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Gap-phase regeneration in longleaf pine wiregrass ecosystems

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Abstract

Naturally regenerated seedlings of longleaf pine are typically observed to cluster in the center of tree fall canopy gaps and be encircled by a wide zone from which they are generally excluded. Twelve representative canopy gaps distributed across 600 ha of a naturally regenerated uneven-aged longleaf pine forest in the sandhills of north central Florida were examined to determine which aboveground and belowground factors are responsible for development of this seedling exclusionary zone. Within 12 m of adult trees growing along the gap edge, significantly fewer longleaf pine seedlings were present. The canopy of overstory trees, however, extended only 4–5 m into the gap. The relatively open structure of the longleaf pine canopy (57% cover) allowed photosynthetically active radiation (PAR) to be evenly distributed upon the forest floor across each canopy gap. Thus, light avail-ability was not related to pine seedling clustering near gap centers. Significantly greater forest litter mass beneath adult trees (5 Mg ha^{-1}) could result in fires more intense than would be supported by the litter mass near gap centers (2.5 Mg ha^{-1}). However, litter mass was significantly elevated only within 4 m of the gap edge. The fine root biomass within 12 m of the gap edge (3–4.5 Mg ha^{-1}) was two to six times that measured near the gap center and most closely coincided with the width of the seedling exclusionary zone along the margin of each gap. Thus, while the canopy of adjacent adult trees may indirectly influence seedling mortality through deposition of needle litter and greater fire intensity within 4 m of the gap edge, the root systems of these adults also appear to directly compete with seedlings within 12–16 m of the gap edge for limited site resources. To effectively regenerate and sustain longleaf pine wiregrass ecosystems, caution should be used in prescribing single-tree selection harvest methods so as not to create gap openings so small (< 30 m diameter) that intraspecific competition from adult trees totally excludes seedlings. Group selection methods may prove more effective in creating canopy gaps of sizes suitable (≥ 40 m diameter) for ensuring that intraspecific competition from adults is maintained at a level which allows for survival and growth of seedlings. Shelterwood and deferment methods may also prove useful where more open canopy conditions are desired. However, the pine seedlings' need for light cannot be used as an appropriate rationale for application of clearcutting methods. © 1998 Elsevier Science B.V.

Keywords: *Pinus palustris* Mill.; *Aristida stricta* Michx.; Uneven-aged forest; Disturbance; Canopy gaps; Root gaps

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1. Introduction

Longleaf pine (*Pinus palustris*) forests were at one time among the most extensive ecosystems in North America (Landers et al., 1995). These forests occupied over 37 million ha prior to European settlement (Frost, 1993), ranging from poorly-drained flatwoods to xeric sandhills and rocky ridges (Boyer, 1990) along the Coastal Plain from Texas to Virginia extending well into central Florida and the Piedmont and mountains of northern Alabama and Georgia (Stout and Marion, 1993). Clearing land for crops and pasture (Myers and White, 1987; Ewel, 1990), converting to other southern pines such as loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii*), interrupting natural fire regimes (Streng et al., 1993), impeding longleaf pine regeneration and invasion by hardwood trees (Burns and Hebb, 1972) and more aggressive pines, including loblolly pine, slash pine and sand pine (*Pinus clausa*), have since then caused a progressive decline in longleaf pine, with current levels estimated at less than 1.2 million ha (Outcalt and Sheffield, 1996). Most remaining longleaf pine forests are aging without replacement (Kelly and Bechtold, 1990) and, with this ecosystem now occupying only about 4% of its original extent, habitat reduction has resulted in the increased rarity of 191 taxa of vascular plants (Hardin and White, 1989; Walker, 1993) and several vertebrate species.

In the eastern half of the Coastal Plain, longleaf pine is associated with wiregrass (*Aristida stricta*) in ecosystems often characterized by an open, park-like stand structure (Harper, 1914; Laessle, 1942; Edmisten, 1963). Few shrubs or hardwood trees are present, because understory grasses facilitate the ignition and spread of fire during the growing season (Landers, 1991). Longleaf pine and wiregrass function as keystone species that facilitate but are resistant to fire (Platt et al., 1988; Noss, 1989). They exhibit substantial longevity and demonstrate nutrient and water retention to a degree that reinforce their site dominance and minimize change in the plant community following disturbance (Landers et al., 1995). The longleaf pine wiregrass ecosystem exists in an environment influenced by large scale catastrophic disturbance, such as damaging tropical storms. Lightning is an important agent in individual tree mortality and creation of small scale disturbance in longleaf pine stands (Komarek, 1968; Taylor, 1974). The structure, pattern and diversity of this ecosystem is maintained by a combination of disturbance events and site factors (including lightning strikes, tree mortality and animal interactions at local scales and wind storms, soils and hydrologic regimes at broader scales), which result in large living trees, snags, coarse woody debris, forest canopy gaps and hardwood thickets (Snedaker and Lugo, 1972). Numerous organisms are adapted to this disturbance-prone, yet largely stable ecosystem. The high diversity of understory plants per unit area makes this one of the most species-rich plant communities outside the tropics (Peet and Allard, 1993).

The sandhills component of the longleaf pine wiregrass ecosystem is regarded by many as an endangered plant community (Means and Grow, 1985). Concern about loss of these unique forests (Noss et al., 1995) has stimulated discussion regarding how to effectively sustain this ecosystem. Success in this endeavor will depend on identifying the ecological processes needed to create conditions that ensure reliable regeneration of longleaf pine. Natural regeneration methods employing a regime of frequent fire are reportedly compatible with maintaining the longleaf pine wiregrass ecosystem (Boyer and White, 1990). However, the reproductive dynamics of sandhills longleaf pine, typically regenerating in forest canopy gaps, are not well understood and may provide additional insight into how silvicultural methods might be adapted to sustain resource values in this unique ecosystem.

Canopy gaps, resulting from a variety of disturbance agents, have recently become recognized as ecologically important features driving the forest cycle through open, growth and closed phases (Whitmore, 1989). Tree seedlings developing in gaps at differing time intervals result in a network of forest patches at various stages of development dispersed across the landscape (Pickett and White, 1985), similar to the shifting mosaic steady state (Bormann and Likens, 1979). Extensive research has been conducted on the reproductive dynamics of tree seedlings associated with canopy gaps in tropical forests (Putz, 1983; Brokaw, 1985; Denslow, 1987; Lawton and Putz, 1988; Uhl et al., 1988; Brokaw and Schneider, 1989; Schupp et al., 1989; Hartshorn, 1989; Brown, 1996), temperate deciduous forests (Runkle, 1984;

Canham, 1988; Clebsch and Busing, 1989; Lorimer, 1989, Veblen, 1989; Phillips and Shure, 1990; Clinton et al., 1994; Lajtha, 1994; Sipe and Bazzaz, 1995; Poulson and Platt, 1996; Goldblum, 1997) and temperate coniferous forests (Spies and Franklin, 1989; Spies et al., 1990; Waldrop, 1990; Lertzman and Krebs, 1991; Liu and Hytteborn, 1991; Lertzman, 1992; Battles et al., 1995; Lertzman et al., 1996).

Longleaf pine is a shade-intolerant tree species, with its regeneration largely confined to canopy gaps (Wahlenberg, 1946). Abundance and growth of seedlings have long been reported to be negatively related to the presence of adult longleaf pine (Walker and Davis, 1954; Davis, 1955; Smith, 1961). The competitive influence of individual trees and forest walls on seedlings is observed to extend 15 m or more from adult trees into forest gaps (Smith, 1955; Walker and Davis, 1956; Boyer, 1963). This competitive effect is so pronounced that naturally regenerating longleaf pine seedlings typically cluster near the center of canopy gaps and are encircled by a wide zone from which they are generally excluded. The most frequently mentioned mechanisms responsible for this seedling exclusionary zone are: (1) lower levels of light available along the gap edge than near the gap center and (2) greater accumulations of needle litter near overstory trees thus more intense fires along the gap margin than at the gap center (Boyer, 1974; Platt et al., 1988; Grace and Platt, 1995; Farrar, 1996). The relationship between canopy gap formation and root gap development and the potential for belowground interactions to influence gap-phase regeneration in the longleaf pine wiregrass ecosystem have not been fully explored.

Naturally occurring forest canopy gaps in a longleaf pine wiregrass ecosystem on the sandhills of north central Florida were examined to develop an improved understanding of the gap-phase regeneration dynamics of longleaf pine. Overstory attributes, canopy gap dimensions, photosynthetically active radiation (PAR), forest floor and root biomass were compared with the spatial distribution of longleaf pine seedlings within the gaps to: (1) identify the aboveground and belowground factors responsible for development of the seedling exclusionary zone along the interior margin of each canopy gap and (2) assess the importance of these exclusionary zone factors when prescribing single-tree selection, group selection, shelterwood and other silvicultural methods for sustainable management of the longleaf pine wiregrass ecosystem.

2. Methods and materials

2.1. Study site

This study was conducted on the Ocala National Forest in Marion County, north central Florida. The study site is located on Riverside Island (29°28′N, 81°50′W), one of largest remaining longleaf pine wiregrass areas along the Mount Dora Ridge (Laessle, 1958). The climate is humid subtropical (Chen and Gerber, 1990). Annual precipitation is abundant, averaging 1300 mm, with more than half of this arriving during the June to September season (Aydelott, 1966). Average monthly temperatures range from 21 to 28°C for the April to October period and from 14 to 19°C for November to March (NOAA, 1930–1985).

The study area is approximately 50 m above sea level in a sandhills landscape with rolling topography, devoid of surface drainages and characterized by closed depressions. Surface slopes at the study site range from nearly level (0–2%) to moderately inclined (up to 8%). The surface geology is underlaid by a bedrock of Ocala Limestone, a relatively pure calcium carbonate deposit dating to the Eocene, approximately 40 000 000 yrs old (Brooks, 1972). This limestone, also known as the Crystal River Formation, is largely responsible for the karst nature of the locale, forming numerous sinkholes and large springs (Brown et al., 1990). Above this limestone is the Citronelle Formation (Laessle, 1958), which occurs continuously throughout the central ridge of Florida over a distance of 240 km (Pirkle et al., 1963). The Citronelle Formation is composed of sand and gravel intermixed with clay (Brooks, 1972). Over this formation are aeolian dunes which developed during periods of climate and sea level fluctuation in the Pleistocene (Kalisz and Stone, 1984). Lands higher than 30 m above mean sea level remained above the ocean surface during the entire Pleistocene (Alt and Brooks, 1965).

Surface deposits are dominated by sands 2–3 m thick overlying the stratified sand, gravel and kaolinitic clays of the Citronelle Formation (Laessle, 1958). Soils developed in parent materials devoid of easily weathered primary minerals and consist of quartz sand with small amounts of iron and titanium (Kalisz and Stone, 1984). Clay-sized particles are primarily quartz, kaolinite, hydroxy–aluminum interlayered minerals and gibbsite (Carlisle et al., 1978). Soils present on the site are excessively drained entisols and typically exhibit little if any profile development (Brown et al., 1990). The predominant soil is the Astatula series (Typic Quartzipsamments, hyperthermic) which is low in organic matter, nutrients and water holding capacity (Aydelott et al., 1975). The terms 'wet desert' and 'desert in the rain' are commonly used to describe this environment since, while precipitation is abundant, this soil can become extremely dry within one week without substantial rainfall (Outcalt, 1993).

Overstory vegetation in this sandhills area is dominated by an uneven-aged longleaf pine forest, within a larger sand pine landscape matrix (Kalisz and Stone, 1984; Myers and White, 1987; Myers, 1990). Pollen evidence suggests that these have been the two principal ecosystems in this locale for the past 5000 yrs (Watts, 1971; Watts and Hansen, 1988). Repeated fires have maintained this longleaf pine ecosystem relatively free of shrubs and encouraged an abundance of grasses. Fire-suppressed turkey oak, (*Quercus laevis*), Chapman oak (*Quercus chapmanii*), sand live oak (*Quercus geminata*) and myrtle oak (*Quercus myrtifolia*) are associated with dwarf live oak (*Quercus minima*), scrub palmetto (*Sabal etonia*), prickly pear (*Opuntia humifusa*), shiny blueberry (*Vaccinium myrsinites*) and gopherapple (*Licania michauxii*) in the sparse shrub layer. Wiregrass, Curtiss dropseed (*Sporobolus curtissii*), broomsedge bluestem (*Andropogon virginicus*), lopsided indiangrass (*Sorghastrum secundum*), panic grass (*Panicum* spp.), sandgrass (*Triplasis* spp.) and yellow nutsedge (*Cyperus recurvata*) are among the prominent graminoids. Forbs commonly observed include partridge-pea (*Cassia chamaecrista*), tread-softly (*Cnidosculos stimulosus*), doveweed (*Crotan argyranthemus*), buckwheat (*Eriogonum tomentosum*), milkpea (*Galactia* spp.), wild indigo (*Indigofera caroliniana*), silverthread goldaster (*Pityopsis graminafolia*), dollarweed (*Rhynchosia* spp.), blue-eyed grass (*Sisyrinchium solstitiale*) and queens delight (*Stillingia sylvatica*).

2.2. Site history and study design

The study area is occupied by a second-growth uneven-aged longleaf pine forest that has naturally regenerated during the past 90 yrs. Numerous tree fall canopy gaps ranging from 40 to 50 m in diameter (0.1–0.2 ha) are distributed throughout this forest. Lightning is thought to be the principal disturbance agent followed by pathogens and insects in creating these gaps through tree mortality. Tornadoes are also responsible for creating some larger gaps and linear strings. Periodic growing-season fire every 3–4 yrs has maintained forest floor and understory conditions favorable for germination and growth of longleaf pine seedlings. Pine regeneration is abundant near the canopy gap centers.

Following an area reconnaissance in June 1991, twelve representative tree fall gaps within a 600-ha area were selected for study. Adult trees along the edge of each canopy gap were labeled and line transects from each adult tree to the gap center were installed. Along the line transects, data collection points were identified at intervals of 1, 4, 8, 12, 16, 20 and 24 m from the gap edge. The position of longleaf pine trees, saplings and seedlings were mapped in detail for five of the selected gaps.

2.3. Measurements

In July 1991, age, height, diameter at 1.4 m (dbh), crown radius, crown depth and distance to nearest seedling were measured for all adult trees growing along the edge of each canopy gap. Age in years was determined from increment core samples and tree height and crown depth in m were quantified using a Haga altimeter. Crown radius in m was estimated by vertical projection of the canopy and tree dbh in cm and distance to nearest seedling in m were directly quantified with measuring tapes. Along each line transect, seedling density, overstory canopy cover, forest litter mass and root biomass (including total roots, coarse roots and fine roots) were measured. Seedling density was quantified in 2 m × 2 m subplots. Overstory canopy cover was estimated by

Table 1
Overstory longleaf pine characteristics and relationships

	Mean	S.E.
Tree age (yr)	71.2	1.2
Tree height (m)	23.6	0.6
Tree diameter (cm at 1.4 m)	39.2	1.1
Tree crown radius (m)	5.1	0.3
Tree crown depth (m)	13.6	0.7
Tree distance to nearest seedling (m)	7.7	0.6
Sapling height (m)	5.5	1.0
Sapling diameter (cm at 1.4 m)	5.4	1.9

$n = 29$.

vertical projection. Forest litter samples were collected from 1 m × 1 m subplots and placed into paper bags. Soil cores 5.1 cm in diameter to assess root biomass to a depth of 20 cm were collected, placed in plastic bags and stored in a freezer until processed at the laboratory.

In December 1991, photosynthetically active radiation (400–700 nm) was measured using a sunfleck ceptometer (Decagon Devices, Pullman, WA, USA). PAR data were collected on the cloudless days of late fall, so comparisons among points would be valid without correction. The ceptometer was positioned to record PAR ($\mu E\ m^{-2}\ s^{-1}$) 1 m above the ground at regular intervals along all cardinal directions from the gap edge to the gap center. Measurements were begun at 1200, when the sun angle was greatest, and continued hourly until 1600, beyond which the changing sun angle had little if any effect on the solar radiation reading.

Soil samples were dry-sieved on 2-mm mesh and then wet-sieved with a wash bottle to remove all soil particles adhering to the roots. Live roots were then separated by hand from dead roots and divided into coarse root (> 5 mm diameter) and fine root (≤ 5 mm diameter) fractions. Root samples and forest litter samples were dried to a constant mass in a force draft oven at 85°C for 24 h and weighed. These data were then used to construct spatial distribution estimates for forest litter and roots across the canopy gaps. Seedling density, overstory canopy cover and PAR data were also used to construct spatial distribution profiles across the canopy gaps. Overstory data for trees and saplings along the gap edges were statistically summarized.

All data for dependent variables were summarized as estimates of the mean and variance for each data collection interval along the line transect (1, 4, 8, 12, 16, 20 and 24 m from the gap edge). Mean and variance estimates for PAR data were similarly cal-

Fig. 1. Regenerating longleaf pine seedlings clustered near center of canopy gap (note absence of seedlings in close proximity to adult tree in left foreground).

Fig. 2. Seedling exclusionary zone, showing 12–16-m-wide band near adult trees containing few if any regenerating longleaf pine seedlings.

culated, except that these were partitioned by quadrant (N, E, S or W) and time of day (1200, 1300, 1400, 1500 and 1600). For each dependent variable, a comparison of differences among the spatial intervals along the line transect (gap edge to center) was then undertaken. Statistical analysis was completed using a general linear models analysis of variance and covariance (GLM-ANOVA) program, which computes the F-ratio and conducts the Tukey–Kramer multiple comparison test (Hintze, 1995). Response variables were compared along the line transect using a set of seven pairwise contrasts. Except as otherwise noted, a probability level of 0.05 was used to discern significant differences.

3. Results

3.1. Overstory characteristics and seedling distribution

During the past 9 decades, the site had become dominated by a naturally regenerated second-growth longleaf pine forest. This stand was characterized by

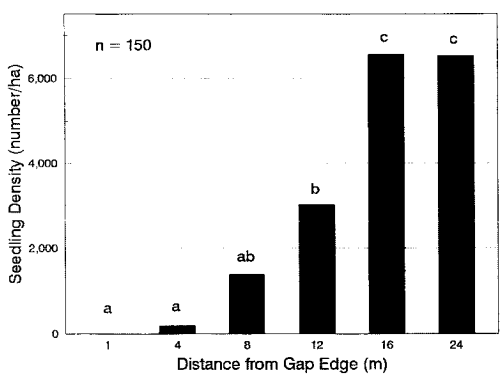

Fig. 3. Distribution of longleaf pine seedlings across canopy gaps (gap edge is at far left and gap center is at far right).

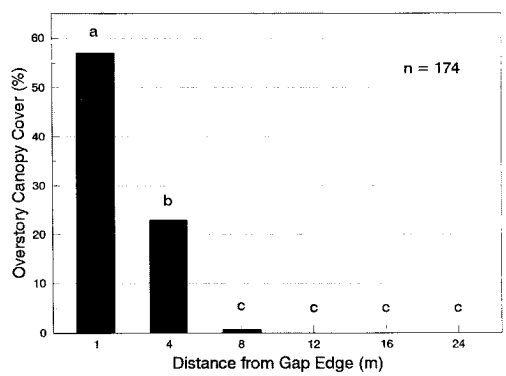

Fig. 4. Distribution of longleaf pine overstory cover across canopy gaps.

an uneven-aged structure, with seedlings, saplings and mature longleaf pine trees well represented. Numerous canopy gaps were distributed throughout the forest. These gaps typically ranged from 40 to 50 m in diameter (0.1–0.2 ha), but gaps of smaller diameter were also present.

Mature longleaf pines adjacent to the canopy gaps were an average age of 71 yrs, approximately 24 m in total height and 39 cm in diameter (Table 1). The mean crown depth for these trees was nearly 14 m and crown radius (the distance the forest canopy extended into the gap) was about 5 m. The average distance from a typical adult tree to the nearest longleaf pine seedling was nearly 8 m. Longleaf pine saplings were on the average 5.5 m tall and 5.4 cm in diameter.

Longleaf pine seedlings were generally confined to canopy gaps which were scattered throughout the stand. These seedlings were observed to cluster near the center of each canopy gap (Fig. 1), with very few if any present in a relatively broad band along the gap margin, the seedling exclusionary zone (Fig. 2). The density of longleaf pine seedlings within 8 m of the gap edge was not significantly different from that beneath overstory trees (Fig. 3). However, seedling density was significantly greater 12 m from the gap edge, with highest seedling densities observed at distances $\geq$ 16 m from the adult longleaf pines.

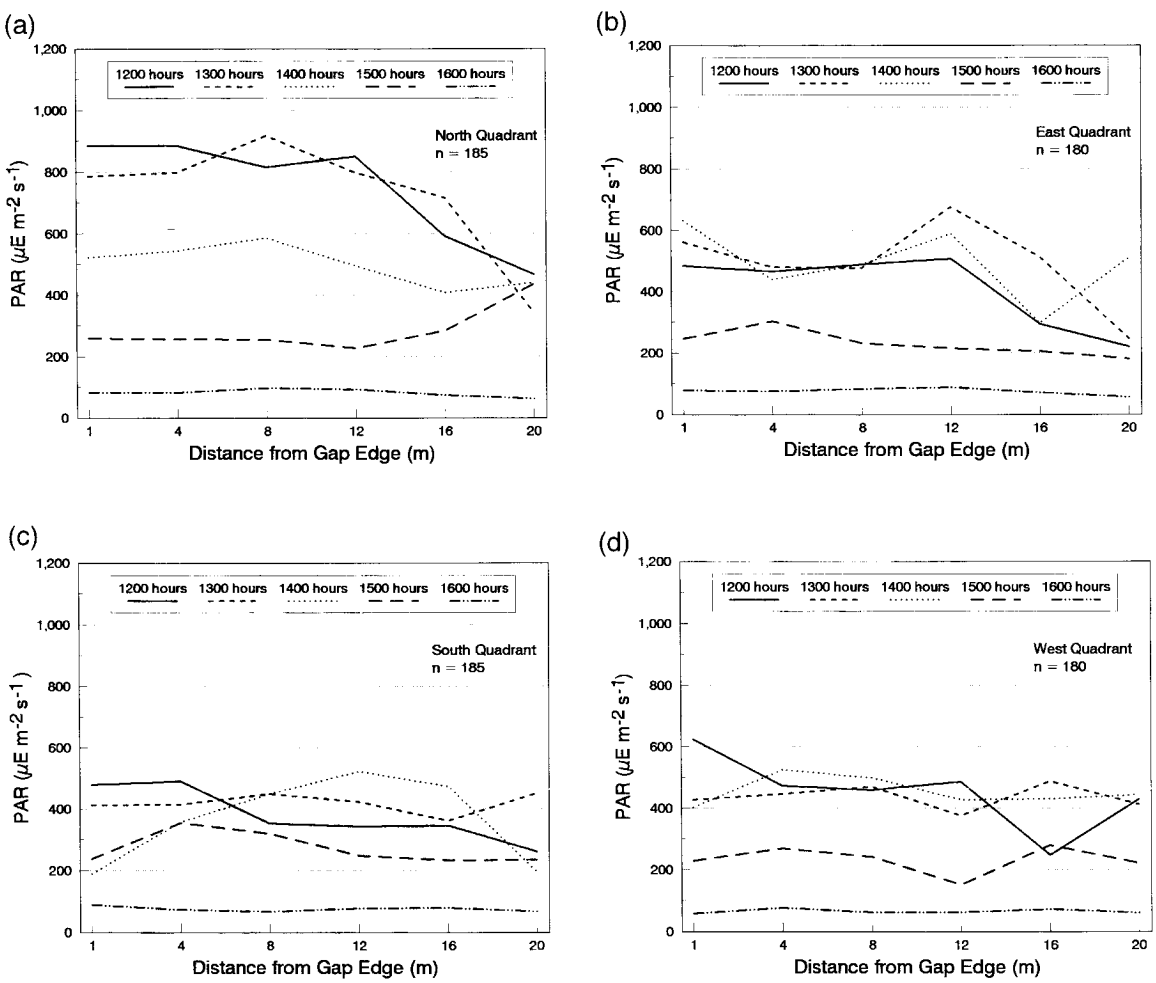

Fig. 5. Distribution of PAR across canopy gaps in four cardinal directions.

3.2. Canopy cover and solar radiation

Total foliar cover for the overstory of this sandhills longleaf pine forest averaged 57%, indicating a moderately open canopy condition (Fig. 4). Along the margin of the typical canopy gap, overstory cover rapidly declined to significantly lower levels. At only 4 m from the gap edge, overstory foliage decreased to 23% cover and, at distances ≥ 8 m from parent trees, overstory cover was essentially absent.

No significant differences in solar radiation across forest canopy gaps were observed (Fig. 5). In all four cardinal directions (quadrants), PAR was in general uniformly distributed from gap edge to gap center. Near midday in the north quadrant of the gaps, only half as much radiation was received at gap centers compared with gap edges, in reverse of conventional expectation. While radiant energy values exhibited modest variation across the canopy gaps, the only consistent trend was a progressive decrease in PAR values with the declining sun angle from 1200 to 1600.

3.3. Forest litter

The forest floor consisted of a well developed mor humus (predominantly forest litter) upon the acidic sandy soil. This litter layer was principally composed of longleaf pine needles which had fallen from overstory trees, with lesser components of pine needles from seedlings and leaves from infrequent hardwood trees and shrubs. The forest litter mass was unevenly distributed across the canopy gaps, with highest values approaching 6 Mg ha^{-1} measured immediately adjacent to adult trees along the gap edge (Fig. 6). Only 4 m from the gap edge, litter mass decreased significantly to less than 4.5 Mg ha^{-1} and, at distances ≥ 8 m from adult trees, the litter mass of ≤ 3 Mg ha^{-1} was not significantly different from that found at the gap center.

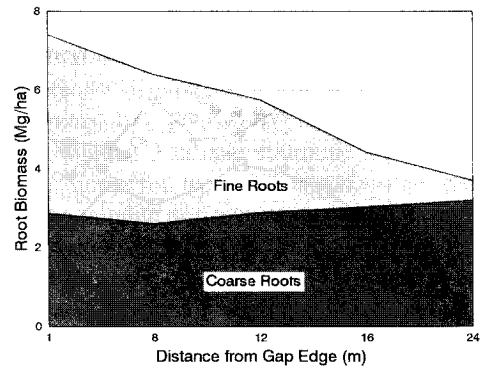

Fig. 7. Distribution of coarse roots and fine roots across canopy gaps (note differential pattern for coarse roots and fine roots).

3.4. Root distribution

The distribution of roots in the upper 20 cm of soil across forest canopy gaps showed a differential pattern for coarse roots and fine roots (Fig. 7). Coarse root biomass of 3 Mg ha^{-1} was distributed relatively evenly across the canopy gaps, showing no significant difference from edge to center. However,

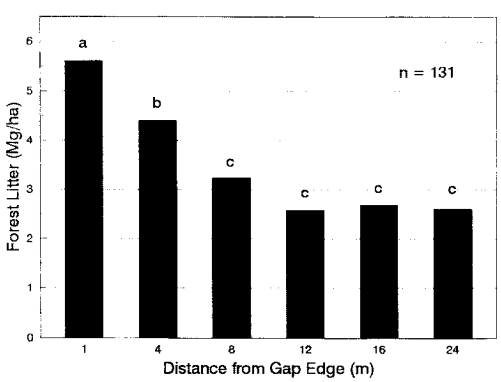

Fig. 6. Distribution of forest litter mass across canopy gaps.

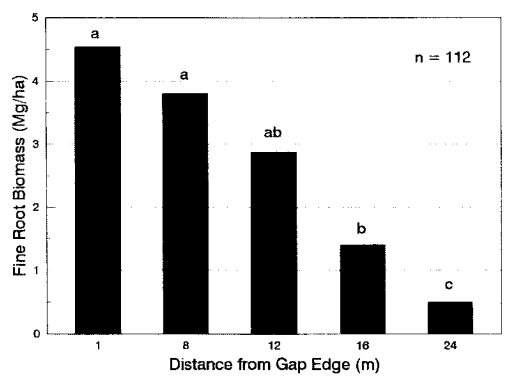

Fig. 8. Distribution of fine root biomass across canopy gaps.

the biomass of fine roots was positively related to the proximity of adult longleaf pines growing along the gap edge (Fig. 8). Fine root biomass of 4.5 Mg ha^{-1} near adult trees progressively declined to 3.8 Mg ha^{-1} at 8 m and 2.9 Mg ha^{-1} at 12 m from the gap edge. Fine root biomass values of 1.5 Mg ha^{-1} at 16 m and 0.5 Mg ha^{-1} at 24 m from the gap edge were significantly less than those measured nearer the adult trees.

4. Discussion

4.1. Regeneration pattern and seedling exclusionary zone

Longleaf pine forests naturally regenerating in periods between large scale disturbances are typically an uneven-aged mosaic consisting of even-aged patches averaging less than 1 ha. Mortality of single longleaf pines or groups of trees caused by a variety of disturbance agents such as lightning, windstorms, insects and pathogens create tree fall canopy gaps throughout the forest. The pyrogenicity of longleaf pine wiregrass ecosystems is adapted to maintain these canopy gaps relatively free of potentially competing hardwood trees and shrubs until longleaf pines have opportunity to occupy these grassy openings (Platt and Rathbun, 1993). This ecosystem occupies a portion of the Southeast that is highly prone to lightning with a high potential for wildfire ignition (Paul et al., 1968; Paul and Waters, 1978; Goodman and Christian, 1993). The longleaf pine wiregrass ecosystem has been described as ideally structured for the purpose of transmuting a localized disturbance (lightning) into a more widespread disturbance (ground fires), thus providing conditions suitable for its own regeneration (Platt et al., 1988). Longleaf pine trees then commonly disseminate seed into adjacent unoccupied grassy openings as well as areas beneath their crowns. Creation of these openings in the tree canopy initiates the forest cycle of renewal via patch or gap-phase regeneration.

Naturally regenerating longleaf pine seedlings on these xeric sandhills were highly aggregated near the center of forest canopy gaps and encircled by a 12–16 m wide zone along the interior margin of each gap from which they were largely excluded. This seedling exclusionary zone commonly develops in these openings when seedlings located distal to adult trees have higher survival and growth rates than those proximal to mature longleaf pines along the gap edge. This phenomenon was also frequently reported by earlier observers (Wahlenberg, 1946; Smith, 1955; Walker and Davis, 1956). Although the suppression effect upon seedlings diminishes rapidly with increasing distance from mature longleaf pines (Boyer, 1963), the negative influence of adult trees upon seedlings extends well beyond overstory crowns and as far as $\geq$ 15 m from the base of mature pines into a canopy gap (Boyer, 1993).

Mechanisms responsible for development of the seedling exclusionary zone have been discussed, with most frequent mention given to (1) higher levels of available sunlight near the gap center and (2) greater seedling mortality resulting from more intense fires in the higher volumes of litter deposited along the canopy edge (Boyer, 1974; Platt et al., 1988; Grace and Platt, 1995; Farrar, 1996). Belowground dynamics, such as root system competition between differing age groups of pine, have received little attention (Putz, 1992). Given the influence of adult longleaf pines well beyond their crowns and the fact that this zone of seedling suppression seems to extend farther from mature pines on poor sites than on good sites, it is possible that the seedling exclusionary zone is a product of competition for moisture and nutrients (Boyer, 1993).

4.2. Canopy cover and solar radiation

Canopy gaps reportedly have heterogeneous distributions of available site resources (Brandani et al., 1988; Canham, 1988; Brown, 1996). Differential availability of sunlight across gaps formed in closed canopy forests leads to gap partitioning between shade tolerant species regenerating under lower light levels along the gap edge and intolerant species under higher radiation levels near the center of the canopy gap (Denslow, 1980; Poulson and Platt, 1989; Canham et al., 1990; Sipe and Bazzaz, 1995). Considering the typical morphology of tree fall gaps in tropical and temperate forests, limited solar radiation levels along canopy gap edges (Ackerly and Bazzaz, 1995) may seem an obvious cause for development

of the seedling exclusionary zone in longleaf pine forests. This is especially so when considering that sufficient sunlight is necessary for the survival and growth of shade intolerant longleaf pines. However, the margins of canopy gaps occurring in most tropical and temperate forests are distinct boundaries of high contrast between little or no canopy cover over the gap and a highly dense canopy beyond the gap edge within the undisturbed portion of forest (Moore and Vankat, 1986; Denslow, 1987). This 'hard edge' present along gaps in closed canopy forests is dramatically different from the 'soft edge' along gaps within longleaf pine forests having a moderately open overstory with < 60% canopy cover.

Although longleaf pine seedlings were present at significantly reduced densities within 12–16 m of adult trees growing along canopy gap edges, significant overstory cover extended only 4–5 m into these openings. While greater sunlight availability near the center of canopy openings than along gap edges was suggested as one possible explanation for development of the seedling exclusionary zone, our data suggest otherwise. In the longleaf pine wiregrass ecosystem on these sandhills, solar radiation was uniformly distributed across the canopy gaps. Apparently, the < 60% canopy cover in this longleaf pine forest allowed solar radiation to laterally reach the forest understory through numerous interstitial spaces in the sparse pine overstory as well as through the canopy gap itself. Thus, the sweep of partial shade across the gaps during the solar day resulted in a relatively even distribution of PAR across the forest floor of entire gaps. Therefore, the null hypothesis that sunlight is evenly distributed across the canopy gap could not be rejected. Clearly, a differential in the distribution of PAR across each canopy gap was not responsible for development of the seedling exclusionary zone.

4.3. Forest litter and forest fire

Frequent low intensity fires are known to be the single most important type of disturbance shaping the ecological nature of longleaf pine wiregrass ecosystems (Christensen, 1981; Streng et al., 1993; Glitzenstein et al., 1995; Landers et al., 1995). Ignition is commonly affected via lightning strikes of tall longleaf pine trees, with fire subsequently spreading throughout the understory of abundant grasses and forest litter (primarily pine needles) which serve as fine fuels (Landers, 1991; Platt and Rathbun, 1993). In areas of the forest floor where greater volumes of pine needles accumulate in the litter layer, ground fire intensity is substantially higher, resulting in high mortality rates among longleaf pine seedlings (Platt et al., 1988; Grace and Platt, 1995). Highest litter accumulation and pine seedling mortality rates are typically observed directly under and adjacent to the crowns of adult longleaf pine trees (Boyer, 1963, 1974; Farrar, 1996).

Higher intensity fire, burning in the greater mass of accumulated litter associated with mature longleaf pine trees, seems a logical mechanism for development of the seedling exclusionary zone along the margin of canopy gaps. However, our findings clearly show that the seedling exclusionary zone ranges 12–16 m from the gap edge and significantly increased volumes of litter extended only 4 m into these grassy openings. Thus, the influence of more intense ground fires in causing greater mortality among longleaf pine seedlings does not extend sufficiently far from the gap edge to serve as the principal mechanism responsible for development of the seedling exclusionary zone. Therefore, while higher rates of litter accumulation beneath and adjacent to adult tree crowns may have an indirect effect (through fire) on pine seedling mortality along the outermost 4 m of each gap, another mechanism must be responsible for seedling exclusionary zone development in longleaf pine canopy gaps.

4.4. Root gaps and intraspecific competition

Formation of tree fall gaps within tropical and temperate forests is suspected to provide higher levels of available nutrients and moisture within these localized canopy openings, but evidence supporting this hypothesis is as yet inconclusive (Vitousek and Denslow, 1986; Denslow, 1987; Lajtha, 1994). Data from temperate deciduous and coniferous forests recently demonstrated the development of root gaps subsequent to the creation of canopy gaps (Wilczynski and Pickett, 1993; Parsons et al., 1994; Bauhus and Bartsch, 1996). These root gaps generally correspond to the geometric configuration of the canopy gaps, but they are somewhat reduced in area by the

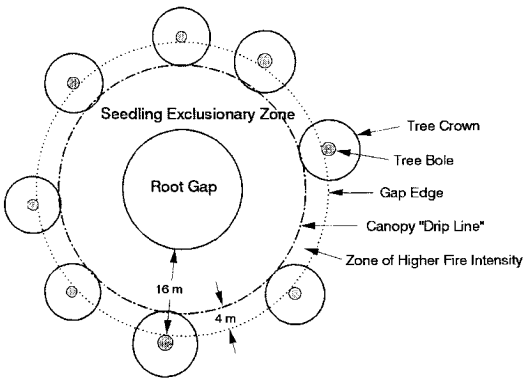

Fig. 9. Vertical view of root gap and canopy gap showing the seedling exclusionary zone (gaps vary in shape from circular and elliptical to attenuated strings).

lateral innervation of fine roots from live adult trees along the canopy gap edge.

Our data clearly indicate the presence of root gaps formed in the sandy soil immediately below the central portion of each longleaf pine canopy gap (Fig. 9). Mature longleaf pine trees are known to have root systems extending radially up to 16.8 m from their mainstems (Stone and Kalisz, 1991) and, in this study, fine root biomass was significantly reduced at distances $\geq$ 16 m from canopy gap edges. Significantly, the highest densities of longleaf pine seedlings were also observed at $\geq$ 16 m from the gap edge. The fine root biomass found within 12 m of the gap edge (3–4.5 Mg ha^{-1}) was two to six times that measured near the gap center and most closely coincided with the dimensions of the seedling exclusionary zone along the margin of each gap. Thus, development of the seedling exclusionary zone in longleaf pine forest canopy gaps is most likely the result of intraspecific competition between the root systems of adults and seedlings for limited soil resources.

4.5. Sustaining the ecosystem through silviculture

Most monotypic pine forests in the southeastern United States are intensively managed as plantations, using a system of clearcutting on relatively short rotations (approximately 30 yrs) followed by artificial regeneration through planting tree seedlings. This even-aged silvicultural system, while often justified on the basis of southern pine intolerance to shade, is more frequently implemented to achieve economic objectives. A major disadvantage of this approach is periodic degradation of numerous nontimber resource values following complete removal of the forest canopy in these ecosystems. While this method has been sporadically applied in longleaf pine forests, the unique reproductive ecology of these ecosystems better suits them to alternative, less disruptive silvicultural systems.

Naturally regenerating longleaf pine forests typically develop as an uneven-aged mosaic of even-aged patches distributed across the landscape (Platt and Rathbun, 1993). This pattern of renewal maintains continuous canopy cover in the ecosystem, while providing for replacement of overstory trees by establishing naturally regenerating seedlings in canopy gaps. Silvicultural systems which mimic this overall regeneration pattern are quite likely best suited in the long-term for sustaining the ecological character and multiple resource values of the longleaf pine wiregrass ecosystem. Such alternative approaches maintain continuously-standing forest, while allowing landowners not to forgo income because their land is locked in a preserve (Farrar, 1996).

The gap-phase regeneration dynamics of longleaf pine are critically important in selecting silvicultural systems suitable for the long-term sustainability of longleaf pine wiregrass ecosystems. Within each canopy gap, a distinct zonation develops between the gap center and surrounding area inside the gap edge. Near the canopy gap center ($\geq$ 16 m from the gap edge), pine seedlings are noted to aggregate at highest densities because of the presence of a belowground gap in the root system of adult pines. This root gap affords the seedlings a refuge from intense intraspecific competition with adult longleaf pines. Along the gap margin (within 16 m of the gap edge), very low densities of seedlings are present in the seedling exclusionary zone. While fire plays an indirect role in seedling mortality within 4 m of the gap edge, the seedling exclusionary zone is largely a product of direct seedling suppression resulting from the presence of mature longleaf pine root systems. Thus, the dimensions of the seedling exclusionary zone have major implications for the minimum size of forest canopy gaps that should be created through silvicultural practice.

Considering these findings and those of others (Platt et al., 1988; Boyer, 1993; Platt and Rathbun, 1993), it is suggested that the minimum size of canopy gaps silviculturally created in longleaf pine forests be limited to diameters of 30 m. However, this minimal diameter canopy opening will likely result in development of a very small root gap area and a relatively large seedling exclusionary zone, thus supporting a very small number of regenerating pine seedlings within the gap. Note that gaps of smaller diameter provide little or no opportunity for root gap development and may preclude gap occupancy by few if any pine seedlings. Therefore, we recommend that canopy gaps created through silvicultural methods in longleaf pine forests be ≥ 40 m in diameter to provide sufficient opportunity for development of root gaps that can support substantial numbers of pine seedlings. Our recommendation coincides with the typical dimensions of naturally occurring gaps (40–50 m diameter) which were commonly observed throughout this longleaf pine forest.

Considering the minimal size of forest gaps suitable for effectively regenerating pines in the longleaf pine wiregrass ecosystem, caution should be used in prescribing the single-tree selection method for gap creation. Single longleaf pine trees removed from the canopy will likely leave gaps averaging < 30 m in diameter. Being below our minimum recommendation, gaps of this small size will probably allow no substantial root gap development and will likely remain occupied by few if any pine seedlings until adjacent trees fall from the canopy to create a larger gap. Conversely, the group selection method may be among the most useful silvicultural techniques for creating canopy gaps (and root gaps) of sufficient size to effectively sustain the longleaf pine wiregrass ecosystem in the long-term. Group selection can be used to create canopy gaps with diameters of 40–50 m (0.1–0.2 ha) or more distributed throughout the forest to simulate the desired uneven-aged mosaic. The volume-guiding diameter limit (GDL) and basal area-maximum dbh-q (BDq) procedures in a modified group selection system are suitable for managing longleaf pine forests when used in combination with prescribed fire on a 3-yr cycle (Farrar, 1996). Shelterwood methods and deferment cutting may also prove useful in regenerating longleaf pine forests, if for some reason more open canopy conditions are desired (Smith et al., 1989; Boyer, 1993). However, the pine seedlings' need for light cannot be used as an appropriate rationale for application of clearcutting methods.

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