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# Characteristics of gaps and natural regeneration in mature longleaf pine flatwoods ecosystems

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## Abstract

Developing uneven-aged structure in mature stands of longleaf pine requires scientifically based silvicultural systems that are reliable, productive and sustainable. Understanding seedling responses to varying levels of site resource availability within forest gaps is essential for effectively converting even-aged stands to uneven-aged stands. A project was initiated on the Apalachicola National Forest in Northwestern Florida to examine these relationships, particularly as they would apply to the group selection forest reproduction method.

This study used a line transect technique to examine gaps formed in mature stands of longleaf pine by either natural disturbances or prior intermediate silvicultural operations (i.e., thinnings). The expanded gap sizes ranged from 32 to 1161 $m^2$; however, 86% of all gaps sampled in this study were less than 600 $m^2$ in size. Mean and median expanded gap sizes were 402 and 334 $m^2$, respectively. Gap shapes were irregular and significantly different from a circle. Seedling stocking ranged from 0 to 43% and density ranged from 0 to 9800 seedlings $ha^{-1}$. Neither gap size nor shape significantly affected seedling numbers or root collar diameters (RCDs). In contrast, proximity to mature longleaf pine affected both seedling numbers and RCD. Seedling numbers increased considerably $\geq$5 m from mature trees. Significant decreases in seedling RCD, resulting from interspecific competition with mature longleaf pine, were detected and most strongly expressed outside the gaps (average RCD = 21 and 16 mm inside and outside gaps, respectively). In general, seedling stocking within the gaps was low (average 16%).
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## 1. Introduction

Temporary increases in site resource availability (i.e., light, water, nutrients) within canopy gaps have been documented in a variety of forest types (Denslow, 1980; Brandani et al., 1988; Canham et al., 1990; Phillips and Shure, 1990; Pacala et al., 1994; Palik et al., 1997; McGuire et al., 2001). The magnitude and

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duration of these increases depend on characteristics of the gap (gap size, shape, height and diameter of surrounding trees; Denslow, 1980) and the structure of the surrounding stand (e.g., basal area). Larger openings tend to support higher levels of available site resources compared to smaller gaps (Denslow, 1980; Phillips and Shure, 1990; Bradshaw, 1992; Gray and Spies, 1996; Palik et al., 1997; Drobyshev and Nihlgård, 2000; McGuire et al., 2001).

Gap shape may also be important in determining site resource availability (Canham et al., 1990; Lertzman and Krebs, 1991; Battles et al., 1996). In general, when the shapes of gaps are more irregular, the effects that edge has on the inner-gap environment become more pronounced because of increased competition for both aboveground (light) and belowground (water, nutrients) resources. These changes in light, soil moisture, nutrient availability and temperature suggest that a microsite resource gradient exists between the gap center and gap edge (Gray and Spies, 1997; Gagnon et al., 2003).

A temporary increase in within-gap site resource availability and its effects on seedling demography may be most apparent in gaps formed in stands having dense overstories (Palik et al., 1997). Conversely, those forest types that characteristically have sparse canopies may have more diffuse and less spatially concentrated increases in site resources (Runkle, 1992; Palik et al., 1997), as observed in longleaf pine (*Pinus palustris* Mill.) stands having less than 50% canopy closure (Palik and Pederson, 1996; Palik et al., 1997). In such cases, it is difficult to assess the role that gap characteristics have on regeneration processes, especially when information on the interactions between gap characteristics and the ecological requirements of a species are not well understood. Some of the characteristics of longleaf pine, such as the requirement of a bare mineral soil seedbed (Wahlenberg, 1946; Croker, 1975; Dennington and Farrar, 1983; Boyer, 1990), rapid germination (Wahlenberg, 1946; Boyer, 1990), and intolerance of understory competition (Dennington and Farrar, 1983; Barnett et al., 1990), might identify it as a pioneer species (large gap specialist; Denslow, 1980; Boyer, 1993). However, other attributes, such as sporadic seed crops (Croker, 1975; Dennington and Farrar, 1983; Boyer, 1990; Boyer and White, 1990) large seeds (Boyer, 1990), poor seed dispersal (Wahlenberg, 1946; Croker and Boyer, 1976; Boyer, 1990), development of extensive root systems (Wahlenberg, 1946; Boyer, 1990) and the ability to persist in the understory (Smith, 1955), are indicative of a small gap specialist (Denslow, 1980).

Although mature overstory trees have been shown to affect the survival and/or growth of nearby longleaf pine seedlings (Smith, 1955; Grace and Platt, 1995; Palik et al., 1997; McGuire et al., 2001; Gagnon et al., 2003), studies characterizing the structure of canopy gaps in these ecosystems are limited (Palik and Pederson, 1996; Palik et al., 1997; Brockway and Outcalt, 1998; McGuire et al., 2001). Quantifying gap size and shape, and the location and size of the regeneration within gaps are essential for understanding the complex interactions between overstory and understory vegetation. A more complete understanding of these processes will also aid in the development of silvicultural systems that are designed to closely mimic patterns of natural disturbance that lead to successful seedling recruitment (Lertzman et al., 1996; Palik and Pederson, 1996; Brockway and Outcalt, 1998).

The objectives of this study were to (1) characterize the size and shape of gaps formed by natural disturbances or intermediate silvicultural operations applied in mature stands of longleaf pine and (2) quantify the location, abundance, and root collar diameter (RCD) of longleaf pine seedlings within and around these canopy gaps.

## 2. Methods

### 2.1. Study site

The study was conducted on the 116,384 ha Apalachicola Ranger District of the Apalachicola National Forest in Northwestern Florida (30°07′N 85°00′W). The flat to gently rolling terrain is interspersed with bayheads and cypress swamps (*Taxodium* spp. Rich.). The climate is humid subtropical, with an annual rainfall of 1670 mm. The soils vary among sites and include Grossarenic Paleudults, Aeric Alaquods, Plinthaquic Paleudults, Typic Quartzipsamments, Typic Albaquults, Plinthic Kandiudults, Aeric Paleaquults, and Umbric Paleaquualts. The dominant understory vegetation consists of wiregrass (*Aristida beyrichiana* Trin. & Rupr), running oak (*Quercus pumila* Walter), dwarf live oak (*Quercus minima* (Sarg.)

Small), saw palmetto (*Serenoa repens* (W. Bartram) Small) and bluestem grasses (*Andropogon* spp. L.).

Eight 12-ha (200 m × 600 m) study sites were selected in mature stands of longleaf pine located on flatwoods sites. The sites were paired by US Forest Service compartment number (i.e., two blocks located in each of four compartments). Advanced regeneration was present in discrete patches throughout the stands and the canopies were dominated by irregularly shaped openings. All study sites were harvested between 1913 and 1927. Suppressed and non-merchantable trees that were left on site provided the seed source to naturally regenerate the second-growth stand. Three pairs of study sites were thinned to a residual basal area of 16 $m^2\,ha^{-1}$ in 1985, 1990 and 1991, respectively; the other pair was thinned to a residual basal area of 11 $m^2\,ha^{-1}$ in 1984. Current stand basal areas varied significantly among sites and ranged from 9 to 17 $m^2\,ha^{-1}$.

### 2.2. Experimental design

The sites used in this study were originally established to monitor the effects of seasonal prescribed burning on avian populations (Engstrom et al., 1996). The eight study sites were subdivided into a permanently marked grid network of 50 m × 50 m plots using metal fence posts. Three 600 m line transects, established at 50 m intervals lengthwise throughout the blocks, were used to locate gaps (Runkle, 1992; Clinton et al., 1993, 1994; Battles et al., 1996). Plot centers were systematically located every 100 m along the transects, resulting in six plot centers per transect, 18 per block, and 144 total for the study. Plot centers in wet depressions that were dominated by slash pine (*Pinus elliottii* var. *elliottii* Engelm.) and hardwood species (permanent gaps) were not sampled. The omission of permanent gaps reduced the sample size to 141. The initial plot centers for transects 1 and 3 were 100 m from the block edge, while the initial plot centers for transect 2 were 50 m from the block edge to prevent repeated sampling.

### 2.3. Procedures

#### 2.3.1. Gap characteristics

Estimates were made of expanded gap area, which included the ground area under the canopy opening and extended to the base of the trees surrounding the opening (Runkle, 1981, 1992). To estimate gap area, the major axis (the longest straight line that would fit into the gap) and the minor axis (the longest straight line that was perpendicular to the first and would fit in the gap) of the openings were measured. These measurements were used in the following formula based on an ellipse to calculate the area of the expanded gap (Runkle, 1981, 1992; Clinton et al., 1993; Battles et al., 1996)

$$A = \frac{1}{4}(\pi LW)$$

where $L$ is the length of major axis and $W$ the length of minor axis.

The openings in the longleaf pine canopy were irregularly shaped and appeared to more closely resemble complex polygons rather than ellipses (as proposed by Runkle (1992)). Battles et al. (1996) encountered a similar situation in an old-growth spruce-fir stand in New York. To account for this discrepancy, a second technique (similar to Lertzman and Krebs (1991) and referred to here as nearest neighbor method) was used to obtain an estimate of the expanded gap area. Distance from plot center to the nearest mature longleaf pine stem located in each of eight directions (N (338–23°), NE (24–68°), E (69–113°), SE (114–158°), S (159–203°), SW (204–248°), W (249–303°), and NW (304–337°)) was measured and a corresponding compass bearing was recorded. A hand-held Global Positioning System (GPS) (Trimble Geo Explorer II, accuracy of 3 m with differential correction) was used to record the location of plot centers. The gap borders were digitized and the areas and perimeters were calculated using the Arc View Geographical Information System (GIS). Wilcoxon's Sign-Rank Test was used to compare the gap areas calculated by the two methods and no significant differences were found ($P > 0.10$). The objectivity of the nearest neighbor method, however, made it the preferred technique, and the results from this method were used in the analyses. In addition, the heights and diameters of the border trees were measured.

#### 2.3.2. Regeneration characteristics

Brockway and Outcalt (1998) reported that gaps on xeric sandhill sites having radii less than 12–16 m had high levels of fine root competition that inhibited establishment and growth of longleaf pine seedlings.

Based on their findings, the gaps in this study were divided into two groups: large gaps (>600 $m^2$) and small gaps ($\leq$600 $m^2$). To characterize seedling demography, circular 0.0001 ha plots were established at 4 m intervals along the major and minor axes of all large gaps and in four randomly selected small gaps per site ($n = 32$). In the largest gaps, or those gaps having highly irregular borders, additional axes were located perpendicular to the major axis to obtain a representative sample. All axes were also extended 4 m outside of the gaps to determine whether seedling recruitment was occurring under closed canopy conditions. In total, 746 seedling plots were established and monitored. Within each plot, distance to the nearest mature longleaf pine was determined, and the number and RCD of germinants (<3 mm) and juveniles (3–25 mm) were recorded.

### 2.3.3. Statistical analyses

SAS software (V. 6.11 for Windows) was used to examine relationships among gap and seedling characteristics. Mixed models were developed using average number and RCD of seedlings as dependent variables. Gap area, the ratio of gap perimeter to gap area (P:A), average height and diameter of surrounding trees, plot location (inside or outside gap), and distance from plot center to the nearest mature competitor were included in the models as independent variables. No statistical differences were found for seedlings and germinants, so the two size classes were pooled for analyses. Relationships were examined at the plot, gap, and block levels and all significance tests were made at the $\alpha = 0.10$ level. Alternative models were compared based on Schwartz's Bayesian Criterion (Littell et al., 1996). Residual values versus predicted values were plotted to examine the models for bias.

## 3. Results and discussion

### 3.1. Gap characteristics

Definable canopy gaps were present at each of the 141 sample plot locations. The area of the expanded gaps ranged from 32 to 1161 $m^2$. The mean and median expanded gap areas were 403 and 334 $m^2$, respectively (Fig. 1). Twenty-one of the gaps were classified as large, but the majority of gaps were small

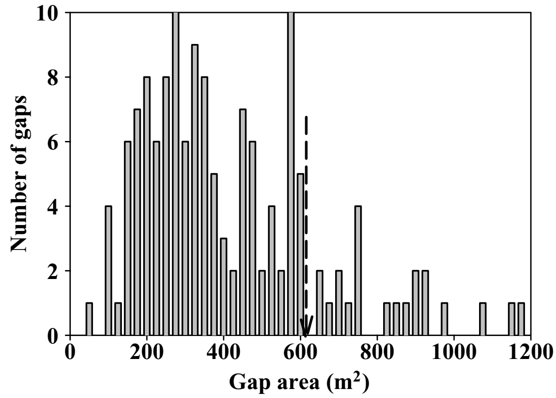


Fig. 1. Distribution of canopy gap areas (25 $m^2$ size-classes) sampled in mature longleaf pine stands on flatwoods sites in Northwestern Florida. The arrow indicates the cutoff point between small gaps (<600 $m^2$) and large gaps (>600 $m^2$) as proposed by Brockway and Outcalt (1998).

(86%, $n = 120$). Palik and Pederson (1996) also identified numerous small gaps in mature longleaf pine stands on mesic uplands, but Brockway and Outcalt (1998) reported the presence of larger forest gaps (1000–2000 $m^2$) on xeric sandhill sites and did not regard the small interstitial spaces between the tree crowns as functional canopy gaps.

Gap shapes were irregular and differed significantly from that of a circle (Fig. 2). Battles et al. (1996) identified the P:A ratio as a useful ecological indicator for assessing the irregularity of an opening, with a

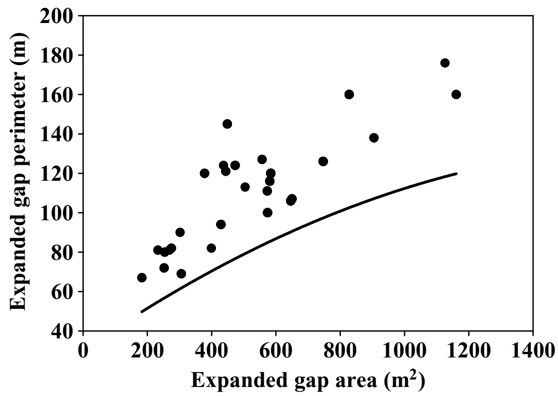


Fig. 2. Perimeter–area relationships for expanded canopy gaps in mature longleaf pine stands. The line plots the area–perimeter relationship for a circle (after Lertzman and Krebs, 1991; Battles et al., 1996) and the circles plot the actual data.

Table 1
Comparison of characteristics of canopy openings (gaps) in a variety of forest types in North America

| Forest type | Location | Range of gap areas ($m^2$)[a] | Mean ($m^2$) | Median ($m^2$) | Gap shape |
|---|---|---|---|---|---|
| Mature longleaf pine (current study) | Northwestern Florida, USA | 32–1161[b] | 402 | 334 | Irregular polygon |
| Upland mixed deciduous (Goldblum, 1997) | New York, USA | 5–130 (canopy gap) | – | – | Elliptical |
| Old-growth sub-alpine spruce-fir (Battles et al., 1996) | New York, USA | 10–575 | – | – | Non-convex polygon |
| Mixed oak (Clinton et al., 1993) | Southern Appalachians, USA | 40–850 | 239 | 152 | Elliptical |
| Sub-alpine old-growth western/mountain hemlock, Pacific silver-fir, Alaska yellow-cedar (Lertzman and Krebs, 1991) | Southwest British Columbia, Canada | 25–1127 | 286 | 203 | Irregular |
| Old-growth Douglas-fir/western hemlock (Spies et al., 1990) | Western Oregon, Washington, USA | 25–380 (canopy gap) | – | 85 | Irregular |
| Mature Douglas-fir/western hemlock (Spies et al., 1990) | Western Oregon, Washington, USA | 25–309 (canopy gap) | – | 19 | Irregular |
| Old-growth mesic (Runkle and Yetter, 1987) | Eastern USA | 1–1490 | 65 | – | Elliptical |

[a] All gap areas reported were calculated based on the expanded gap definition, unless otherwise noted.
[b] These stands were previously thinned.

higher P:A indicating a stronger influence of the forest edge on the interior of an opening. The P:A ratio for gaps in this study ranged from 0.1 to 0.5. Both the mean and median P:A ratios were 0.3 and reflected greater amounts of edge per unit area than found for a circle. Edge effect has been shown to have a strong influence on resource availability within gaps in closed canopy forests (Canham et al., 1990; Battles et al., 1996). In this study, however, we found that the P:A ratio did not significantly influence longleaf pine seedling stocking, density or RCD. The low basal area of the stand surrounding the gaps may have moderated the edge effects so that differences in site resource availability between the gap and the intact canopy were negligible in terms of meeting the ecological requirements for longleaf pine germination, survival and growth.

Table 1 compares characteristics of canopy openings in a variety of forest types in North America. The range of expanded gap areas found in this study was similar to that measured in sub-alpine old-growth forests in southwestern British Columbia, Canada (Lertzman and Krebs, 1991) and old-growth mesic forests in the eastern United States (Runkle and Yetter, 1987). Yet, the mean and median patch sizes found in these mature longleaf pine stands were larger than corresponding values reported for these other forest types. This suggests that the longleaf pine stands had a higher frequency of larger patches that was presumably associated with lower basal areas (9–17 $m^2$ $ha^{-1}$) and limited canopy closure. The larger gap sizes may also be attributed to anthropogenic disturbances (i.e., thinning) which occurred in these stands.

### 3.2. Regeneration characteristics

Longleaf pine seedling stocking (averaged by gap size class) ranged from 0 to 43% and densities ranged from 0 to 9800 seedlings $ha^{-1}$ (Table 2). Although a correlation between number of seedlings and size of gaps has been demonstrated with other species (Clinton et al., 1994; Goldblum, 1997), seedling stocking and density were unrelated to gap size in these mature longleaf pine stands. The number of seedlings in the expanded gaps was also not significantly related to location of the plots or the average height or diameter of the trees surrounding the opening. However, the number of seedlings noticeably increased at a distance of approximately 5 m from mature competitors (Fig. 3). This threshold distance may have resulted from intense competition between seedlings and mature trees, which produced smaller seedlings in this zone which were not able to survive periodic prescribed fires (Grace and Platt, 1995; Brockway and Outcalt, 1998). In a related study, Gagnon et al. (2003) found light availability decreased by 24% along gaps edges in mature longleaf

Table 2
Longleaf pine seedling density and stocking (by gap area size class) within gaps in mature longleaf pine stands in Northwestern Florida, USA

| Gap area ($m^2$) | Number of gaps | Percent stocking | Range (%) | Density (seedlings $ha^{-1}$) | Range (seedlings $ha^{-1}$) |
|---|---|---|---|---|---|
| 0–100 | 3 | 0 | N/A | 0 | 0 |
| 101–200 | 3 | 17 | 0–29 | 60 | 0–180 |
| 201–300 | 11 | 11 | 0–30 | 240 | 0–1320 |
| 301–400 | 7 | 12 | 0–40 | 229 | 0–600 |
| 401–500 | 8 | 14 | 0–33 | 1000 | 0–4160 |
| 501–600 | 10 | 19 | 0–59 | 1316 | 0–5750 |
| 601–700 | 2 | 43 | N/A | 2730 | 2100–3360 |
| 701–800 | 2 | 36 | 0–71 | 2730 | 0–5460 |
| 801–900 | 4 | 6 | 0–25 | 2450 | 0–9800 |
| 901–1000 | 1 | 13 | N/A | 2760 | N/A |
| 1001–1100 | 0 | N/A | N/A | N/A | N/A |
| 1101–1200 | 2 | 7 | 6–9 | 1195 | 640–1750 |

pine forests, resulting in significant decreases in RCD. In addition, high fuel loads near mature longleaf pine may have resulted in hotter prescribed fires and increased seedling mortality (Grace and Platt, 1995).

Seedling RCD was not affected by gap size, shape or the average height and diameter of the surrounding trees. However, the RCD of seedlings inside gaps was larger (21 mm inside versus 16 mm outside). A significant, but weak, relationship between seedling RCD and the distance to the nearest mature competitor was also identified. Seedling RCD increased as distance to mature overstory competition increased for seedlings located both inside ($r^2 = 0.07$) and outside ($r^2 = 0.20$) the gaps (Fig. 3). Grace and Platt (1995),

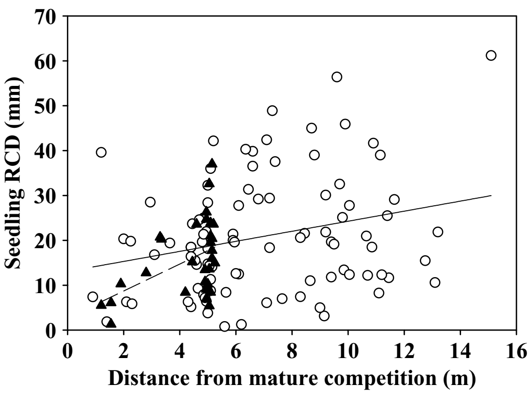


Fig. 3. Relationship between distance to nearest mature longleaf pine competitor and RCD of longleaf pine seedlings located both inside (○, solid line) and outside (▲, broken line) of canopy gaps.

Smith (1955) and Gagnon et al. (2003) found a similar correlation between the proximity of mature trees and longleaf pine seedling growth. This effect was strongest for seedlings located outside the gaps, where intraspecific competition increased due to higher densities of mature longleaf pine. Moderate increases in site resource availability within the gaps may have tempered the competitive interactions between the seedlings and the mature trees, resulting in a lower (although significant) correlation between seedling RCD and distance to mature competition inside the gaps. However, this regression was rather weak, leaving 93% of the variability unexplained, suggesting that other factors may strongly influence seedling RCD within gaps.

As shown in previous studies (Jackson, 1959; Spies et al., 1990; Gray and Spies, 1996), the presence of gaps affected seedling development by providing more opportunities for seedlings to become established further away from canopy trees, in areas with lower competition for limiting site resources. Seedling RCD increased as distance to mature trees increased, so the openings should have encouraged the growth of larger seedlings. The influence of gap size on seedling demography may have been obscured in this study by low stocking (average 16%). To achieve adequate longleaf pine regeneration, minimum gap sizes of 1400 $m^2$ have been recommended for mesic uplands (Palik et al., 1997, 2002) and 1250 $m^2$ for xeric sandhills (Brockway and Outcalt, 1998). In our study, the largest gaps identified were somewhat smaller (1161 $m^2$) than these recommendations.

## 4. Implications for longleaf pine management

The results of this study provide information on the patterns of gap formation and the nature of regeneration at the stand level. The abundance of small gaps suggests that silvicultural systems which create small canopy openings may adequately emulate naturally occurring gap dynamics. However, the low stocking levels suggest that these smaller gaps may not provide favorable microsites for seedling recruitment. Longleaf pine seedling abundance was not associated with gap size, possibly because the range of gap sizes identified did not include gaps larger than 1200 $m^2$. There was also variable production of seed, poor microsites, and seedling failures. In addition, longleaf pine seedling RCD, although not directly affected by gap size, was influenced by distance to mature overstory competition. Larger gaps should minimize competitive interactions between seedlings and mature trees and encourage seedling growth. These results suggest that silvicultural reproduction methods which create gaps of sufficient size and suitable shape to minimize the amount of edge-effect competition (larger, circular, elliptical or polygon openings) may be the most successful in obtaining and maintaining longleaf pine regeneration on flatwoods sites.

Studies examining the causes of gap formation (Palik and Pederson, 1996) and the availability of both aboveground and belowground site resource availability (Palik et al., 1997; Brockway and Outcalt, 1998; McGuire et al., 2001; Gagnon et al., 2003) have been conducted in mature stands of longleaf pine. However, the effects of site resource availability on natural regeneration processes need to be quantified at the stand level. In addition, the timing of periodic prescribed fires and their interactions with gap regeneration processes and long-term seedling survival and growth should be addressed.

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