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Relating the survival and growth of planted longleaf pine seedlings to microsite conditions altered by site preparation treatments

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ABSTRACT

Pine plantations in the southeastern United States are often created using site preparation treatments to alleviate site conditions that may limit survival or growth of planted seedlings. However, little is understood about how site preparations affect longleaf pine (*Pinus palustris* P. Miller) seedlings planted on wet sites. In a 2-year study (2004 and 2005) on poorly drained, sandy soils of Onslow County, North Carolina, we examined the effects of common site preparation treatments on microsite conditions and quantified relationships between microsite conditions and longleaf pine seedling survival and growth. Treatments used in the study included site preparations designed to control competing vegetation (chopping and herbicide) combined with those that alter soil conditions (mounding and bedding). During both years, mounding and bedding treatments reduced the amount of moisture within the top 6 cm of soil and increased soil temperatures when compared to flat planting ($p < 0.001$). Soil moisture was inversely related to seedling mortality in 2004 ($r^2 = 0.405$) and inversely related to root collar diameter in 2005 ($r^2 = 0.334$), while light was positively related to root collar diameter in 2005 ($r^2 = 0.262$). Light availability at the seedling level was highest on treatments that effectively reduced surrounding vegetation. Herbicides were more effective than chopping at controlling vegetation in 2004 ($p < 0.001$) and 2005 ($p = 0.036$). Controlling competing vegetation, especially shrubs, was critical for increasing early longleaf pine seedling growth.

1. Introduction

Restoring the longleaf pine (*Pinus palustris* P. Miller) ecosystem is currently a major focus of land managers throughout the southeastern United States. Widespread reduction since European settlement has left longleaf pine occupying approximately 3% of its original range (Frost, 1993; Landers et al., 1995), largely due to land conversion and fire exclusion. Areas still containing longleaf pine may be maintained successfully with natural regeneration and frequent prescribed fire. However, the majority of the original range no longer contains longleaf pine in the overstory to provide seed and therefore requires artificial regeneration (Barnett, 1999).

Land managers in the southeastern United States frequently use site preparation in conjunction with artificial regeneration of southern pine species. Previous studies have demonstrated the effectiveness of various types of site preparation for increasing early growth of loblolly pine (*Pinus taeda* L.) and/or slash pine (*Pinus elliottii* Engelm.) (e.g. Burger and Pritchett, 1988; Nilsson and Allen, 2003; Rahman and Messina, 2006). For example, Knowe et al. (1992) reported that herbicides and chopping increased loblolly pine height (2.65 m) and diameter (4.47 cm) after 4 years of growth when compared to an untreated control (1.46 m, 1.45 cm, respectively). Moreover, studies have indicated that site preparation intensity is positively related to seedling growth (Nilsson and Allen, 2003). Burger and Pritchett (1988) compared the effects of low intensity site preparation (chopping) and high intensity site preparation (windrowing, disc harrowing, and bedding) on loblolly pine seedling response. After two growing seasons, seedling height and diameter were significantly greater on the high intensity treatment (79.9 cm and 2.33 cm, respectively) than on the low intensity treatment (68.5 cm and 1.41 cm, respectively).

Barnett (1992) identifies well-prepared sites as a critical prerequisite for successful artificial regeneration of longleaf pine. Although limited to only a few studies, previous research has demonstrated the beneficial effects of mechanical treatments on survival and growth of planted longleaf pine seedlings (Croker, 1975; Croker and Boyer, 1975; Boyer, 1988). For instance, Boyer (1988) reported greater seedling survival 3 years after planting on sites treated with two passes of mechanical competition control

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(chop or harrow) (73% survival) when compared to sites with one mechanical pass (58% survival). Additionally, plots treated with herbicides shortly after planting resulted in 77% of seedlings in height growth after 3 years, compared to 58% of seedlings in height growth on untreated plots. The importance of competition control for longleaf pine establishment (Wahlenburg, 1946; Boyer, 1990) has prompted additional studies focused on understanding the effects of using herbicides for seedling release (e.g. Nelson et al., 1985; Creighton et al., 1987; Ramsey et al., 2003; Ramsey and Jose, 2004). Although the type of herbicide and method of application vary across published studies, competition control provided by herbicides typically results in improved seedling establishment. Haywood (2000) found that after 3 years of growth, 59% of surviving seedlings had emerged from the grass stage on plots treated with herbicides and only 17% had emerged on untreated check plots. After 5 years, seedlings out of the grass stage were nearly twice as tall on herbicide plots as those on check plots, indicating potentially long-term benefits for stand production.

Although longleaf pine naturally occurs on a range of site types that includes poorly drained flatwoods (Boyer, 1990), wet sites are often planted with faster growing pine species, and artificial regeneration of longleaf pine is commonly restricted to drier soils. Little is understood about how mechanical site preparation influences longleaf pine seedlings on wet sites. Studies on other southern pines have associated greater growth rates with improved drainage following mechanical treatments (e.g. bedding or mounding) on poorly drained sites (Outcalt, 1984; McKee and Wilhite, 1986; Haywood, 1987). For example, in a study in the flatwoods of Florida, Pritchett (1979) found that slash pines planted on bedded sites averaged 1.25 m taller than those planted on burn-only sites after eight growing seasons and suggested that increased drainage within the root zone was responsible for the growth difference. We would expect that improved drainage on wet sites would also benefit longleaf pine seedlings, although we are aware of no studies designed to evaluate the impact of mechanical treatments that alter soil conditions on longleaf pine seedling response.

The effectiveness of a site preparation treatment, in regard to seedling growth and survival, is typically determined by the magnitude of the target seedling's response; the treatment resulting in a higher growth rate or greater survival is considered the better treatment. However, effects of site preparations on seedling response are complex and vary with specific site, seasonal, and climatic conditions. Therefore, to implement site preparation most efficiently, it is important to understand the underlying mechanisms responsible for improving seedling growth and survival. According to Morris and Lowery (1988), two primary functions of site preparation include (1) manipulation of soil conditions and (2) competition control, and they discuss the benefit of separating the effects of each when evaluating site preparation treatments. However, many types of site preparation, especially mechanical treatments such as bedding and mounding, inherently alter both the immediate soil conditions and the abundance of competing vegetation. Therefore, it is necessary to directly quantify resource availability, soil conditions, and abundance of competing vegetation when identifying primary effects of a site preparation treatment.

This study was designed to investigate the effectiveness of common site preparations for use in longleaf pine regeneration on poorly drained soils by relating seedling response to direct measurements of microsite conditions. Our specific objectives were to: (1) quantify soil conditions (moisture and temperature), abundance of competing vegetation, and light availability following low to medium intensity site preparation treatments, and (2) determine relationships between seedling survival/growth and the measured microsite conditions.

2. Materials and methods

2.1. Study area

The study was conducted on Marine Corps Base Camp Lejeune (34°7′N, 77°4′W), in Onslow County, North Carolina. Camp Lejeune is located within the Atlantic Coastal Flatlands Section of the Outer Coastal Plains Mixed Forest Province (Bailey, 1995). The climate is classified as warm humid temperate with an average annual temperature of 17.4 °C and an average annual precipitation of 145 cm (National Climate Data Center, Hofmann Forest Station, 34°5′N, 77°2′W). Study sites were on Leon fine sand (sandy, siliceous, thermic, Aeric Alaquod), which is characterized by light-gray to white sand within the first 30–60 cm, underlain by a dark B horizon of organic accumulation. The B horizon was sufficiently cemented to form a hardpan of varying thickness (15–25 cm). This soil type is poorly drained, with internal drainage impeded by the hardpan layer (Barnhill, 1992; NRCS, 2005). Natural vegetation on Leon sand in this area is longleaf pine savanna, consisting of longleaf pine overstories with herbaceous ground layers dominated by grasses and sedges, including wiregrass (*Aristida* spp.), bluestems (*Andropogon* spp., *Schizachyrium* spp.), panic grasses (*Panicum* spp., *Dichanthelium* spp.), and beak rushes (*Rhynchospora* spp.) (Frost, 2001). Additionally, the ground layer includes a diverse mix of forbs. With frequent fire, this site type is favorable for rare species such as roughleaf loosestrife (*Lysimachia asperulifolia* Poir.) and Venus flytrap (*Dionaea muscipula* Ellis). Common shrubs include *Ilex glabra* (L.) Gray, *Gaylussacia frondosa* (L.), and *Vaccinium* spp.

2.2. Experimental design and implementation

The study design was a randomized complete block consisting of 8 treatments replicated on 5 blocks, for a total of 40 experimental units. Study treatments were randomly assigned to approximately 0.4 ha experimental units with 15 m buffers between plots to reduce treatment overlap. Prior to site preparation, all blocks were harvested and sheared to remove standing vegetation. Eight experimental treatments were applied in August 2003: a check (no site preparation), six treatments that combined two initial vegetation control treatments (chopping or herbicide) with three planting site conditions (flat [no additional treatment], mounding, or bedding), and a more intense treatment including chopping, herbicide, and bedding. In this paper, the treatments are often referred to by their initials as follows: flat or check (F), chopping and flat (CF), herbicide and flat (HF), chopping and mounding (CM), herbicide and mounding (HM), chopping and bedding (CB), herbicide and bedding (HB), and chopping, herbicide, and bedding (CHB). Details on treatment application are given in Knapp et al. (2006), and all treatments were applied before planting.

Study plots were hand planted in December 2003 with container-grown seedlings from locally collected seed. The average root collar diameter of planted seedlings was 6.6 mm with a standard deviation of 1.2 mm. Planting was done by contracted crews who exhibited a wide range of planting skill, occasionally leaving plugs exposed or buried too deeply in the soil. To avoid problems with planting variability, only seedlings planted with the root collar from one centimeter above the soil to three centimeters beneath the soil (i.e. terminal bud exposed and plug buried) were considered for measurement.

2.3. Data collection

In May 2004, a sub-sample of 45 seedlings was identified in each experimental unit by randomly determining a seedling within the first planted row and selecting the other seedlings at a regular interval to distribute selected seedlings evenly throughout the plot. The sample interval was based on the number of rows per plot and approximate number of seedlings per row. This sub-sample of seedlings was used to monitor seedling survival and growth throughout the 2004 and 2005 growing seasons (Knapp et al., 2006). Microsite conditions measured during 2004 and 2005 included soil moisture at a 6 cm depth, soil temperature at a 15 cm depth, soil surface temperature, percent full sunlight at the seedling level, and percent cover of vegetation surrounding selected seedlings.

Soil moisture at 6 cm, soil temperature at 15 cm, and soil surface temperature were measured adjacent to 10 seedlings randomly selected from the measurement sub-sample in each experimental unit. To reduce variability from weather conditions, all measurements within a single block were taken within a two-hour period just after noon. Soil moisture was measured with a Theta Probe Moisture Meter (Delta-T Devices, Ltd.), which was calibrated with soil samples from the study sites. Soil temperatures at the surface and a depth of 15 cm were recorded using digital thermometers at locations directly east of soil moisture measurements. Means for each variable were calculated for the 2004 and 2005 growing seasons based on measurements taken in June, July, and August 2004, and May and August 2005.

Percent full sunlight reaching each selected seedling was calculated by measuring photosynthetically active radiation (PAR) once during each growing season (August 2004 and August 2005) with an AccuPAR model LP-80 ceptometer (Decagon Devices, Inc.). Two readings were taken at the level of each seedling and the mean was recorded. Care was taken to avoid the shadow of selected seedlings. Similarly, two readings were taken approximately one meter above each selected seedling and the mean was recorded for an open sky measurement. Open sky readings were taken immediately following seedling level readings to maintain consistent light conditions. On check treatments, vegetation was often tall enough to require the open sky reading to be taken higher than one meter above the seedlings, but otherwise did not interfere with the measurements. Due to a lack of uniformity on cloudy days, readings were taken under clear sky conditions. Percent full sunlight was calculated with Eq. (1):

$$Y = \left(\frac{\mathrm{PAR_{below}}}{\mathrm{PAR_{above}}}\right) \times 100 \tag{1}$$

where Y is percent full sunlight, $\mathrm{PAR_{below}}$ is the average seedling level light reading, and $\mathrm{PAR_{above}}$ is the average open sky light reading for each seedling.

Competing vegetation immediately surrounding 15 seedlings selected from the sub-sample on each experimental unit, including the 10 associated with soil moisture/temperature measurements, was quantified during August 2004 and August 2005. Approximately 1 m^2 circular plots (0.6 m radius) were established around selected seedlings to determine percent cover of vegetation within each sampling plot. Visual estimates of percent cover were made for total vegetation and the following plant groups: ferns, forbs, shrubs, and graminoids. The cover classes used were modified from the North Carolina Vegetation Survey (Peet et al., 1998), as follows: (1) <1%, (2) 1–2%, (3) 3–5%, (4) 6–10%, (5) 11–25%, (6) 26–50%, (7) 51–75%, (8) 76–90%, and (9) 91–100%.

2.4. Data analysis

For each growing season (2004 and 2005), means of soil moisture at 6 cm, soil temperature at 15 cm, soil surface temperature, percent full sunlight, and percent cover of total vegetation and each vegetation group were analyzed with analysis of variance using PROC GLM in SAS (SAS Institute, 2003). The analysis was conducted in two ways: (1) all eight treatments were used as factors to determine differences among the treatment combinations, and (2) the treatment with both chopping and herbicide (CHB) and the check (F) were disregarded, creating a 3×2 factorial analysis of variance to distinguish between effects of vegetation control treatments (chopping or herbicide) and of the planting site conditions (flat planting, mounding, or bedding). Significant differences among treatments were determined using Tukey's LSD post hoc test. When necessary, transformations were used to normalize data prior to analysis.

We used regression analysis to determine relationships between dependent variables (seedling mortality and root collar diameter) and the environmental variables measured in each growing season (soil moisture at 6 cm, soil temperature at 15 cm, soil surface temperature, percent full sunlight, and total percent cover). Because percent full sunlight and vegetation cover were measured in August 2004 and 2005 (8 and 20 months after planting, respectively), we used seedling mortality and root collar diameter measurements from 8 to 20 months after planting for the regression analysis. Scatterplots and linear regression were used to determine the type and strength of relationships between the dependent variables and each environmental variable. Additionally, we used multiple regression analysis with all independent variables to create predictive models for seedling mortality and root collar diameter after 20 months of growth (August 2005 data). Percent cover of separate plant groups was used to create the predictive models, and square root transformations were used to normalize the data for each plant group. Significant variables were determined using Mallow's Cp method of variable selection (Mallows, 1973; Ott and Longnecker, 2001), and many models were tested to determine the best fit. We used SAS (SAS Institute, 2003) and SYSTAT (SYSTAT Software Inc., 2002) software for the analyses, with a level of statistical significance at $\alpha = 0.05$.

3. Results

3.1. Soil moisture and temperature

One-way ANOVA indicated that there were significant differences in the amount of moisture within the upper 6 cm of the soil among the eight treatment combinations (Table 1). In 2004, HF had greater soil moisture than any other treatment, followed by F and CF ($F_{7,28} = 12.1$, $p < 0.001$). In 2005, HF, F, and CF had significantly more moisture in the soil than any of the other treatments ($F_{7,28} = 7.3$, $p < 0.001$). The 3×2 factorial ANOVA indicated there was no significant interaction between planting site condition and vegetation control treatments in 2004 ($F_{2,20} = 1.9$, $p = 0.175$) or 2005 ($F_{2,20} = 2.7$, $p = 0.093$). Among the planting site conditions, bedding and mounding reduced soil moisture by at least 10% when compared to flat treatments in both 2004 and 2005 (Table 2). Between the vegetation control treatments, the herbicide treatment resulted in more soil moisture than the chop treatment in 2004 ($F_{1,20} = 4.7$, $p = 0.043$), although there was no difference in 2005 ($F_{1,20} = 0.0$, $p = 0.997$).

Soil temperature at 15 cm also significantly differed among the treatment combinations in both 2004 ($F_{7,28} = 6.8$, $p < 0.001$) and 2005 ($F_{7,28} = 10.3$, $p < 0.001$) (Table 1). The greatest temperatures in 2004 were on CM and HM, while the lowest temperature was on the check (F). In 2005, the same trend continued, with the greatest temperature on CM, HM, and CB, and the lowest on F. There was no significant interaction between planting site condition and vegetation control treatments in 2004 ($F_{2,20} = 0.3$, $p = 0.730$) or 2005 ($F_{2,20} = 2.2$, $p = 0.134$). In 2005, mounded sites had the greatest temperatures among planting site conditions, although bedding also raised temperatures when compared to flat sites

Table 1
Least square means of percent soil moisture at 6 cm, soil temperature (°C) at 15 cm, and soil surface temperature (°C) for each treatment combination in 2004 and 2005

Treatment	Soil moisture (%) at 6 cm				Soil temperature (°C) at 15 cm				Soil surface temperature (°C)			
	2004		2005		2004		2005		2004		2005	
F	28.8^{b}	(5.4)	31.8^{a}	(4.7)	25.7^{f}	(1.3)	24.2^{d}	(1.3)	31.6^{a}	(3.2)	31.4^{e}	(2.0)
CF	28.1^{b}	(7.4)	30.1^{a}	(2.9)	26.3^{e}	(1.3)	24.8^{c}	(0.4)	32.8^{a}	(2.2)	31.8^{de}	(1.2)
HF	33.7^{a}	(7.3)	32.8^{a}	(4.7)	26.3^{e}	(1.3)	25.1^{bc}	(1.0)	32.3^{a}	(3.5)	31.6^{de}	(1.1)
CM	19.8^{c}	(9.8)	22.0^{b}	(5.7)	28.2^{a}	(1.9)	26.6^{a}	(1.2)	31.7^{a}	(4.0)	32.8^{bc}	(1.8)
HM	20.1^{c}	(8.0)	16.7^{c}	(2.3)	28.0^{ab}	(1.4)	26.4^{a}	(0.7)	32.2^{a}	(4.1)	32.2^{cde}	(1.9)
CB	18.8^{c}	(6.8)	18.4^{bc}	(4.0)	27.7^{bc}	(0.8)	26.2^{a}	(0.9)	32.9^{a}	(2.7)	32.3^{bcd}	(1.8)
HB	21.9^{c}	(7.6)	21.2^{bc}	(5.2)	27.2^{cd}	(1.9)	25.4^{b}	(0.6)	32.2^{a}	(2.4)	33.0^{b}	(2.7)
CHB	21.1^{c}	(7.7)	20.6^{bc}	(9.6)	27.0^{d}	(0.7)	25.4^{bc}	(0.6)	30.9^{a}	(2.2)	34.2^{a}	(1.4)
p-Value	<0.001		<0.001		<0.001		<0.001		0.154		0.011	

Similar letters indicate no significant differences within a column ($\alpha = 0.05$); *p*-values are significance of treatment effect in ANOVA. Means are followed by standard deviation in parenthesis.

Table 2
Least square means of percent soil moisture at 6 cm, soil temperature (°C) at 15 cm, and soil surface temperature (°C) from 2004 to 2005 factorial analysis

Treatment	Soil moisture at 6 cm (%)		Soil temperature at 15 cm (°C)		Soil surface temperature (°C)	
	2004	2005	2004	2005	2004	2005
Flat	32.0^{a}	31.5^{a}	26.3^{b}	25.0^{c}	32.5^{a}	31.7^{a}
Mound	20.9^{b}	19.3^{b}	28.0^{a}	26.5^{a}	32.0^{a}	32.5^{a}
Bed	21.2^{b}	19.8^{b}	27.4^{a}	25.8^{b}	32.6^{a}	32.7^{a}
p-Value	<0.001	<0.001	0.001	<0.001	0.424	0.168
Chop	23.4^{b}	23.5^{a}	27.3^{a}	25.9^{a}	32.5^{a}	32.3^{a}
Herbicide	26.0^{a}	23.5^{a}	27.1^{a}	25.7^{a}	32.2^{a}	32.3^{a}
p-Value	0.043	0.997	0.505	0.298	0.607	0.956

Similar letters indicate no significant difference within a treatment type and column ($\alpha = 0.05$); *p*-values are significance of treatment effect in ANOVA.

(Table 2). There were no differences in soil temperature between chopping and herbicide treatments in 2004 ($F_{1,20} = 0.5$, $p = 0.505$) or 2005 ($F_{1,20} = 1.1$, $p = 0.298$).

There were no significant differences among the eight treatment combinations for 2004 soil surface temperature measurements ($F_{7,28} = 1.7$, $p = 0.154$) (Table 1). In 2005 ($F_{7,28} = 3.3$, $p = 0.011$) CHB resulted in the greatest surface temperature and F resulted in the lowest temperature. The factorial analyses from 2004 to 2005 (Table 2) indicated no significant differences among the planting site conditions ($F_{2,20} = 0.9$, $p = 0.424$ and $F_{2,20} = 2.0$, $p = 0.168$, respectively) or vegetation control treatments ($F_{1,20} = 0.3$, $p = 0.607$ and $F_{1,20} = 0.0$, $p = 0.956$, respectively).

3.2. Light and total competition

Availability of sunlight was significantly different among the eight treatment combinations in both 2004 ($F_{7,28} = 6.6$, $p < 0.001$) and 2005 ($F_{7,28} = 7.8$, $p < 0.001$). In 2004, seedlings on F received less sunlight than any other treatment (Fig. 1A). The check also received the least amount of sunlight in 2005, although CF, CB, and HF received significantly less sunlight than HM, CM, HB, and CHB. There was no significant interaction between planting site condition and vegetation control treatment in 2004 ($F_{2,20} = 1.1$, $p = 0.338$) or 2005 ($F_{2,20} = 2.4$, $p = 0.121$). Planting site condition had a significant treatment effect in both years ($F_{2,20} = 3.9$, $p = 0.024$ and $F_{2,20} = 10.0$, $p = 0.001$, respectively), with the mounded treatments receiving more sunlight than flat treatments and the bedded treatments not different from flat planting or mounding (Table 3). The vegetation control treatments did not significantly differ in 2004 ($F_{1,20} = 0.1$, $p = 0.762$), but the herbicide treatments resulted in more sunlight at the seedling level in 2005 ($F_{1,20} = 5.7$, $p = 0.027$).

Table 3
Least square means of percent sunlight at the seedling level and total percent cover of surrounding vegetation from 2004 to 2005 factorial analysis

Treatment	Percent full sunlight		Vegetation cover (%)	
	2004	2005	2004	2005
Flat	88.0^{b}	60.9^{b}	41.3^{a}	61.6^{a}
Mound	93.8^{a}	78.5^{a}	9.9^{b}	30.4^{c}
Bed	92.5^{ab}	68.8^{ab}	15.2^{b}	51.0^{b}
p-Value	0.024	0.001	<0.001	<0.001
Chop	90.7^{a}	65.6^{b}	30.3^{a}	51.1^{a}
Herbicide	92.2^{a}	73.2^{a}	14.0^{b}	44.2^{b}
p-Value	0.762	0.027	<0.001	0.036

Similar letters indicate no significant difference within a treatment type and column ($\alpha = 0.05$); *p*-values are significance of treatment effect in ANOVA.

Significant treatment differences in total percent cover of surrounding vegetation are displayed by treatment combination in Fig. 1B for 2004 ($F_{7,28} = 40.4$, $p < 0.001$) and 2005 ($F_{7,28} = 17.1$, $p < 0.001$). In both years, the greatest abundance of vegetation was on F and CF, with the least on HM, HB, and CHB in 2004, and CM and HM in 2005. The factorial analysis indicated no significant interaction between the planting site condition and vegetation control treatment in 2004 ($F_{2,20} = 1.9$, $p = 0.178$) or 2005 ($F_{2,20} = 1.1$, $p = 0.268$). Among the planting site conditions, flat treatments had the greatest percent cover of surrounding vegetation and mounded treatments had the least (Table 3). Herbicides reduced abundance of surrounding vegetation more than chopping in 2004 and 2005 ($F_{1,20} = 51.8$, $p < 0.001$ and $F_{1,20} = 5.0$, $p = 0.036$, respectively).

3.3. Vegetation by groups

Among the treatment combinations, there were significant differences in forb ($F_{7,28} = 9.8$, $p < 0.001$), shrub ($F_{7,28} = 24.5$, $p < 0.001$), and graminoid ($F_{7,28} = 11.1$, $p < 0.001$) cover in 2004,

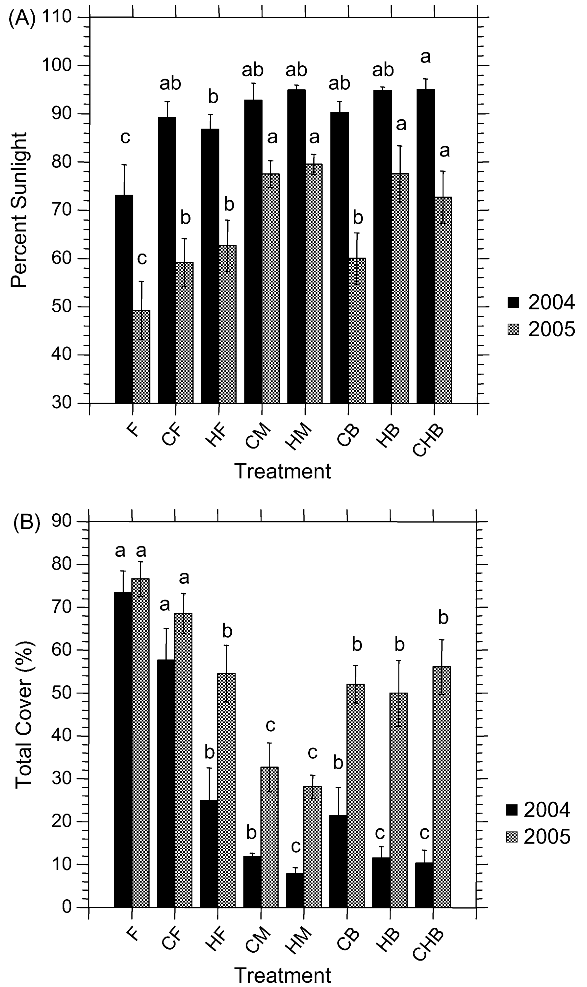

Fig. 1. Least square means of (A) percent sunlight at the seedling level and (B) total percent cover of surrounding vegetation for each treatment combination in 2004 and 2005. Similar letters indicate no significant differences within each year ($\alpha = 0.05$).

and shrub ($F_{7,28} = 9.9$, $p < 0.001$) and graminoid ($F_{7,28} = 3.5$, $p = 0.008$) cover in 2005 (Fig. 2). Only shrubs and graminoids provided greater than 10% cover on any treatment combination. In both years, the greatest amount of shrub cover occurred on F and CF. Similarly, 2004 graminoid cover was greatest on F and CF and least on HB, CHB, and HM. By the second growing season, graminoid cover was highest on CF, HF, HB, and CHB and in the lowest abundance on CM and HM. The factorial analysis in each growing season indicated no significant interactions between planting site condition and vegetation control treatment for any group. Shrub cover was significantly greater on flat sites than either bedded or mounded sites in 2004 ($F_{2,20} = 16.5$, $p < 0.001$), although by 2005 shrub cover on bedded sites was no longer significantly different than flat sites (Table 4). Additionally, the herbicide treatment significantly reduced shrub cover when compared to the chop treatment during both years ($F_{1,20} = 67.2$, $p < 0.001$, and $F_{1,20} = 41.8$, $p < 0.001$, respectively). In 2004, there was significantly more graminoid cover on chopped sites than those treated with herbicides ($F_{1,20} = 14.5$, $p = 0.001$), but no difference in 2005 ($F_{1,20} = 0.1$, $p = 0.753$).

3.4. Regression analysis

In 2004, mortality was negatively related to percent soil moisture ($r^2 = 0.405$) (Fig. 3A). No other single variable accounted for over 5% of the variability in seedling mortality after 1 year. In 2005, the relationship between seedling mortality and percent soil moisture was much weaker than in 2004, accounting for only 8% of the variability. The strongest predictors of mortality in 2005 were soil temperature at 15 cm ($r^2 = 0.295$) and soil surface temperature ($r^2 = 0.124$) (Fig. 3B and C, respectively). The predictive model for second year seedling mortality was best fitted with the following equation:

$$Y = -214.046 + 7.154 \times X_1 + 3.015 \times X_2 + 1.688 \times X_3 \quad r^2 = 0.451,\ n = 40,\ \mathrm{SSE} = 4284.66,\ p < 0.001 \tag{2}$$

where Y is mortality (%), X_1 is soil temperature at 15 cm (°C), X_2 is the square root transformation of graminoid percent cover, and X_3 is soil surface temperature (°C).

In 2004, the individual variable most strongly related to root collar diameter was percent soil moisture, with an inverse relationship that accounted for 7.5% of the variability. In 2005, the relationship between root collar diameter and percent moisture was much stronger, with an r^2 value of 0.334 (Fig. 4). The next strongest relationship was a positive relationship with percent full sunlight, accounting for 26.2% of the variability. Abundance of surrounding vegetation was inversely related to growth ($r^2 = 0.148$). In 2005, the model that best fit the data accounted for 58.5% of the variability:

$$Y = 21.819 - 0.139 \times X_1 - 0.742 \times X_2 + 1.203 \times X_3 \quad r^2 = 0.585,\ n = 40,\ \mathrm{SSE} = 171.50,\ p < 0.001 \tag{3}$$

where Y is root collar diameter (mm), X_1 is percent soil moisture at 6 cm, X_2 is the square root transformation of shrub percent cover, and X_3 is the square root transformation of fern percent cover.

4. Discussion

4.1. Microsite response to site preparation

We classified our site preparation treatments in two groups based on the primary treatment function; "planting site conditions" included mounding and bedding, which are used to alter soil conditions and alleviate limitations associated with flat planting, and "vegetation control treatments" included chopping and herbicide, which are primarily used to reduce competition for resources from surrounding vegetation. The function of each treatment inherently suggests the respective ability of the treatment to impact the response variables. For instance, bedding and mounding would be expected to have a stronger affect on soil moisture and temperature than either chopping or herbicide. For the most part, we found that microsite conditions responded as expected to the site preparation treatments applied.

Table 4
Least square means of percent cover for ferns, forbs, shrubs, and graminoids from 2004 to 2005 factorial analysis

Treatment	Ferns		Forbs		Shrubs		Graminoids	
	2004	2005	2004	2005	2004	2005	2004	2005
Flat	3.1^a	2.8^a	3.4^a	6.7^a	11.7^a	18.1^a	15.4^a	37.7^a
Mound	2.4^a	4.9^a	0.8^b	5.2^a	2.8^b	8.8^b	2.1^b	11.4^b
Bed	3.0^a	5.3^a	1.6^{ab}	6.8^a	5.2^b	15.6^{ab}	2.9^b	24.7^{ab}
p-Value	0.991	0.223	0.011	0.104	<0.001	0.038	<0.001	0.001
Chop	2.5^a	2.6^b	2.9^a	6.4^a	9.9^a	19.8^a	9.3^a	24.3^a
Herbicide	3.1^a	6.1^a	1.0^b	6.1^b	3.2^b	8.5^b	4.3^b	24.9^a
p-Value	0.599	0.018	0.002	0.045	<0.001	<0.001	0.001	0.753

Similar letters indicate no significant difference within a treatment type and column ($\alpha = 0.05$); p-values are significance of treatment effect in ANOVA.

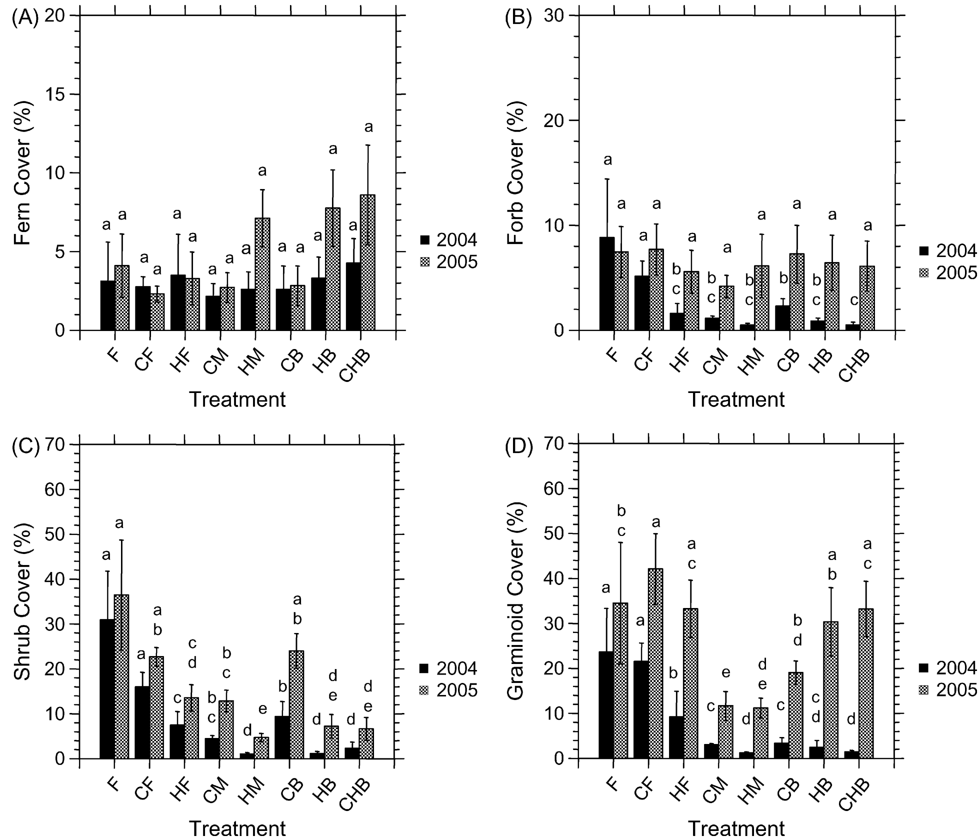

Fig. 2. Least square means of percent cover of (A) ferns, (B) forbs, (C) shrubs, and (D) graminoids for each treatment combination in 2004 and 2005. Similar letters indicate no significant differences within each year ($\alpha = 0.05$).

Consistent with previous reports, we found that bedding and mounding treatments resulted in a reduction in soil moisture and an increase in soil temperatures. Bedding is commonly used to alleviate limitations from excess moisture by improving soil drainage and increasing aeration near the soil surface (Pritchett, 1979; McKee and Wilhite, 1986), and one of the main purposes of mounding is reducing excess soil moisture on a growing site (Sutton, 1993; Londo and Mroz, 2001). The greatest soil temperatures at 15 cm reported in this study occurred on mounded sites. Mounding is used in northern latitudes to raise soil temperatures by increasing site exposure, inverting and "capping" the insulating surface organic layer with mineral soil, and bringing the mounded soil above the ground level (McMinn, 1985; Sutton, 1993; Londo and Mroz, 2001). Although bedding is not used for this purpose in the southeastern United States, increased soil temperatures have been associated with bedding as well (Trettin et al., 1996). Vegetation control treatments did not have very strong effects on temperature within the soil, suggesting that the soil disturbance created by bedding and mounding is largely responsible for increased temperatures at 15 cm.

With exception to the untreated check, all treatment combinations included either chopping or herbicide for the control of surrounding vegetation. However, in both growing seasons the plots treated with only chopping (CF) did not significantly reduce vegetation cover when compared to the check. Chopping primarily crushes above-ground biomass, but does not control stump sprouts and often results in rapid regrowth of woody vegetation (Fredericksen et al., 1991). Previous studies have demonstrated limited success of chopping for reducing vegetation when compared to more intensive mechanical treatments (Miller, 1980). Because we found no significant interactions between planting site conditions and vegetation control treatments, our results suggest that reductions in vegetation caused by CM and CB treatments can be attributed to effects of mounding and bedding, respectively, rather than the chopping treatment.

We found the treatment combinations that included mounding (HM and CM) had the lowest percent cover of surrounding vegetation after two growing seasons. At the local seedling level, where vegetation measurements were taken, mounding was perhaps the most intensive treatment used in the study. To create each individual mound, soil was scooped from the ground, inverted, and then deposited adjacent to the pit. Scooping the soil pulls vegetation from the ground and severs roots, and the inverted mineral soil on which each seedling was planted provides a barrier to returning vegetation (Sutton, 1993). Vegetation is effectively eliminated from the immediate vicinity of the planted seedling, but is often unaffected between mounds. It is unclear, however, how long the inhibitory effect of mounding on nearby vegetation will persist as the mounds shift and settle over time.

Herbicides provided additional vegetation control when used in combination with mounding or bedding and were clearly more effective at reducing surrounding vegetation than chopping. However, we found a greater increase in vegetation abundance from 2004 to 2005 on sites treated with herbicides (14% cover in 2004 to 44% cover in 2005) than sites treated with chopping (30% cover in 2004 to 51% cover in 2005), consistent with previous studies that show the effects of herbicides diminish significantly by the second year after application (Blake et al., 1987; Zutter and Zedaker, 1987). We found that the increase in total vegetation cover on herbicide sites from 2004 to 2005 was largely attributed to an increase in graminoids, which as a taxon typically respond well to site disturbance. The herbicide treatment used in our study, which was formulated to target woody vegetation, effectively controlled shrub cover through two growing seasons.

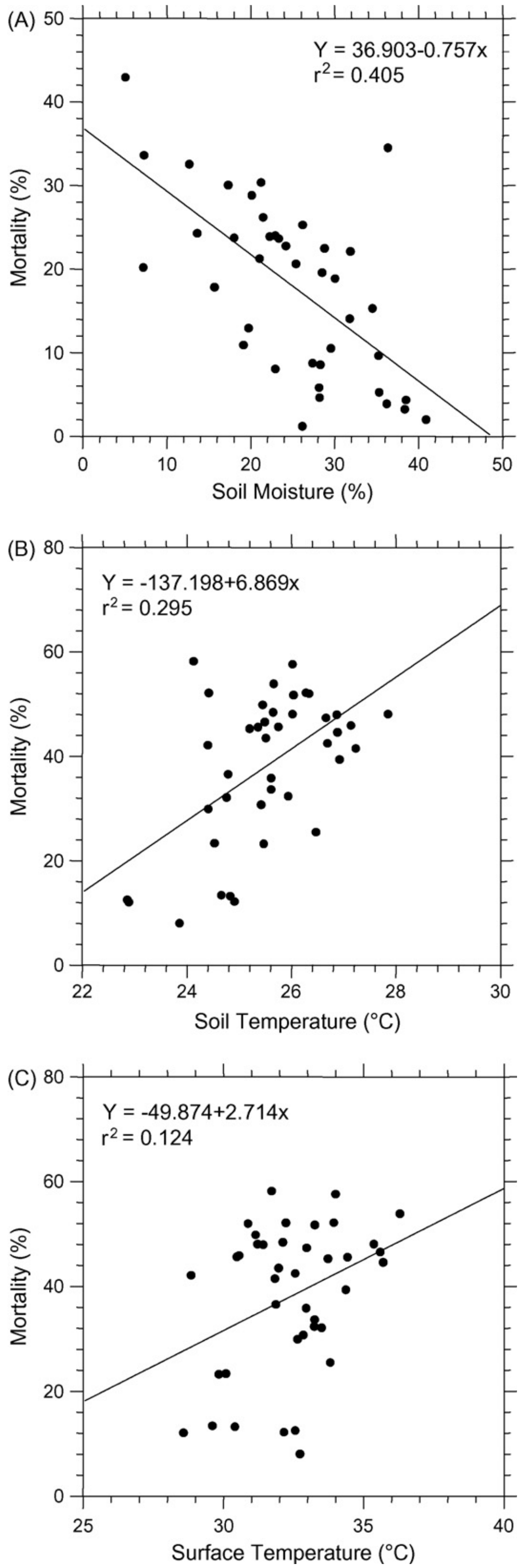

Fig. 3. Scatterplots with regression lines and r^2 values for (A) 2004 percent mortality vs. percent soil moisture at 6 cm, (B) 2005 percent mortality vs. soil temperature (°C) at 15 cm, and (C) 2005 percent mortality vs. soil surface temperature (°C).

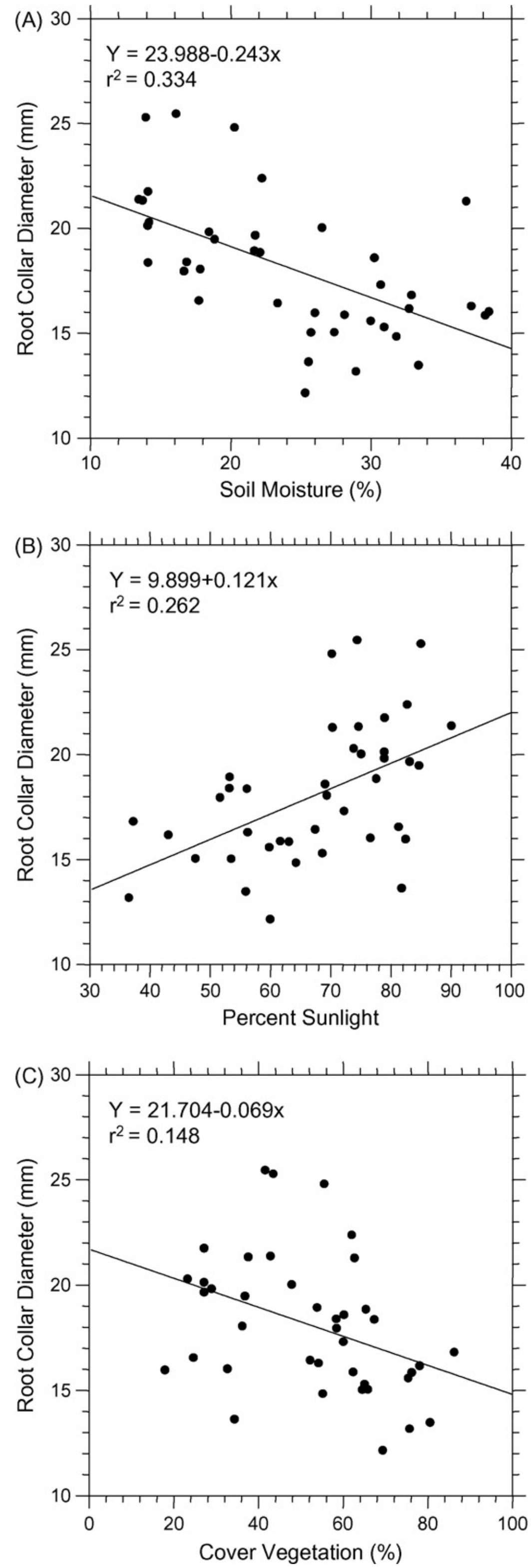

Fig. 4. Scatterplots with regression lines and r^2 values for (A) 2005 root collar diameter (mm) vs. percent soil moisture at 6 cm, (B) 2005 root collar diameter (mm) vs. percent sunlight, and (C) 2005 root collar diameter (mm) vs. percent cover of surrounding vegetation.

Reducing shrubs and preserving or increasing the herbaceous component of the understory is desirable for restoration and may provide the opportunity to increase biological diversity, a defining characteristic of properly managed longleaf pine ecosystems (Peet and Allard, 1993; Walker, 1993). Previous studies have demonstrated pronounced shifts in community structure following the use of site preparation (Schultz and Wilhite, 1974; Conde et al., 1983; Swindel et al., 1986). Understanding effects of site preparation on the structure and composition of understory vegetation is critical for ecological restoration (Noss, 1989; Glitzenstein, 1993; Hedman et al., 2000). Although we observed changes in percent cover of vegetation groups in response to our treatments, a detailed analysis of understory response is beyond the scope of this report.

4.2. Seedling response to microsite conditions

The strong inverse relationship between seedling mortality and soil moisture in 2004 suggests that greater soil moisture (within the range reported in this study) improves seedling survival during the first year after planting. Similarly, Larson (2002) found that dry conditions at the root system increased the likelihood of seedling mortality, and Haywood (2007) associated drought conditions in the first growing season with reduced survival of planted longleaf pine seedlings. It is important to note that our study was conducted on poorly drained sites, where we would expect soil moisture levels to be relatively high. Despite significant reductions in soil moisture caused by mounding and bedding treatments, we previously reported no significant treatment effects on survival at 12 months (Knapp et al., 2006). A high degree of within-treatment variability in seedling mortality may have masked some treatment effects; inconsistent depths to the hardpan affecting local drainage patterns likely resulted in drier conditions in some areas within plots. According to data from the National Climate Data Center (Hofmann Forest Station, 34°5′N, 77°2′W), precipitation during the study years was approximately normal when compared to the 30-year mean (2004 = 149.0 cm, 2005 = 153.9 cm, 30-year mean = 145.0 cm), suggesting that seedlings were not stressed by unusual conditions. Overall, we would expect that planting longleaf pine on sites with uniformly and/or excessively low moisture levels would result in higher mortality rates than we observed in this study (e.g. Rodriguez-Trejo et al., 2003).

With the exception of soil moisture, individual microsite factors were poor predictors of seedling survival or growth in 2004. The use of container-grown seedlings may have obscured other relationships because the growth medium surrounding the root system moderates local conditions, allowing seedlings to gradually adjust to the new growing environment after planting (Schultz, 1997; Barnett and McGilvray, 2000; Barnett, 2002). The plug of nutrient-rich medium creates favorable conditions for early root growth regardless of site conditions. Therefore, seedling response may not be representative of growing conditions during the very early stages of growth, resulting in weak relationships after the first growing season.

The predictive model for 2005 seedling mortality indicates that soil temperature and competition from graminoids were significant factors affecting seedling survival. In a study on artificial regeneration of longleaf pine in canopy gaps in Georgia and Florida, Rodriguez-Trejo et al. (2003) reported that extreme temperatures increased first year mortality by drying out and desiccating the root systems of longleaf pine seedlings during a severe drought. Our study was not conducted under droughty conditions, but our results also suggest that hot, dry conditions increase early mortality of planted longleaf pine seedlings. Additionally, Rodriguez-Trejo et al. (2003) found grass cover to be negatively related to seedling survival. Grasses typical of the longleaf pine ecosystem, primarily bunchgrasses and specifically wiregrass within the region of our study, have shallow but dense and fibrous root systems that make them strong competitors for soil moisture and nutrients, especially when recently planted longleaf pines seedlings have not yet developed extensive root systems.

Although previous studies on resource availability have reported poor relationships between longleaf pine growth and soil moisture (Palik et al., 1997; McGuire et al., 2001), we found soil moisture to have the strongest relationship with root collar diameter in 2005. In contrast to the well-drained sites of previous studies, the poorly drained growing conditions of our study appear to limit the seedling growth rate because of too much moisture. Similarly, studies on other southern pine species found that site preparations used to increase drainage on poorly drained sites resulted in greater seedling growth rates (Pritchett, 1979; McKee and Wilhite, 1986). Shoulders (1976) reported that poor soil aeration reduced growth rates of slash pine seedlings by inhibiting root growth and the ability of existing roots to absorb water and nutrients. Therefore, the strong relationship between soil moisture and seedling growth is not surprising on poorly drained sites where excess moisture limits seedling growth potential. In addition, if weaker seedlings died on the drier microsites of our study, proportionally more of the healthier, strong-growing seedlings would remain to contribute to growth means at the plot level.

It is well known that longleaf pine is a shade-intolerant species (Boyer, 1990), and light may be a limiting factor for seedling growth under intact canopies. Gagnon et al. (2003) report significantly larger increments of diameter growth at the center of gaps (where light levels are highest) and decreasing growth rates toward the forest edge. Other studies on resource availability within forest gaps identify light as the most limiting factor for early longleaf pine growth (Palik et al., 1997; McGuire et al., 2001). In these studies and ours, seedling growth increased as light levels rose from 30% to around 70% full sunlight, above which additional sunlight did not appear to correspond with additional growth. In our study, sites had been clear-cut, sheared, and burned prior to treatment application. With no canopy to provide shade, first-year light levels exceeded 73% full sunlight on all treatments. By the end of the second year, however, understory vegetation had grown tall enough on some of the treatments (F, CF, HF, and CB) to bring light levels below 70%. As competing vegetation continues to grow around seedlings, we expect reduced light levels to further inhibit root collar growth of seedlings remaining in the grass stage.

We were not surprised to find that abundance of surrounding vegetation was inversely related to seedling growth. Based on field observation, the height and density of the shrub group made it the most likely to reduce light levels reaching the seedling, and our predictive model for 2005 root collar diameter included shrub cover as a significant variable. Previous reports suggest that shrub control is critical for longleaf pine establishment because seedlings cannot compete with fast growing woody vegetation (Croker and Boyer, 1975; Van Lear et al., 2005). In addition to reducing light levels reaching the seedling, surrounding vegetation competes for soil nutrients. Soil nutrients, especially available nitrogen, have been found to be significantly correlated to longleaf pine seedling growth (Palik et al., 1997; McGuire et al., 2001). In our study, we did not quantify nutrient availability and therefore cannot differentiate the competitive effects of surrounding vegetation as primarily above-ground or below-ground. However, it is clear that controlling competition, especially shrubs, is critical for increasing seedling growth.

An interesting result from our study was the positive relationship between fern abundance and root collar diameter in the 2005 predictive growth model. The dominant fern species throughout the study area was bracken fern (*Pteridium aquilinum* (L.) Kuhn), which is a common pioneer species in plantations following disturbances such as logging, burning, and site preparation. Herbicides, specifically those that target shrub species, aid establishment of bracken fern by reducing competition for resources (McDonald et al., 1999, 2003). Our results suggest that similar site conditions (including an absence of woody competitors) favor both longleaf pine seedlings and bracken fern through 2 years after site preparation. Bracken fern has also been reported to inhibit growth of surrounding vegetation, particularly herbaceous plants, through allelopathy (Stewart, 1975; Gliessman and Muller, 1978; McDonald et al., 2003). Consequently, the presence of bracken fern may provide additional competition control and result in increased availability of resources for longleaf pine seedlings, although herbaceous species richness and diversity could be adversely affected by the same allelopathic mechanisms.

5. Conclusion

Understanding the effects of resource availability on longleaf pine seedling survival and growth can help land managers choose appropriate site preparation treatments for regeneration efforts. Our study has shown that excess moisture on poorly drained sites is an important limiting factor for root collar growth. Site preparation treatments that improve drainage, as well as reduce competition for light and other resources, can be expected to maximize longleaf pine seedling growth. Therefore, mounding or bedding combined with herbicides are appropriate treatments for land managers wishing to rapidly establish planted longleaf pine seedlings on this site type.

However, if the management goal is to restore the longleaf ecosystem with its component species and processes, managers will need to consider broader effects of site preparation decisions. Site preparation techniques, particularly those that alter the micro-topography by changing soil conditions, may have lasting influence on other aspects of the ecosystem. For example, it is not clear how these treatments will affect the frequency or continuity of surface fires, which have traditionally maintained this ecosystem. Raised soil from mounding or bedding, along with decreased vegetation as a fuel source, may disrupt the spread of fire and result in future encroachment by woody vegetation. Our study also suggests short-term changes in the structure of ground layer vegetation, which in turn may alter other ecosystem components or processes.

While our results indicate that appropriate site preparation can increase early growth of longleaf pine seedlings, it is not clear if advantages will persist throughout stand development. Previous studies on longleaf pine (Boyer, 1985, 1996) and other southern pines (Haywood, 1980; Nilsson and Allen, 2003) suggest that short-term increases in seedling growth associated with site preparation may diminish with time. Therefore, understanding the long-term effects of site preparation for longleaf pine restoration on poorly drained sites will require additional research throughout all stages of stand development.

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