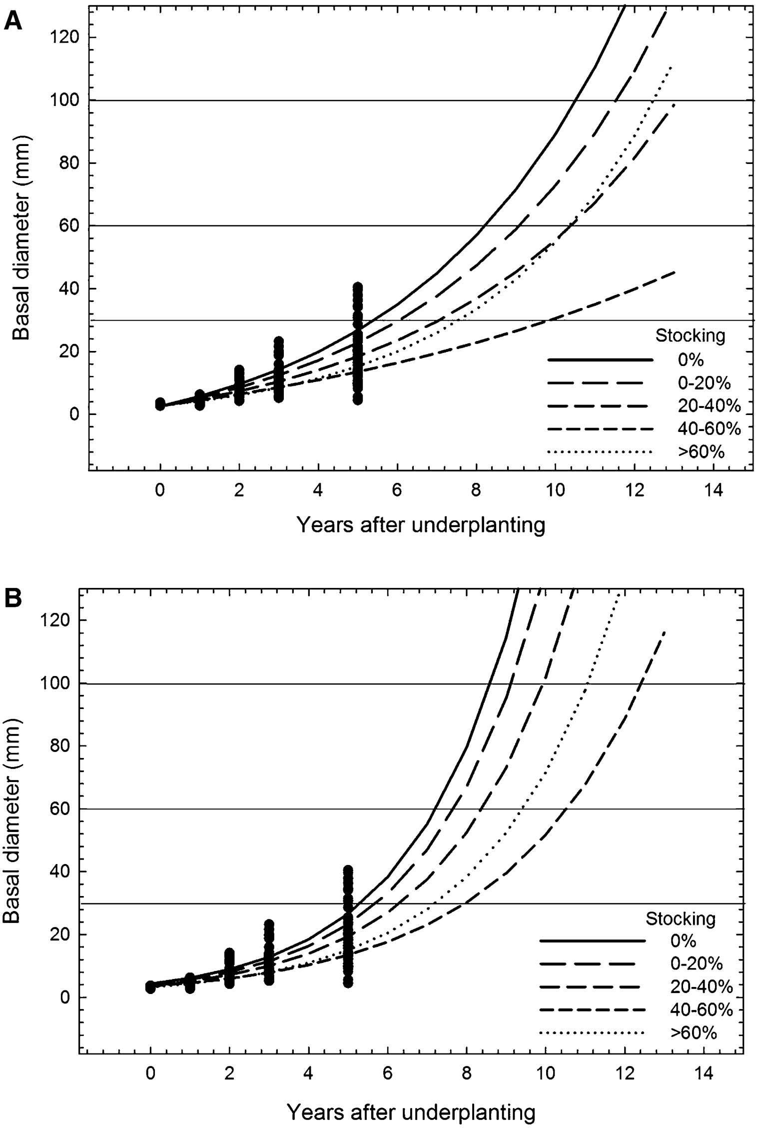

Fig. 6 Projection of shortleaf pine seedling basal diameter for 13 years after planting using the model forms **a** $y = y_0 + a(e^{(bx)})$ and **b** $y = a(e^{(bx)})$. *Horizontal lines* represent 30, 60, and 100 mm basal diameter, previously reported to relate to approximately 50, 75, and 90 % survival probabilities, respectively, of shortleaf pine seedlings in prescribed burns (Dey and Hartmann 2005)

Growth of shortleaf pine seedlings compared to hardwood competitors

There was evidence in support of the hypothesis that increasing the residual overstory density would decrease both the basal diameter and the height (shoot length) growth of underplanted shortleaf pine seedlings (Table 2; Fig. 2). The strength of the relationships between the basal diameter or height and the residual overstory increased over time, as evidenced by the increasing R^2. The height growth that occurred during the first five growing seasons under a residual overstory stocking of 0 % was similar to the height growth of open-grown bare-root shortleaf pine seedlings elsewhere in the Missouri Ozark Highlands where competing hardwoods within a 1-m radius of each seedling were controlled with glyphosate (Ponder 2004). Gwaze et al. (2007a) reported similar 5th year heights for shortleaf pine seedlings planted in a clearcut stand on similar soils on the Salem Ranger District of the Mark Twain National Forest in southeastern Missouri, USA, but also reported that heights were 1.5 times greater where a subsoiling treatment to loosen the soil had been applied prior to planting. Brandeis et al. (2001) reported that moderately-tolerant conifers including *Abies grandis*, *Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla* underplanted in *Pseudotsuga menziesii–Abies grandis* stands benefited from a reduction of competitors in the understory in the western USA.

As suggested by Paquette et al. (2006), the growth of the competing hardwoods was also reduced with increasing overstory stocking and the growth reductions were similar in magnitude as for the shortleaf pine seedlings (Table 3; Fig. 4). Five years after planting, the shortleaf pine seedlings remained about 0.5 to 1.5 m shorter than competing hardwoods, but the annual height increment of the pine seedlings was about the same as the primary hardwood competitors (*Nyssa*, *Quercus*, *Acer*, and *Prunus*) across a wide range of residual stocking levels. This was counter to the hypothesis that shortleaf pine seedling growth would be reduced more with increasing overstory stocking than would hardwood reproduction. It was also counter to early findings of Brinkman and Liming (1961), who reported that increasing the residual overstory density reduced the growth of shortleaf pine seedlings more than that of competing hardwood regeneration and concluded that the shoot growth of oaks would exceed that of shortleaf pine if the residual stand basal area remained above 6 m^2 ha^{-1}. This basal area threshold is the equivalent to approximately 20 % stocking in oak-hickory stands (Gingrich 1967). This result was surprising because shortleaf pine is classed as shade intolerant (Lawson 1990).

It appears that there were two reasons that the shortleaf pine seedlings remained shorter than competing hardwoods. First, the shortleaf pine seedlings were shorter than the hardwood competitors when the study was initiated. The hardwood competitors were primarily comprised of advanced regeneration that was present prior to harvest and persisted or resprouted following top-kill during harvest. In contrast, the shortleaf pine seedlings were true seedlings and approximately 20 cm tall when planted. Second, there appeared to be a lag in the first-year growth of the shortleaf pine seedlings compared to subsequent years (Fig. 5a, b) that was likely due to a combination of planting shock and to the initial root growth at the expense of shoot growth during the first growing season. The hardwood competitors were already established as advance reproduction and as seedlings, seedling sprouts, and small saplings (capable of producing stump sprouts when cut) prior to the initiation of the study and were better able to respond to the overstory release. Despite this apparent delay in growth during the first and possibly the second growing season, the shortleaf pine seedlings were growing at a similar rate as the hardwood competition during the last three growing seasons (Fig. 5b). This also suggests that even when there is an initial size or stock type disadvantage, shortleaf pine seedlings can grow at a similar rate as the hardwood competition once they have overcome planting shock.

Even though the planted shortleaf pine seedlings appeared to be growing at the same rate as the competing hardwood reproduction during the final three growing seasons, the fact that they remained shorter suggests that they will need to eventually be released with additional treatments (Brandeis et al. 2001; Paquette et al. 2006). However, our results suggest that releases do not need to be performed for several years after underplanting regardless of overstory stocking or understory competition levels. Releases will become necessary at canopy closure of the reproduction cohort, which generally occurs about 10–15 years after establishment under an open canopy but longer under a partial canopy (Dey et al. 2012; Dey 2014). During the period prior to canopy closure, individual shortleaf pine seedlings can be released by mechanically or chemically removing competing hardwoods in their immediate growing space to ensure their future survival and continued growth. This suggests that there is considerable flexibility for establishing shortleaf pine seedlings even where there is intense hardwood competition from the regeneration cohort shortly after planting.

Prescribed fire is increasingly being used as a restoration tool in pine–oak woodlands to affect both stand density and herbaceous and woody species composition. It also has been postulated that prescribed fire would benefit shortleaf pine by preferentially controlling some of the competing hardwoods (Cain and Shelton 2002). Shortleaf pine seedlings are considered to be fire adapted because dormant buds occurring along a J-shaped crook above the root collar are capable of surviving low-intensity dormant-season ground fires and producing sprouts if top killed (Shelton and Cain 2000; Lilly et al. 2012). Moreover, shortleaf pine saplings have nearly a 100 % probability of not being top killed by low-intensity dormant-season ground fires if they have a basal diameter >10 cm (Dey and Hartmann 2005). Thus, a restoration strategy would be to delay the application of prescribed fire until an acceptable proportion of the seedlings are sufficiently large to escape being top killed. Growth projections made with regression models (Table 4; Fig. 6) suggested that for our study region, planted shortleaf pine seedlings need to be 8–12 years old to be sufficiently large to avoid being top killed by prescribed low-intensity ground fire (Dey and Hartmann 2005). This time period also compatible with the hypothesis of Stambaugh et al. (2007) who proposed that an 8–12-year fire-free period is required for shortleaf pine recruitment in the Ozark Highlands. Their hypothesis was based on a dendrochronological examination of fire scars on shortleaf pine stumps of large pine trees cut during the extensive timber harvesting period in the Missouri Ozarks, most of which originated when the fire return interval was 8 to 15 years or longer. Our regression models also imply that, on average, half of the planted shortleaf pine seedlings will be smaller than the threshold diameter and are more likely to be top killed by the prescribed fire and would resprout. Lilly et al. (2012) found that >37 % of shortleaf pine seedlings top killed by prescribed fire resprouted.

Although shortleaf pine seedlings have the ability to resprout, it is unlikely that shortleaf pine sprouts can grow at similar rates as hardwood sprouts. Cain and Shelton (2000) and Lilly et al. (2012) each found that shortleaf pine sprouts originating from prescribed fire under a partial overstory canopy regained only about one third to one half of their initial height one growing season after prescribed fire. In contrast, the sprouts of oaks and other hardwoods following dormant-season prescribed fires are capable of returning to their preburn height or basal diameter within a single growing season (Cain and Shelton 2000). Our data also suggested that where the overstory stocking is >60 %, underplanted shortleaf pine seedlings may not grow large enough to escape being top killed by fire prior to canopy closure of the reproduction cohort. This suggests that mechanical or chemical releases may be warranted prior to applying prescribed fire to ensure that shortleaf pine seedlings are sufficiently large to not be top killed.

Increasing overstory stocking appears to affect the species composition of competing hardwoods. As the overstory stocking increased there was a reduction in the proportion of *Prunus* and an increase in the proportion of *Carya* in the reproduction cohort. We observed that the height growth of *Nyssa* and of those in “other” species category appeared to be the least affected by an increasing overstory stocking (Fig. 3). This suggests that the composition of the principal hardwood competitors would shift to those that are more shade tolerant mixture with increasing residual overstory stocking levels. This also suggests that varying the residual overstory is a strategy for favoring different hardwoods where mixed-species stands containing both shortleaf pine and hardwoods is desired.

Conclusions and restoration implications

Findings from this study have many implications for restoring shade-intolerant conifers such as shortleaf pine where retaining a partial overstory is an important objective for meeting restoration goals. First, the survival rate of underplanted seedlings (50 % after five years) is not decreased by retaining a partial overstory. Rather, the most important measured factor positively related to survival of the underplanted trees was initial basal diameter. In this study, survival increased with increasing basal diameter and survival probability exceeded 50 % if the initial basal diameter was >4 mm. Retaining a partial overstory will decrease the growth of underplanted seedlings; diameter or height growth reductions of 50 % or more can to be expected by the fifth year after underplanting where the overstory stocking exceeds 50 % compared to seedlings planted where the overstory was removed. Despite these growth reductions, the growth of competitors in the understory is also reduced by retaining a partial overstory competition, even for species that have a greater shade tolerance than shortleaf pine. Except during the first two growing seasons, the growth rates of underplanted shortleaf pine were comparable to those of moderate to shade-tolerant hardwood competitors at each overstory stocking level during the third through fifth growing seasons. Releasing the shortleaf pine seedlings from hardwood competition appears to be inevitable, but because of the similar growth rates of shortleaf pine seedlings and competitors, there is flexibility in the timing when releases are performed. Releases can be delayed until the canopy reproduction cohort closes. Because of the reduced growth of underplanted seedlings, the application of prescribed fire applied for restoring other ecosystem functions must be delayed for several years to allow underplanted shortleaf pine seedlings to exceed a threshold basal diameter of 10 cm so they are not likely to be top killed. Our data suggest for this region that this occurs about 8–12 years after planting depending on the overstory density.

Appendix

See Table 5.

Table 5 Pre-treatment, post-treatment, and post-storm basal area (m^2 ha^{-1}) and stocking (Gingrich 1967) by experimental unit

Experimental unit	Pre-treatment (2006)		Post-treatment (2008)		Post-storm (2009)	
	Basal area	Stocking	Basal area	Stocking	Basal area	Stocking
1	26	96	6	19	5	13
2	30	105	15	47	16	49
3	30	111	12	42	13	45

Table 5 continued

Experimental unit	Pre-treatment (2006)		Post-treatment (2008)		Post-storm (2009)	
	Basal area	Stocking	Basal area	Stocking	Basal area	Stocking
4	37	136	0	0	0	0
5	26	103	0	0	0	0
6	34	131	8	31	6	25
7	41	147	16	52	15	47
8	35	131	0	0	0	0
9	26	103	8	26	1	4
10	34	130	23	78	15	52
11	26	104	13	44	11	40
12	27	100	24	82	22	73
13	34	129	0	0	0	0
14	29	110	21	69	10	36
15	30	110	24	80	18	58
16	33	126	17	54	5	15
17	31	112	0	0	0	0
18	29	113	18	61	18	59
19	29	111	9	31	7	24
20	44	149	21	58	19	55
21	19	86	0	0	0	0
22	29	116	14	50	14	51
23	33	118	16	51	10	32
24	29	104	21	64	22	65
25	26	101	18	60	16	55
26	27	102	0	0	0	0
27	28	103	15	49	8	27
28	37	124	26	80	15	47
29	36	141	26	91	17	63
30	27	101	0	0	0	0
31	28	100	14	46	14	44
32	23	87	16	50	2	7
33	41	140	24	72	11	34
34	36	129	24	79	20	63
35	38	130	0	0	0	0
36	36	127	0	0	0	0
37	28	109	11	38	2	6
38	25	103	16	55	11	40
39	24	98	11	37	9	31
40	24	91	11	32	9	30
41	30	113	14	45	6	21
42	33	116	17	51	14	41
43	27	106	15	51	4	13
44	27	99	21	70	10	32
45	22	82	5	16	3	10

Table 5 continued

Experimental unit	Pre-treatment (2006)		Post-treatment (2008)		Post-storm (2009)	
	Basal area	Stocking	Basal area	Stocking	Basal area	Stocking
46	28	101	0	0	0	0
47	33	114	0	0	0	0
48	37	133	12	36	5	14

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