ELSEVIER

Forest Ecology and Management 172 (2003) 133–144

Forest Ecology and Management

www.elsevier.com/locate/foreco

Dynamics of artificial regeneration in gaps within a longleaf pine flatwoods ecosystem

J.L. Gagnon[a,1], E.J. Jokela[b,*], W.K. Moser[c,2], D.A. Huber[b,3]

[a]*Joseph W. Jones Ecological Research Center, Rt. 2 Box 2324, Newton, GA 31770-9651, USA*

[b]*School of Forest Resources and Conservation, University of Florida, P.O. Box 110410, Gainesville, FL 32611-0410, USA*

[c]*Missouri Department of Conservation, 1110 S. College Avenue, Columbia, MO 65201, USA*

Received 10 September 2001; accepted 26 November 2001

Abstract

The selection silvicultural system has gained popularity as a means for developing and maintaining uneven-aged stand structure in a variety of forest types. Only limited information exists, however, regarding regeneration dynamics and growth of longleaf pine (*Pinus palustris* Mill.) managed under the group selection silvicultural system in the southeastern USA. A replicated artificial gap study, established in a 65-year-old, second-growth stand in northwest Florida, was used to examine the interactions between site resource availability (light, nutrition, water) and canopy gap position on survival and growth of containerized longleaf pine seedlings over two growing seasons. A gradient in site resource availability was created using fertilizer and hand weeding treatments. Levels of light transmittance (averaged over the growing season) within the gaps varied by location and ranged from 72% near the uncut edge to 96% in the gap center. Seedlings growing in the gap center had significantly lower survival rates (e.g., 1999, center = 23%, edge = 51%), but larger diameter increments (e.g., 2000, center = 3.6 mm, edge = 1.4 mm) than those found in lower light environments along the gap edge. Soil moisture content had little apparent impact on these differences in survival and growth, as surface (0–15 cm) moisture contents did not vary significantly among gap positions in either growing season. Although seedling survival was significantly reduced by the fertilizer and hand weeding (control = 41%, treated = 31%), diameter increment was 44% greater than the untreated control. Results of this study suggest that a group selection silvicultural system that provides sufficient light and relief from competition (for nutrients) for seedlings may be a suitable silvicultural method for effectively regenerating longleaf pine forests.

Keywords: Competition control; Light interception; Fertilization; Group selection silvicultural system

1. Introduction

Prior to European settlement, the longleaf pine (*Pinus palustris* Mill.) ecosystem covered more than 37 million ha in the southeastern USA. Since that time, a steady decline has occurred (Wahlenberg, 1946; Croker and Boyer, 1976; Croker, 1979; Dennington and Farrar, 1983) and today less than 1.2 million ha remain (Brockway and Outcalt, 2000). The

* Corresponding author. Tel.: +1-352-846-0890; fax: +1-352-846-1277.
E-mail addresses: jennifer.gagnon@jonesctr.org (J.L. Gagnon), ejokela@ufl.edu (E.J. Jokela), 4ester@compuserve.com (W.K. Moser), dahuber@ufl.edu (D.A. Huber).
[1] Tel.: +1-229-734-4706; fax: +1-229-734-4707.
[2] Tel.: +1-573-882-9880.
[3] Tel.: +1-352-846-0898; fax: +1-352-846-1277.

PII: S0378-1127(01)00808-8

reduction in land area occupied by this forest type can be attributed to several factors. First, extensive harvesting that occurred between 1900 and 1930 greatly reduced the levels of longleaf pine growing stock (Wahlenberg, 1946; Boyer, 1979; Dennington and Farrar, 1983; Boyer and White, 1990). Second, an inadequate understanding of the biological requirements of this species and poor fire management led to frequent regeneration failures (Wahlenberg, 1946; Dennington and Farrar, 1983; Barnett et al., 1990). In addition, the intolerance of longleaf pine to both shade and understory competition (Barnett et al., 1990) along with sporadic seed production (Croker, 1975; Boyer, 1990; Boyer and White, 1990), seed predation (Croker and Boyer, 1976; Boyer and White, 1990) and bare mineral soil seedbed requirements (Croker, 1975; Boyer, 1990), contributed to difficulties in achieving successful regeneration. Many longleaf pine sites were also converted to other land uses, or to other commercially important species such as loblolly pine (*P. taeda* L.) and slash pine (*P. elliottii* var. *elliottii* Englem, Wahlenberg, 1946; Boyer, 1979; Croker, 1979; Dennington and Farrar, 1983).

The majority of second-growth longleaf pine forests existing today resulted from even-aged, natural regeneration processes. In many stands, fire suppression and sparse stocking have led to hardwood encroachment and changes in the native ground cover (Brockway and Outcalt, 2000). Over the last decade, interest has grown considerably in conserving and restoring the longleaf pine ecosystem. Both conventional and alternative management systems are being studied to determine the most effective approach for achieving this goal.

Traditionally, longleaf pine stands have been managed using silvicultural systems that create and maintain even-aged structure. The clear-cut and shelterwood silvicultural systems have historically been the most commonly used regimes for managing this species (Croker and Boyer, 1976; Maple, 1977; Boyer, 1979, 1990, 1993; Croker, 1979; Dennington and Farrar, 1983; Boyer and White, 1990). Recently, there has also been increasing interest in developing and maintaining uneven-aged stand structure in longleaf pine stands using the irregular shelterwood and group- and single-tree selection silvicultural systems (Baker, 1991; Farrar, 1996; USDA Forest Service, 1999a,b; McGuire et al., 2001). The group selection system attempts to mimic uneven-aged, gap-phase regeneration dynamics through periodic harvest disturbances that form canopy openings and encourage seedling recruitment over extended periods of time.

To date, few landscape-level examples exist where the principles of uneven-aged management have been applied to the longleaf pine ecosystem. Recently, however, the USDA Forest Service's Revised Land and Resource Management Plan for National Forests in Florida (1999b) declared that over 50,000 ha of even-aged longleaf pine and mixed longleaf pine–slash pine stands on the Apalachicola National Forest would be converted to a diverse patch-size structure using a modified group selection system. The proposed silvicultural regime would focus on creating many small (<0.5 ha) patches (gaps) and fewer large gaps within stands. Additional goals of the modified group selection system would include enhancing red-cockaded woodpecker (*Picoides borealis*) habitat, production of poletimber and large sawtimber, and provision for a wide range of recreational opportunities for visitors (USDA Forest Service, 1999a,b).

For the group selection system to be successfully applied in the longleaf pine ecosystem, a better understanding of the regeneration dynamics within canopy gaps is required. Few studies are available as a basis for making specific management recommendations for this species (Palik and Pederson, 1996; Palik et al., 1997; McGuire et al., 2001). Previous research with other species has demonstrated that site resource availability (i.e., light, water, nutrients) may vary within canopy gaps (Minckler and Woerheide, 1965; Canham et al., 1990; McDonald and Abbott, 1994; Brown, 1996; Gray and Spies, 1996, 1997; McDonald and Reynolds, 1999), and thereby affect both seedling survival and growth. For example, shade cast from surrounding mature trees may serve to initially enhance seedling survival and thereby promote the regeneration process. Conversely, belowground competition for water and nutrients from adjacent mature trees may hinder seedling development as lateral root expansion occurs into newly established openings (Brockway and Outcalt, 1998).

Fundamental questions related to the importance of gap size, residual stand basal area, and interactions of understory and mature tree competition on seedling survival and development within harvested groups remain unanswered, but should be addressed for the successful implementation of the group selection system in longleaf pine. This study examined the interactions between site resource availability and canopy gap position, and their effects on survival and growth of containerized longleaf pine seedlings over two growing seasons. To accomplish this objective, we utilized a replicated artificial gap study established in a mature, second-growth longleaf pine stand in northwest Florida. A gradient in site resource availability was created using fertilizer and hand weeding treatments.

2. Materials and methods

2.1. Study area and management history

The study site is located on the Apalachicola Ranger District of the Apalachicola National Forest in northwest Florida, USA (30°10′N, 84°43′W). The terrain is flat to gently rolling, with many wet depressions. The soils are mapped as loamy, siliceous, subactive, thermic Grossarenic Paleudults (Albany series). The Albany series is somewhat poorly drained, having formed in marine deposits of sandy material underlain by loamy sediments. The soil nutrient reserves are inherently low, as the A horizon has both low organic matter content and extractable nutrient levels (Table 1). The climate is humid subtropical and annual precipitation averages 1670 mm.

The overstory was a second-growth, naturally regenerated longleaf pine stand (average age 65 years), with minor interspersion of slash pine. Prior to treatment, the average diameter and basal area of the stand were 26 cm and 26 $m^2\ ha^{-1}$, respectively. Major understory species were those common to flatwoods sites and included gallberry (*Ilex glabra* (L.) Gray), saw palmetto (*Serenoa repens* (W. Bartram) Small), wiregrass (*Aristida beyrichiana* Trin. and Rupr.), bluestem grasses (*Andropogon viginicus* L., *A. capillipes* Nash.), blueberry (*Vaccinium myrsinites* Lam.), runner oak (*Quercus pumila* Walter) and dwarf live oak (*Q. minima* (Sarg.) Small).

The site was harvested in the late 1920s. Suppressed and non-merchantable stems that remained following harvest provided the necessary seed source to naturally regenerate the area. Historically, the stand has not been thinned, and prescribed surface fires have been used on a 3-year cycle to reduce fuel loads. The site was last burned in the spring of 1998, 1 year prior to implementation of this study. Advanced longleaf pine regeneration was sparse across the area.

Table 1
Soil characteristics prior to treatment for a loamy, siliceous, subactive, thermic, Grossarenic Paleudult (Albany series) in northwest Florida (values were averaged across all gaps, gap positions and treatments)[a]

Nutrient concentration	Depth (cm)	Average
Phosphorus ($mg\ l^{-1}$)	0–15	1.8
	16–30	1.1
	31–45	0.7
Potassium ($mg\ l^{-1}$)	0–15	7.2
	16–30	3.5
	31–45	2.9
Magnesium ($mg\ l^{-1}$)	0–15	3.3
	16–30	1.5
	31–45	1.2
Calcium ($mg\ l^{-1}$)	0–15	16.6
	16–30	11.0
	31–45	9.5
pH	0–15	4.8
	16–30	4.9
	31–45	5.0
Organic matter (%)	0–15	0.9
	16–30	0.4
	31–45	0.2

[a] Extractable nutrient concentrations were determined using the Mehlich I procedure and organic matter content was determined using the Walkley–Black procedure (Nelson and Sommers, 1982; SRIEG 18, 1983; Hanlon et al., 1994).

2.2. Experimental design and treatments

A randomized complete block, split–split-plot design was used to examine the main effects and interactions between canopy gap position (distance from mature canopy and direction within the canopy gap) and site resource availability on regeneration dynamics of longleaf pine. Four 0.3 ha circular gaps (radius = 30.9 m) were whole-tree harvested in January 1999. An uncut buffer of at least 25 m, providing an intact canopy, separated each gap.

Based on anticipated within-gap gradients in site resource availability (Minckler and Woerheide, 1965; Canham et al., 1990; Brown, 1996; Brockway and Outcalt, 1998), each gap was divided into three zones

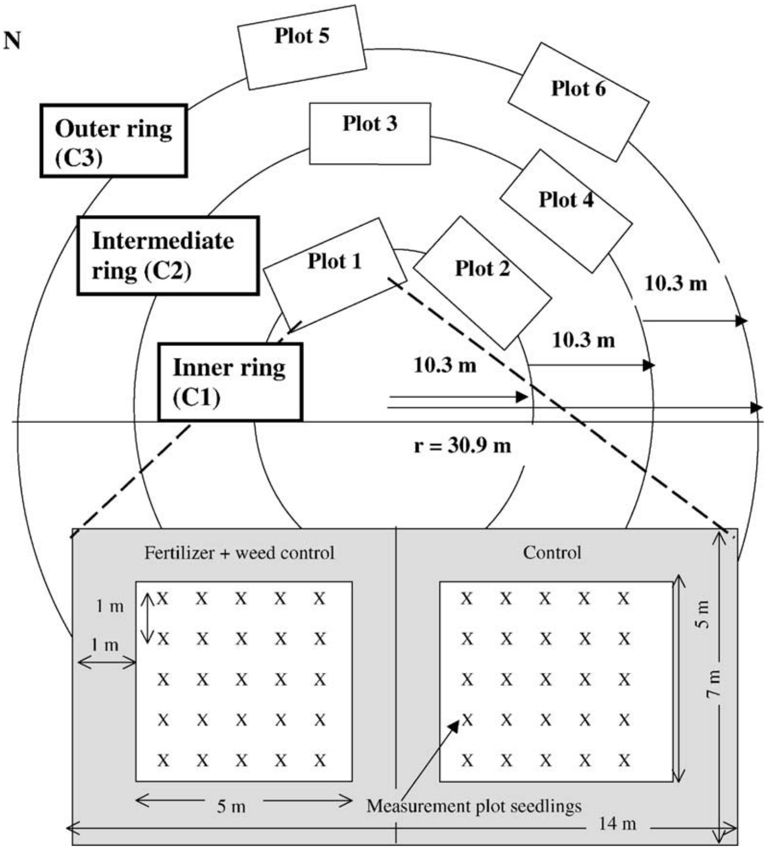

Fig. 1. Experimental layout (randomized complete block split–split-plot design) used to test the effects of distance from gap edge, direction within a gap and fertilizer plus hand weed control treatments on survival and growth of containerized longleaf pine seedlings planted in four 0.3 ha canopy gaps in northwest Florida. Plot arrangements were identical in the southern zone.

of competitive influence (Fig. 1). Each zone represented a different level of edge effect competition, ranging from minimal edge effects (C1, center of gap) to strong competitive edge effects (C3, perimeter of opening, under the intact canopy). The rings of competitive influence were fixed at 10.3, 20.6 and 30.9 m from the center of all four gaps. The gaps were further divided into a north and a south zone to isolate the effects of gradients in solar radiation within gaps on seedling survival and growth from those associated with different levels of edge effect competition (Gray and Spies, 1996). Along each gap ring and the two cardinal point positions, two 7 m × 14 m whole plots were established, for a total of four whole plots along each ring, and 12 whole plots per gap. The locations of the plot centers along the rings of competitive influence were determined randomly by selecting compass directions. Each plot was then divided into two 7 m × 7 m paired subplots for a total of 24 subplots per gap.

Following harvest, understory vegetation was removed manually from all plots using rotary cutters. In February 1999, containerized longleaf pine seedlings were hand-planted in the subplots. A 5 m × 5 m measurement plot was formed in each subplot by planting five rows of seedlings at a 1 m × 1 m spacing ($n = 25$ seedlings). Seedlings were also planted in a 1 m buffer that was maintained around each measurement plot. A total of 2832 seedlings were planted across the four experimental gaps. Only seedlings having root collar diameters greater than 0.5 cm were planted to help ensure high survival rates (Barnett et al., 1990). Treatments were then randomly assigned to the subplots. One paired subplot served as a control (i.e., no treatments imposed after the initial removal of understory vegetation to facilitate planting) and the other was fertilized 2 weeks after planting in February 1999, with 560 kg ha^{-1} of 10–10–10. Competing vegetation was again manually removed on those plots receiving fertilizer additions in May of 1999 and 2000.

2.3. Sampling procedures

Prior to assigning the experimental treatments, soil samples were collected from three depths (0–15, 16–30 and 31–45 cm) in each subplot. All soils were air-dried, sieved and extracted using the Mehlich I procedure (Hanlon et al., 1994). Extractable nutrient levels were determined using an inductively coupled argon plasma unit. Soil pH was determined using a 1:2 (w/v) soil/water slurry and the Walkley–Black procedure (Nelson and Sommers, 1982; Hanlon et al., 1994) was used to determine soil organic matter content (Table 1).

Over the 1999 and 2000 growing seasons, all four gaps were visited monthly. Photosynthetically active radiation (PAR; 400–700 nm; μmol m^{-2} s^{-1}) was determined for each subplot on nearly cloudless days between 11:00 and 14:00 h. PAR levels were measured 1 m above the ground simultaneously at (a) the center of each of the subplots (with a sunfleck ceptometer; Decagon Devices, Pullman, WA; $n = 4$ per subplot) and (b) the center of each gap (with an LI-COR 190 SA Quantum Light Sensor; LI-COR, Lincoln, NE). Corresponding PAR values were used to calculate PAR transmittance using the following formula:

$$\text{PAR transmittance} = \left(\frac{\text{PAR subplot}}{\text{PAR gap center}}\right) \times 100$$

PAR transmittance was calculated for June, July and August of 1999, and monthly, May–September of 2000. Monthly soil moisture content (0–15 cm) was determined gravimetrically (May–October of 1999, and May–September of 2000) at the center of each subplot ($n = 2$ samples per subplot). Survival and root collar diameter of longleaf pine seedlings were recorded at the beginning (May) and end (October of 1999 and September of 2000) of both growing seasons. Seedling diameter increments (mm growing per season) were calculated as the increase in root collar diameters over the course of each growing season. Seedling heights were not determined, as the majority of the plants had not emerged from the grass stage even after the 2000 growing season.

2.4. Statistical analyses

Data were analyzed separately for each growing season (1999 and 2000) using analysis of variance techniques for a randomized complete block, split–split-plot design (SAS Institute, 1996). Differences in seedling survival, growth and average growing season, soil moisture content by gap position, direction within gap, and fertilizer plus hand weeding treatments were tested ($\alpha = 0.10$) using the PROC GLM procedure. Significant treatment effects were separated using contrasts in the PROC MIXED procedure and linear correlations between variables were tested using the PROC CORR procedure. PAR data were analyzed using analysis of variance techniques for a randomized complete block split-plot design because measurements were unaffected by fertilization plus hand weeding treatments.

3. Results and discussion

Wide-scale implementation of uneven-aged silvicultural systems (e.g., group- and single-tree selection) has focused the need to acquire information on important processes regulating seedling development within various-sized canopy gaps created from either natural disturbances or through the removal of overstory trees. Although recent studies have begun to explore gap regeneration dynamics in longleaf pine ecosystems (Palik et al., 1997; Brockway and Outcalt, 1998; McGuire et al., 2001), knowledge concerning the competitive effects that mature canopy trees have on within-gap site resource availability (light, water, nutrients) and seedling survival and growth is still quite limited.

3.1. Within-gap site resource availability

3.1.1. Soil moisture

Surface soil moisture content over both the 1999 and 2000 growing seasons averaged 12% (Fig. 2). Although within-gap gradients in soil moisture content have been identified in other forest types (Minckler and Woerheide, 1965; McDonald and Abbott,

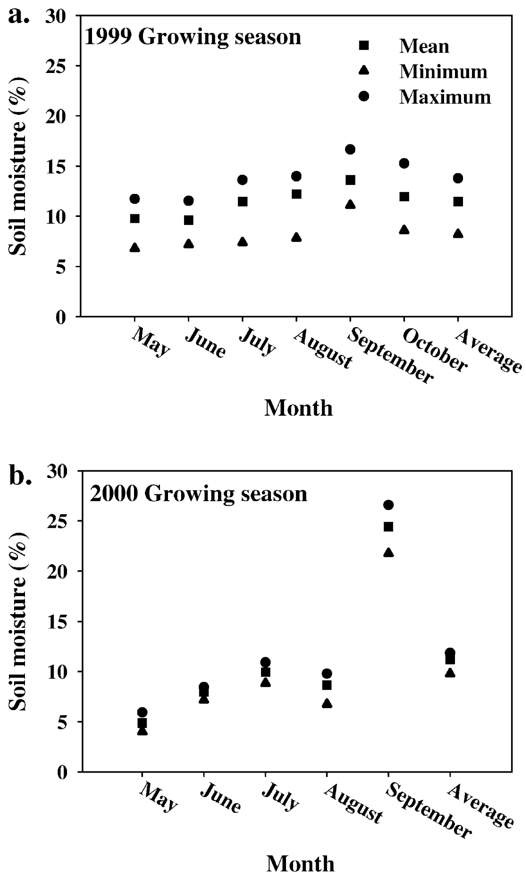

Fig. 2. Monthly soil moisture contents (0–15 cm) found within artificially created canopy gaps (0.3 ha) in northwest Florida during the (a) 1999 and (b) 2000 growing seasons. Note: monthly values were averaged across all gaps and gap positions, as no significant differences were detected.

1994) and were anticipated for longleaf pine based on the findings of Brockway and Outcalt (1998) on xeric sandhill sites, no significant differences were observed in relation to distance from gap edge or direction within a gap. Our findings are similar to those for temperate deciduous forests (Wilczynski and Pickett, 1993) and longleaf pine stands on mesic uplands (Palik et al., 1997). The drought conditions that prevailed in Florida from 1998 to 2000 undoubtedly contributed to the low within-gap variation in growing season soil moisture contents. For example, annual precipitation levels were 23 and 37% below normal in 1999 and 2000. During the 2000 growing season soil moisture content ranged from 6 to 11% and did not change substantially until September, when a tropical depression contributed heavy rainfall to the site (increasing soil moisture content to 24%). McGuire et al. (2001) similarly found that soil moisture contents did not vary from gap edge to gap center for a range of gap sizes (0.11–1.63 ha) during a period of drought in southwestern Georgia, USA.

3.1.2. PAR transmittance

Light availability has been shown to vary within canopy openings (Canham et al., 1990; Phillips and Shure, 1990; Gray and Spies, 1996; Palik et al., 1997; McGuire et al., 2001). In this study, a significant increase in PAR transmittance was found as distance from the gap edge increased. For example, during the 1999 growing season, PAR transmittance was highest in the gap center (C1 = 96%) and lowest near the gap edge (C3 = 72%). Consistent findings were also observed during the 2000 growing season (C1 = 92%, C3 = 73%). Significant within-gap differences in growing season PAR transmittance were also found between the northern and southern zones. During both growing seasons, average PAR transmittance was highest in the northern zone (92%) compared to the southern zone (77%). PAR transmittance along each ring within the northern zone was also generally higher than the corresponding ring in the southern zone (Figs. 3a and 4a), and could be attributed to differences in sun angle and solar track. As expected, a steady decline in monthly PAR transmittance occurred among gap positions over the course of the growing season. For example, PAR transmittance within the gap center (C1) ranged from about 100% in May to 83% in September; corresponding monthly values for the gap edge position (C3) varied from about 83 to 62%. By December, PAR transmittance values did not vary significantly among gap positions (C1 = 69%, C3 = 58%); however, differences still persisted between gap directions (north = 78%; south = 49%).

Measurements of PAR transmittance in this study were instantaneous and representative of light levels at solar noon during the growing season. Data representing cumulative seasonal PAR levels in tropical forest gaps (Brown, 1996) and in tropical and temperate forests (Canham et al., 1990) support the findings of this study. However, Brockway and Outcalt (1998) found that cumulative PAR levels (within canopy gaps in mature stands of longleaf pine on

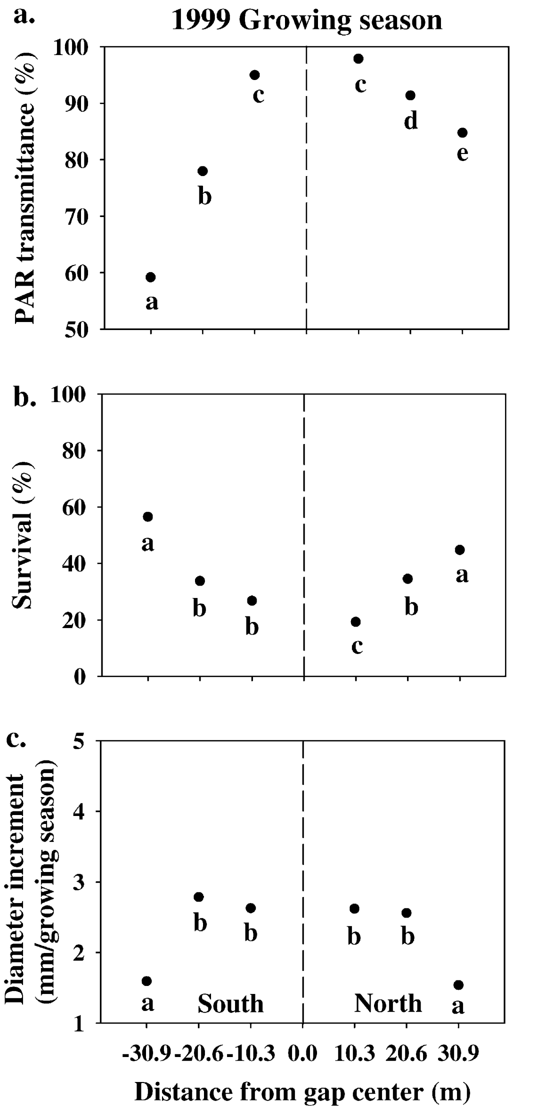

Fig. 3. Within-gap variation in 1999: (a) average growing season PAR transmittance; (b) longleaf pine seedling survival; (c) diameter increment (the increase in seedling root collar diameter over the growing season). Means (averaged across all gaps) followed by different letters denote significant differences ($\alpha = 0.10$) using linear contrasts in the PROC MIXED procedure.

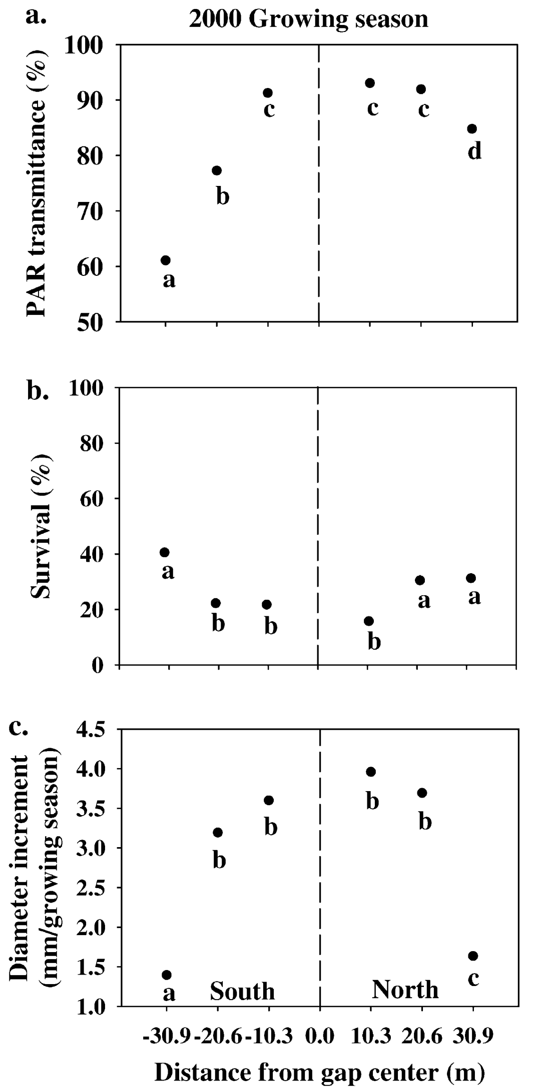

Fig. 4. Within-gap variation in 2000: (a) average growing season PAR transmittance; (b) longleaf pine seedling survival; (c) diameter increment (the increase in seedling root collar diameter over the growing season). Means (averaged across all gaps) followed by different letters denote significant differences ($\alpha = 0.10$) using linear contrasts in the PROC MIXED procedure.

xeric sites) were uniformly distributed from gap edge to gap center, regardless of measurement direction within the opening. Their results may differ from our findings because of differences in density of the surrounding stands. Longleaf pine canopies on xeric sandhill sites tend to be sparser than those on flat-woods sites, resulting in more uniform light conditions within gaps. Discrepancies may also be attributed to the temporal measurement period used, as they recorded PAR levels in December, when the sun was low in the south, further increasing the uniformity of light conditions within the gaps. McGuire et al.

(2001) calculated a gap light index using hemispherical photographs in longleaf pine stands and observed findings similar to those reported here. They also noted that the proportion of gap area receiving full sun light increased as gap size increased.

3.2. Longleaf pine seedling response to within-gap environment

Longleaf pine seedling survival decreased significantly over both the 1999 and 2000 growing seasons. Average seedling survival for all plots in May 1999 was 77% and by September 2000 it averaged 27%. Initial root collar diameter was not significantly related to seedling survival. The presence of mature longleaf pines surrounding the uncut gap edges, however, initially had a positive effect on within-gap seedling survival. In October 1999, survival was significantly lower in the gap center (C1 = 23%) than along the gap edge (C3 = 51%; Fig. 3b). Similar results were found during the 2000 growing season (C1 = 19%, C3 = 36%; Fig. 4b); however, the relative advantage associated with the gap edge position on seedling survival diminished over time, i.e., decreases in relative seedling survival rates between years was greater along the gap edge (−15%) than in the gap center (−4%). This represented a reversal from that observed in 1999 and suggests that the protective shelter effect provided by overstory trees near the gap edge diminished after the seedlings became established.

During the 1999 growing season, seedling survival was inversely related to PAR transmittance. PAR transmittance was highest near the gap center, where survival was lowest. Conversely, PAR transmittance was lowest along the gap edge, where survival was highest ($r^2 = 0.22$; Fig. 5a). This relationship was strongest ($r^2 = 0.28$) for the southern rings (Fig. 5b). Correlations between PAR transmittance and survival were similar for the 2000 growing season ($r^2 = 0.10$ for all plots; $r^2 = 0.19$ for the southern plots alone). Within-gap direction did not significantly affect seedling survival during either growing season; however, seedlings planted in the northern zone, along the gap center, had the lowest first year survival (19%; Fig. 3b) of all gap positions.

Longleaf pine seedling growth was also affected by variation in the within-gap environments for both the

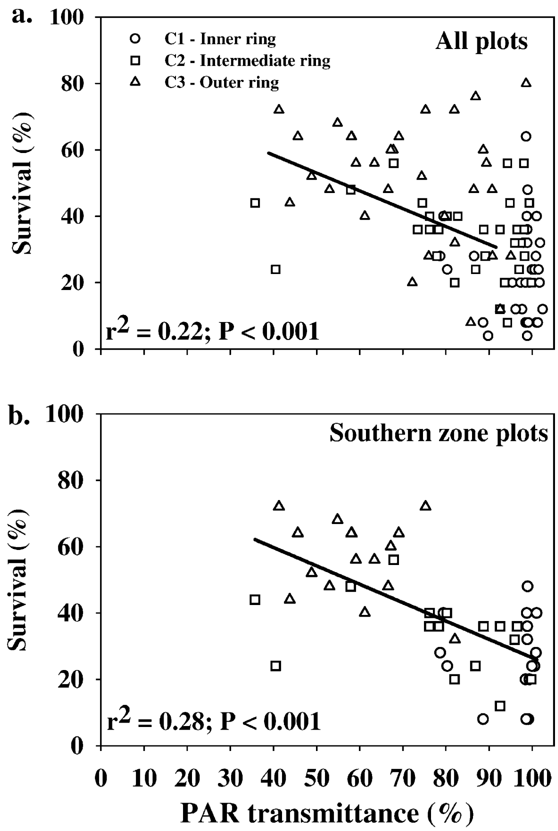

Fig. 5. PAR transmittance and longleaf pine seedling survival by ring (distance from gap edge) and gap direction (north vs. south) during the 1999 growing season in artificially created canopy gaps in northwest Florida. Survival was averaged across all gaps for (a) all longleaf pine seedlings (averaged across both gap directions), and (b) longleaf pine seedlings in the southern canopy gap only.

1999 and 2000 growing seasons. Seedling diameter increments increased significantly as distance from the gap edge increased and levels of PAR transmittance increased. Diameter increments were largest along the gap center and the intermediate rings (C1 = 2.6 mm, C2 = 2.7 mm in 1999; C1 = 3.6 mm, C2 = 3.2 mm in 2000; Figs. 3c and 4c), where average growing season PAR transmittance was highest. Seedling diameter increments were smallest along the gap edge (C3 = 1.7 mm in 1999; C3 = 1.4 mm in 2000), where average growing season PAR transmittance was lowest.

In a related study, Smith (1955) found that longleaf pine seedlings established within 3 m of mature pines were significantly smaller than those seedlings located 6–9 m from the base of the trees. The negative effects that mature trees have on seedling growth could be attributed in part to decreased light availability near the intact canopy edge. For example, decreased seedling growth in response to decreased light availability has been found in a variety of forest types (Minckler and Woerheide, 1965; McDonald and Abbott, 1994; Pacala et al., 1994; Brown, 1996; Palik et al., 1997; McDonald and Reynolds, 1999; Drobyshev and Nihlgård, 2000; McGuire et al., 2001). In this study, however, PAR transmittance only partially explained the differences in seedling growth. PAR transmittance was significantly higher in the northern zone of the gap, yet there were no significant differences in seedling diameter increments between the two directions (north = 2.2 mm, south = 2.3 mm in 1999; north = 2.7 mm, south = 3.1 mm in 2000). Therefore, although PAR transmittance significantly increased as distance from gap edge increased, the lack of differentiation in growth between gap directions indicated that other limiting factors, such as soil nutrient availability (Palik et al., 1997; McGuire et al., 2001), could also be affecting growth. Continued monitoring of the seedling growth dynamics will be needed to fully understand these interactions. In addition, studies conducted over an array of site conditions (from wet savannas to xeric sandhills) are needed to determine if similar processes occur across the range of the longleaf pine ecosystem.

The survival and growth of longleaf pine seedlings in this study were recorded in the absence of prescribed fire. Other studies in longleaf pine stands have suggested that these survival patterns may be reversed following the introduction of prescribed fire (Grace and Platt, 1995; Brockway and Outcalt, 1998). For example, the presence of mature trees along the gap edges may indirectly affect seedling survival by first reducing diameter increment due to shading effects (Croker and Boyer, 1976; Grace and Platt, 1995) and, second, by increasing fuel loads along the gap edges, resulting in higher fire temperatures (Grace and Platt, 1995; Brockway and Outcalt, 1998). Brockway and Outcalt (1998) suggested that, in xeric sandhill longleaf pine forests, a seedling exclusionary zone extended 12–16 m from the gap edge, and was caused by increased fire intensity and increased fine root competition from mature trees adjacent to the gap openings. An indication that this pattern may emerge in this study, even in the absence of fire, was the reversal in relative seedling survival trends noted previously between the center and the edge of the gaps.

3.3. Longleaf pine seedling response to fertilization and hand weeding

Longleaf pine seedlings that received the fertilizer plus hand weeding treatment had significantly lower survival rates during the 1999 growing season compared to the untreated control (control = 41%, treated = 31%; Fig. 6a). No significant differences were detected, however, between treatments in seedling survival during the 2000 growing season (control = 29%, treated = 25%; Fig. 6b). Decreases in seedling survival in 1999 on the treated subplots may have been accentuated by the drought conditions that began soon after the seedlings were planted and treated with fertilizers. There were no significant interactions between treatment and gap position (distance and direction within a gap), although the negative effects of the fertilizer and hand weeding treatment on survival in 1999 appeared to be less severe along the gap edge (C1 = 23%, C3 = 51%).

In contrast, seedling growth responses were positive to the fertilizer and hand weeding treatment. In 1999, diameter increments were 41% greater for the fertilizer and hand weeding treatment compared to the untreated control (control = 1.7 mm, treated = 2.9 mm; Fig. 6c). Similar results were found in 2000, with growth responses averaging 47% (control = 2.0 mm, treated = 3.8 mm; Fig. 6d). As soil nutrient levels were low and well below published critical levels for southern pines (Pritchett and Comerford, 1983; Allen, 1987), growth responses should continue to be strong on the treated plots. Phosphorus deficiencies have been especially common in this region of Florida, and growth responses to fertilization exceeding 2-fold have been documented over a 25-year rotation with slash pine (Jokela et al., 1989).

4. Summary and implications for longleaf pine management

Over the course of two growing seasons, surface soil moisture content did not vary significantly within the canopy gaps of a mature longleaf pine stand in

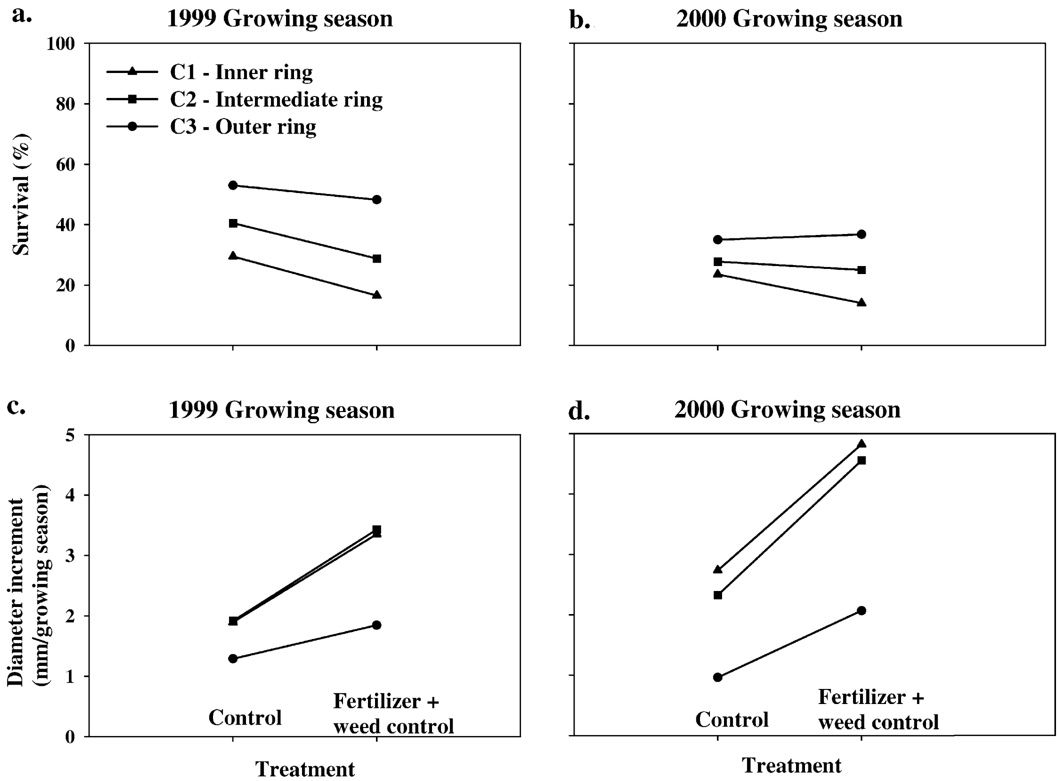

Fig. 6. The effects of fertilizer additions and competition control on longleaf pine: (a) survival in 1999; (b) survival in 2000; (c) diameter increment in 1999; (d) diameter increment in 2000.

northwest Florida. Light levels within canopy gaps, however, were heterogeneous. Seedlings growing in the center gap position had significantly lower survival rates, but larger diameter increments, than those seedlings growing along the gap edges that were exposed to corresponding lower levels of PAR.

The fertilizer and hand weeding treatment significantly decreased seedling survival during the 1999 growing season. However, seedling growth response, measured as diameter increment over both growing seasons, averaged 44% greater on the fertilizer and weeded plots than the untreated controls. There were no significant growth interactions between gap positions and the fertilizer and weeding treatment during either growing season.

In this study, seedling response to increased site resource availability (i.e., expressed as increasing distance from gap edge or through the fertilizer and weeding treatment) involved a trade-off. Larger seedlings were generally located in gap areas having lower initial survival and higher resource availability (i.e., center of gap), while smaller seedlings were located in gap areas having higher initial survival and lower resource availability (i.e., edge of gap). A similar trade-off between seedling survival and growth was found in a canopy gap study conducted with western conifers (Gray and Spies, 1996).

Based on these results, a group selection silvicultural system that creates canopy openings large enough to provide relief from competition (for light and nutrients) may facilitate gap-phase regeneration on flatwoods sites, while maintaining continuous canopy cover. Fertilization and weed control treatments would also prove effective in promoting seedling growth on similar sites, but they may be more beneficial if delayed until the seedlings have become established (e.g., age 2–3 years) to prevent lower survival rates, especially during periods of prolonged drought.

Before specific recommendations for the group selection silvicultural system can be made for longleaf pine, at least two additional areas of research are required. First, the optimal size and shape of canopy openings that promote high seedling survival and growth must be determined for both artificially and naturally regenerated stands. Previous studies have generally suggested that larger seedlings will be associated with larger canopy openings. There will likely be a maximum gap size, however, after which enlarging the opening would not provide additional benefits for growth (Minckler and Woerheide, 1965). For example, as gap size and light availability increases, competition from herbaceous and shrubby understory plants may be accentuated and thereby decrease pine growth, especially on sites having low soil nutrient capital (Neary et al., 1990; Jokela and Martin, 2000; McGuire et al., 2001). In addition, the appropriate arrangement of these openings across the landscape needs to be determined (i.e., how many openings per hectare, and how much variation in size and shape is desirable). Although the shade-intolerant nature of longleaf pine makes it a reasonable candidate for the group selection silvicultural system, recent evidence also suggests that gaps as small as 0.1 ha were large enough to promote acceptable seedling growth and, hence, the potential application of the single-tree selection system (McGuire et al., 2001).

To begin answering these questions, a larger network of designed studies (i.e., artificially created gap openings), replicated across a range of site types, is needed to assemble the long-term data required to understand regeneration processes and the subsequent growth and development of multi-cohort stands. Alternatively, regeneration studies could be conducted in canopy openings formed by natural disturbances. In either case, selecting silvicultural systems for effectively managing longleaf pine forests (e.g., group selection, single-tree selection, shelterwood, clearcut) should be based on satisfactorily meeting the ecological requirements of this species and satisfying the management objectives of the landowner.

Acknowledgements

This research was supported by the Florida Agricultural Experiment Station and is approved for publication as Journal Series No. R-08545. The Tall Timbers Research Station and the Apalachicola National Forest are gratefully acknowledged for providing financial and logistical support for this research. Special thanks are extended to R.J. English, R. Duncan, D. Farnsworth, E. Bain, H. Heckathorne and K. Owen for technical field assistance.

References

Allen, H.L., 1987. Forest fertilizers: nutrient amendment, stand productivity, and environmental impact. J. For. 85, 37–46.

Baker, J.B., 1991. Alternative silvicultural systems—south. In: Proceedings of the National Silviculture Workshop on Silvicultural Challenges and Opportunities of the 1990s, Petersburg, AK, July 10–13, 1989. US Forest Service, New Orleans, LA, pp. 51–60.

Barnett, J.P., Lauer, D.K., Brissette, J.C., 1990. Regenerating longleaf pine with artificial methods. In: Proceedings of the Symposium on the Management of Longleaf Pine, New Orleans, LA, April 4–6, 1989. US Forest Service, New Orleans, LA, pp. 72–92.

Boyer, W.D., 1979. Regenerating the natural longleaf pine forest. J. For. 77, 572–575.

Boyer, W.D., 1990. Longleaf pine. In: Burns, R.M., Honkla, B.H. (Eds.), Silvics of North America. US Department of Agricultural Handbook 654.

Boyer, W.D., 1993. Long-term development of regeneration under longleaf pine seedtree and shelterwood stands. South. J. Appl. For. 17, 10–15.

Boyer, W.D., White, J.B., 1990. Natural regeneration of longleaf pine. In: Proceedings of the Symposium on the Management of Longleaf Pine, New Orleans, LA, April 4–6, 1989. US Forest Service, New Orleans, LA, pp. 94–113.

Brockway, D.G., Outcalt, K.W., 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. For. Ecol. Mgmt. 106, 125–139.

Brockway, D.G., Outcalt, K.W., 2000. Restoring longleaf pine wiregrass ecosystems: hexazinone application enhances effects of prescribed fire. For. Ecol. Mgmt. 137, 121–138.

Brown, N., 1996. A gradient of seedling growth from the centre of a tropical rain forest canopy gap. For. Ecol. Mgmt. 82, 239–244.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20, 620–631.

Croker, T.C., 1975. Seedbed preparation aids natural regeneration of longleaf pine. US Forest Service Research Paper SO-112.

Croker, T.C., 1979. Longleaf pine: the longleaf story. J. For. Hist. 23, 32–43.

Croker, T.C., Boyer, W.D., 1976. Regenerating longleaf pine naturally. US Forest Service Research Paper SO-105.

Dennington, R.W., Farrar, R.M., 1983. Longleaf pine management. US Forest Service For. Report R8-FR 3.

Drobyshev, I., Nihlgård, B., 2000. Growth response of spruce saplings in relation to climatic conditions along a gradient of gap size. Can. J. For. Res. 30, 930–938.

Farrar, R.M., 1996. Fundamentals of uneven-aged management in southern pine. In: Moser, W.K., Brennan, L.A. (Eds.), Tall Timbers Research Station Miscellaneous Publication No. 9, Tallahassee, FL.

Grace, S.L., Platt, W.J., 1995. Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). J. Ecol. 83, 75–86.

Gray, A.N., Spies, T.A., 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. J. Ecol. 84, 635–645.

Gray, A.N., Spies, T.A., 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78, 2458–2473.

Hanlon, E.A., Gonzalez, J.S., Bartos, J.M., 1994. IFAS Extension Soil Testing Laboratory Chemical Procedures and Training Manual. IFAS Circular 812. Florida Cooperative Extension Service, University of Florida, Gainesville, FL, pp. 15–16, 19.

Jokela, E.J., Martin, T.A., 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. Can. J. For. Res. 30, 1511–1524.

Jokela, E.J., Harding, R.B., Nowak, C.A., 1989. Long-term effects of fertilization on stem form, growth relations, and yield estimates of slash pine. For. Sci. 35, 832–842.

Maple, W.R., 1977. Planning longleaf pine regeneration cuttings for best seedling survival and growth. J. For. 75, 25–27.

McDonald, P.M., Abbott, C.S., 1994. Seedfall, regeneration, and seedling development in group-selection openings. US Forest Service Research Paper PSW-RP-220.

McDonald, P.M., Reynolds, P.E., 1999. Plant community development after 28 years in small group-selection openings. US Forest Service Research Paper PSW-RP-241.

McGuire, J.P., Mitchell, R.J., Moser, E.B., Pecot, S.D., Gjerstad, D.H., Hedman, C.W., 2001. Gaps in a gappy forest: plant resources, longleaf pine regeneration, and understory response to tree removal in longleaf pine savannas. Can. J. For. Res. 31, 765–778.

Minckler, L.S., Woerheide, J.D., 1965. Reproduction of hardwoods 10 years after cutting as affected by site and opening size. J. For. 64, 103–107.

Neary, D.G., Jokela, E.J., Comeford, N.B., Colbert, S.R., Cooksey, T.E., 1990. Understanding competition for soil nutrients—the key to site productivity on southeastern Coastal Plain Spodosols. In: Gessel, S.P., Lacate, D.S., Weetman, G.F., Powers, R.F. (Eds.), Sustained Productivity of Forest Soils. Proceedings of the Seventh North American Forest Soils Conference, Vancouver, BC, July 24–28, 1988. Faculty of Forestry, University of British Columbia, Vancouver, BC, pp. 432–450.

Nelson, D.W., Sommers, L.E., 1982. Total carbon, organic carbon and organic matter. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis II, Vol. 9. American Society of Agronomy, Madison, WI.

Pacala, S.W., Canham, C.D., Silander, J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. 24, 2172–2183.

Palik, B.J., Pederson, N., 1996. Overstory mortality and canopy disturbances in longleaf pine ecosystems. Can. J. For. Res. 26, 2035–2047.

Palik, B.J., Mitchell, R.J., Houseal, G., Pederson, N., 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. Can. J. For. Res. 27, 1458–1464.

Phillips, D.L., Shure, D.J., 1990. Patch-size effects on early succession in southern Appalachian forests. Ecology 71, 204–212.

Pritchett, W.L., Comerford, N.B., 1983. Nutrition and fertilization of slash pine. In: Stone, E.L. (Ed.), The Managed Slash Pine Ecosystem. Proceedings of the Symposium held at the University of Florida, Gainesville, FL, June 9–11, 1981, pp. 69–90.

SAS Institute, 1996. SAS Software for Windows, Release 6.11. SAS Institute, Inc., Cary, NC.

Smith, L.F., 1955. Development of longleaf pine seedlings near large trees. J. For. 53, 289–290.

SRIEG 18, 1983. Reference soil test methods for the southern region of the United States. Southern Cooperative Series Bulletin 289. University of Georgia, Athens, GA.

USDA Forest Service, 1999a. Final environmental impact statement for the revised land and resource management plan for National Forests in Florida. US Forest Service Management Bulletin R8-MB-83B.

USDA Forest Service, 1999b. Revised land and resource management plan for National Forests in Florida. US Forest Service Management Bulletin R8-MB-83A.

Wahlenberg, W.G., 1946. Longleaf Pine: Its Use, Ecology, Regeneration, Protection, Growth, and Management. Charles Lathrop Pack Forestry Foundation, Washington, DC.

Wilczynski, C.J., Pickett, S.T.A., 1993. Fine root biomass within experimental canopy gaps: evidence for a belowground gap. J. Veg. Sci. 4, 571–574.