

Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem

Brian J. Palik, Robert J. Mitchell, Greg Houseal, and Neil Pederson

Abstract: Competition between mature trees and regeneration has been well studied in closed-canopy forests, but less so in open-canopy woodlands. We examined competition in a longleaf pine (*Pinus palustris* Mill.) woodland to understand effects of overstory abundance on resource availability and seedling responses to resource levels. We examined resources and planted seedling performance across a gradient from intact canopies to the centers of large gaps. Growth of seedlings increased slowly across a wide range of decreasing overstory basal area, but increased substantially only in the center of gaps. Seedling survival was unrelated to overstory abundance. Overstory basal area was negatively related to light and nitrogen. Light increased from 40% of full sunlight in intact forest to 80% in gaps. Nitrogen only increased in the center of gaps, suggesting that below-ground and above-ground gaps are spatially distinct. Correlations between seedling growth and light and nitrogen were positive and curvilinear upward. The data suggest that increases in both light and nitrogen may be required for seedling growth increases. We use our results to propose a silvicultural approach for green tree retention that minimizes inhibition of regeneration through clumping of residuals to maximize gap size, even while holding remaining basal area constant.

Résumé : La compétition entre les arbres mûrs et la régénération a été bien étudiée dans les forêts à voûte fermée, moins par contre dans les forêts claires à voûte ouverte. La compétition dans une forêt claire de pin des marais (*Pinus palustris* Mill.) a été examinée afin de comprendre les effets de l'abondance de l'étage dominant sur la disponibilité des ressources et la réaction des semis par rapport au niveau de ces dernières. Les ressources et la performance des semis plantés ont été examinées le long d'un gradient allant des voûtes intactes jusqu'au centre des larges trouées. La croissance des semis augmentait lentement à mesure que diminuait la surface terrière de l'étage dominant, mais elle augmentait considérablement seulement au centre des trouées. La survie des semis n'était pas reliée à l'abondance de l'étage dominant. Il y avait, par contre, une relation négative entre la surface terrière de l'étage dominant et la lumière ainsi que l'azote. La lumière est passée de 40% de luminosité totale dans les forêts intactes à 80% dans les trouées. L'azote a augmenté uniquement au centre des trouées, suggérant que les trouées hypogées et épigées ne correspondent pas dans l'espace. Les corrélations entre la croissance des semis et la lumière ainsi que l'azote étaient positives et curvilignes ascendantes. Les données suggèrent que l'accroissement de la lumière, comme de l'azote, pourrait être requis pour augmenter la croissance des semis. Les résultats de cette étude sont utilisés pour proposer une méthode sylvicole de conservation des arbres vivants qui minimise l'inhibition de la régénération par les arbres résiduels. Elle consiste à garder ces derniers par groupes afin de maximiser la taille des trouées, tout en maintenant la surface terrière résiduelle constante.

[Traduit par la Rédaction]

Introduction

Forest regeneration often depends on canopy disturbances that open gaps and reduce competition from mature trees (Canham and Marks 1985; Runkle 1985). Most work on gap regeneration has been conducted in dense forests where openings are distinct against the background of a closed canopy. In contrast, the effects of canopy disturbances are not so distinct in woodland ecosystems, such as longleaf pine (*Pinus palustris* Mill.) in the southeastern United States, where canopies are already

open (Christensen 1988; Platt et al. 1988). Canopy closure in mature longleaf pine stands may average only around 50% (Palik and Pederson 1996) and may be as low as 20 or 30% in old-growth stands (Penfound and Watkins 1937). Still, exploitive resource competition is believed to be an important mechanism controlling regeneration of longleaf pine, and patterns of regeneration consistent with competition have been reported (Platt et al. 1988; Boyer 1993; Grace and Platt 1994, 1995). No study of longleaf pine, however, has actually quantified competitive effects, i.e., the influence of competitors on resource availability, and the responses of target plants to resources (Goldberg 1990; Mitchell et al. 1993; Burton and Bazzaz 1995). For competition to be important, both the effects and response components must be significant and of the proper direction (Goldberg 1990).

Predicting seedling performance under varying levels of overstory competition is important for understanding the consequences of silvicultural systems that include green tree retention. There are ecological benefits to retaining mature trees

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B.J. Palik,¹ R.J. Mitchell, G. Houseal, and N. Pederson.
Joseph W. Jones Ecological Research Center, Route 2, Box
2324, Newton, GA 31770, U.S.A.

¹ Author for correspondence at Forestry Sciences
Laboratory, 1831 Hwy. 169 E., Grand Rapids,
MN 55744, U.S.A.
e-mail: bpalik/nc_grandrapids@fs.fed.us

in harvested stands (Swanson and Franklin 1992), but these same trees can also reduce regeneration success by limiting resources (Birch and Johnson 1992; Seymour and Hunter 1992). Understanding competitive mechanisms between mature trees and seedlings may point to silvicultural approaches that minimize this competition while still retaining the benefits of residual trees.

We studied competition between overstory trees and seedlings of planted longleaf pine to (i) quantify relationships between overstory competitors and growth and survival of seedlings, (ii) examine the effects of overstory abundance on resource availability, and (iii) describe relationships between seedling growth and survival and resource availability. We examined the components of competition across a structural gradient from the center of large canopy disturbances to the understory of intact forest. As an additional objective, we present a silvicultural model for green tree retention that may minimize competitive inhibition of regeneration by mature trees, by controlling the spatial distribution of different resource levels in a stand.

Methods

Study area

Our study was conducted in longleaf pine forests at the Joseph W. Jones Ecological Research Center in southwestern Georgia, U.S.A. Most of the forests are 70–90 years old and have been prescribed burned between February and April on a 2- to 3-year basis for many decades. We worked on sandy soils (Typic Paleudult, Norfolk series; Arenic Paleudult, Wagram series) having site indices of 22 m at 50 years (USDA 1986). Longleaf pine on these sites comprises 85–100% of relative basal area in the overstory, while several species of oaks (particularly *Quercus falcata* Michx. and *Quercus margaretta* Ashe) are minor components (Palik and Pederson 1996).

Sampling design and vegetation measurements

We used four large canopy openings as sites for resource and seedling measurements (see next two sections). The openings formed between 1990 and 1992 and resulted from mortality after excessive crown scorch during a surface fire (one opening) or group lightning strikes (three openings). We estimated the size of each opening as the area of an ellipse that fit just within the crowns of the border trees. Sizes of the four openings were 1553, 2027, 1067, and 1225 m², respectively. Within the gaps, the number of dead trees (all longleaf pine) ranged from 18 to 33. The number of live pines remaining ranged from two to seven.

In each gap, we established nine sample points as locations for planted seedlings and resource measurements. The points were arrayed in a crossed design, with one at the center of the gap, one at each edge on the north, south, east, and west peripheries, and one equidistant between each gap edge and the center. We measured basal area of live overstory trees (diameter at breast height (DBH) ≥ 10 cm) at each point using a five-factor (English units) wedge prism. With this prism factor, the sampling radius extended up to 25 m for large-diameter trees (DBH > 30 cm), the approximate maximum distance at which competitive inhibition of seedlings by large longleaf pines has been detected (Grace and Platt 1995; Platt and Rathbun 1995).

Each gap was paired with an adjacent area of equal size having an intact overstory. These areas were selected by choosing random compass bearings and distances of at least 75 m from the center of the gaps. The same array of nine sample points was established in each intact canopy plot and the basal area of trees ≥ 10 cm DBH was measured at each point with prism sampling.

Seedling planting and measurements

Four weeks before planting seedlings, a 2-m² quadrat was centered over each point and a nonselective herbicide (glyphosate) was applied in and around the outside of the quadrat (up to a 50-cm distance) to eliminate herbaceous (mostly *Aristida stricta* Michx.) and small woody vegetation. The quadrats were periodically hand-weeded over the course of the study. We eliminated understory vegetation so that trends related to overstory competition alone could be better quantified.

We hand-planted eight 1-year-old containerized longleaf pine seedlings in each 2-m² quadrat in early March of 1994. Two seedlings were planted along the periphery of the quadrat near each corner. Seedlings were graded to reduce mortality from out-planting shock. We used only healthy seedlings with root collar diameters ≥ 10 mm. Thirty additional seedlings, spanning the same diameter range as those planted, were destructively sampled to estimate initial above- and below-ground biomass of the planted seedlings. The stems of these seedlings were severed at the root collar and above- and below-ground components were dried at 70°C for 48 h and weighed.

Seedling survival was 100% soon after planting. Survival was assessed again in early March 1995, approximately 12 months after planting. At that time, four to six seedlings (depending on survival in the particular quadrat) were selected randomly and harvested. Two seedlings were left unharvested in each quadrat for future measurements. The tops of the harvested seedlings were clipped at the root collars. The root systems were excavated by hand. Sandy surface soils facilitated recovery of roots. Above- and below-ground biomass was determined as above. Biomass increment (grams per 12 months) was estimated as the difference between final weight and initial weight (based on the average of the 30 seedlings destructively sampled at the start of the study).

Resource measurements

Hemispherical photographs were used to measure canopy openness above each quadrat. Photographs were taken after full extension of the current-year needles (approximately June 15, 1994) on calm, cloudless mornings just prior to sunrise. The lens was situated 2.5 m above the ground on a tripod.

Soil moisture was measured using time domain reflectometry (TDR; Topp et al. 1980). Measurements were made across depths of 0–30 and 30–90 cm. For each depth, one pair of parallel steel rods was placed vertically in the soil near the center of each quadrat. TDR measurements were taken with a cable tester every 2 weeks from May 1994 to May 1995.

Soil nitrogen (NH_4^+ plus NO_3^-) and phosphorus (PO_4) availability was measured monthly in each quadrat from May 1994 to May 1995. Availability of nitrogen was determined using mixed ion exchange resin bags (Sigma 1-9005, mixed-bed exchanger on polystyrene, 20–50 mesh) (Binkley and Matson 1983). Anion resin bags (Dowex 1 \times 8, Cl⁻ form, 20–50 mesh) were used to measure phosphorus (Walbridge 1991). Exchange resins provide relative indices of nutrient availability that are appropriate for comparisons among different conditions. Three mixed-bed bags and three anion bags were buried in each quadrat at a depth of 5 cm at the beginning of the measurement period. The bags were retrieved and replaced at the end of each month and processed immediately.

Data analysis

The hemispherical photographs were digitized using an image analysis system. The digitized images were used with the computer program Sunshine (Smith and Somers 1991) to estimate direct and diffuse beam radiation above each quadrat on a daily basis over a 6-month period (June 1 to November 30, 1994). Sunshine estimates daily light measurements by accounting for canopy openness, the diurnal path of the sun, seasonal changes in sun angle, and climatic conditions. Gap light indices (sensu Canham 1988b) were calculated for each quadrat as cumulative seasonal light availability relative to light availability in the open.

Table 1. Regression equations (standard errors of regression coefficients in parentheses) relating longleaf pine seedling biomass growth (g/12 months), gap light index (%), and nitrogen ($\mu\text{g}\cdot\text{bag}^{-1}\cdot 30\text{ days}^{-1}$) to overstory basal area (m^2/ha) (eqs. [1–4]), and biomass growth to resource levels (eqs. [5–8]).

Dependent variable (y) ^{**}	a	b	r ²	SEE [‡]	F
Independent variable (x): basal area					
[1] Above-ground biomass	8.67 (0.98)	0.15 (0.032)	0.53	1.36	58.64 ($p < 0.001$)
[2] Below-ground biomass	6.94 (0.81)	0.18 (0.039)	0.59	1.06	73.49 ($p < 0.001$)
[3] Gap light index	85.51 (3.78)	0.068 (0.008)	0.71	7.34	174.63 ($p < 0.001$)
[4] Nitrogen	146.60 (10.95)	0.060 (0.012)	0.45	19.79	42.30 ($p < 0.001$)
Independent variable (x): gap light index					
[5] Above-ground biomass	1.64 (0.18)	-0.0098 (0.0006)	0.39	1.55	33.49 ($p < 0.001$)
[6] Below-ground biomass	1.10 (0.14)	-0.010 (0.0005)	0.40	1.27	34.81 ($p < 0.001$)
Independent variable (x): nitrogen					
[7] Above-ground biomass	2.09 (0.23)	-0.0040 (0.0004)	0.22	1.75	14.59 ($p = 0.004$)
[8] Below-ground biomass	1.38 (0.15)	-0.0044 (0.0003)	0.31	1.36	23.75 ($p < 0.001$)

*All models have the form $y = a/(1 + bx)$.

† $n = 54$ for all equations (excludes flooded quadrates) except eq. [3] ($n = 72$).

‡Standard error of y .

TDR measurements were converted to volumetric soil moisture following Topp et al. (1980). The biweekly measurements were averaged across time to derive a single measure of soil moisture at each depth. Similarly, monthly soil nitrogen and phosphorus measurements were averaged across time within each quadrat to derive seasonal measures of nutrient availability.

Nonlinear regression models were used to examine (i) the interaction between overstory competitor abundance and seedling growth and survival, (ii) competitive effects of the overstory on resource availability, and (iii) the performance of seedlings in relation to resource levels. For these analyses, the 18 quadrats from each pair of gap and intact canopy plots were pooled ($n = 72$). Although quadrats within plots were not necessarily independent for all factors, we felt justified in pooling them because our study was a mensurative experiment, rather than a manipulative one (Hurlbert 1984). All data sets were fit with a power function of the form

$$[1] \quad y = a/(1 + bx)$$

where y is the predicted value, a and b are estimated regression coefficients, and x is either overstory basal area or resource level. For all models, standardized residuals plotted against predicted and independent variables revealed no strong violations of distribution assumptions.

In July 1994, Tropical Storm Alberto flooded one of the pairs of gap and intact canopy plots for 1 day. Most of the seedlings were submerged during this time but survived until the end of the study. Soil nutrient availability and seedling growth were reduced in these quadrats, relatively to nonflooded ones. The regression analyses were assessed without the flooded quadrats, although data for all the quadrats are presented graphically.

Results

Competitive interactions between overstory trees and seedlings

Survival of the planted seedlings after 12 months was high, averaging (\pm SD) 97 (8)% among the 72 quadrats. There was no obvious relationship between survival and overstory basal area (data not shown). Survival was significantly lower in the flooded quadrats, averaging 90 (10)%, compared with the

others, which averaged 97 (8)% ($p = 0.005$, t -test, flooded and nonflooded quadrats pooled separately).

Seedling biomass increment increased significantly with decreasing overstory basal area (above-ground: $r^2 = 0.53$, $p < 0.001$; below-ground: $r^2 = 0.59$, $p < 0.001$; Table 1). The relationships were exponential; both above- and below-ground growth increased slowly across a wide range of decreasing basal area, from around 27 to 9 m^2/ha , but began to increase substantially below about 8 m^2/ha basal area (Fig. 1). Root to shoot ratios increased slightly (but not significantly) from about 0.5 to 0.75 with decreasing basal area ($r^2 = 0.17$; data not shown).

Effects of overstory abundance on resource availability

Gap light indices increased significantly ($r^2 = 0.71$; $p < 0.001$; Table 1) from the intact canopies to the gap centers (Fig. 2), although light availability still averaged around 40% under an intact canopy. Overall, the relationship was curvilinear (Fig. 2); however, below about 15 m^2/ha , gap light index increased approximately linearly with decreasing basal area.

Soil moisture was not related to overstory basal area at either depth (data not shown). The quadrats that were flooded were not distinguishable from the larger pool of samples. Across the range of basal area, soil moisture rarely fell below 10% at either depth and was probably not limiting to survival or growth of the pine seedlings during the sample period.

Nitrogen availability increased exponential with decreasing overstory basal area ($r^2 = 0.45$; $p < 0.001$; Table 1). Nitrogen remained low across a wide range of basal area (27–10 m^2/ha) and began to increase substantially below about 7 m^2/ha (Fig. 3). Phosphorus availability did not vary consistently as a function of overstory basal area, although phosphorus did appear to remain consistently low above a basal area of about 21 m^2/ha (data not shown).

Seedling responses to resource availability

Significant portions of seedling biomass growth were explained by gap light index (above-ground: $r^2 = 0.39$, $p < 0.001$;

Fig. 1. Longleaf pine seedling biomass increment as a function of overstory basal area (DBH \geq 10 cm). Open circles are unflooded quadrats, solid circles are flooded quadrats, and solid lines are regression functions fitted to unflooded quadrats only.

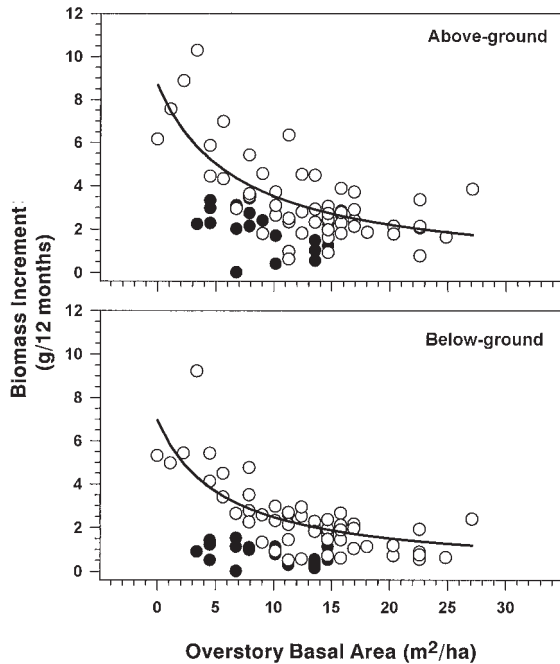
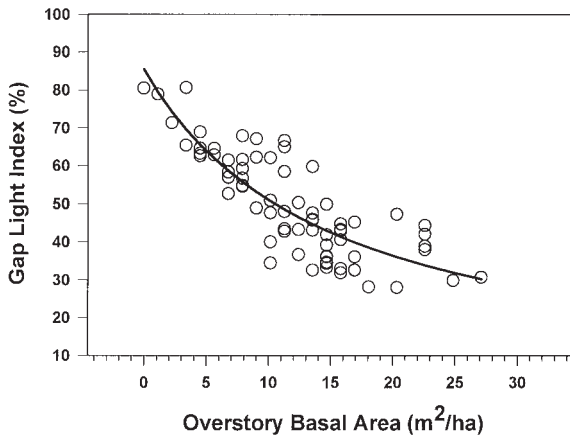


Fig. 2. Gap light index as a function of overstory basal area (DBH \geq 10 cm). Open circles are individual quadrats and the solid line is a regression function fitted to all quadrats.



below-ground: $r^2 = 0.40$, $p < 0.001$; Table 1). The relationships were curvilinear (Fig. 4) and similar in form (although opposite in sign) to those between basal area and both nitrogen availability and seedling growth.

Nitrogen availability also explained a significant portion of seedling growth (above-ground: $r^2 = 0.22$, $p = 0.004$; below-ground: $r^2 = 0.31$, $p < 0.001$; Table 1). As with light, the growth increases with increasing nitrogen were curvilinear in form (Fig. 5). Both phosphorus availability and soil moisture at both depths were poorly related ($p > 0.10$) to seedling growth (data not shown).

Fig. 3. Nitrogen availability as a function of overstory basal area (DBH \geq 10 cm). Open circles are unflooded quadrats, solid circles are flooded quadrats, and the solid line is a regression function fitted to unflooded quadrats only.

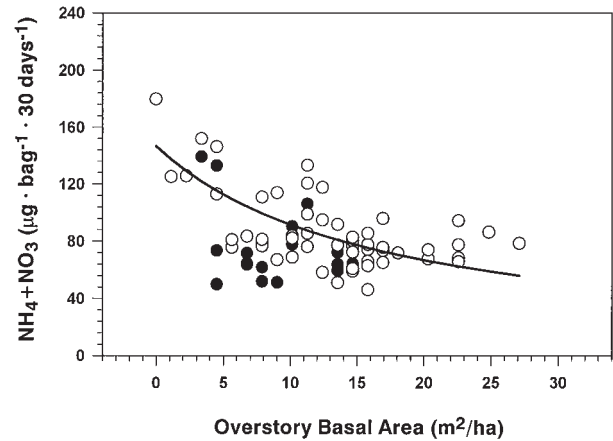
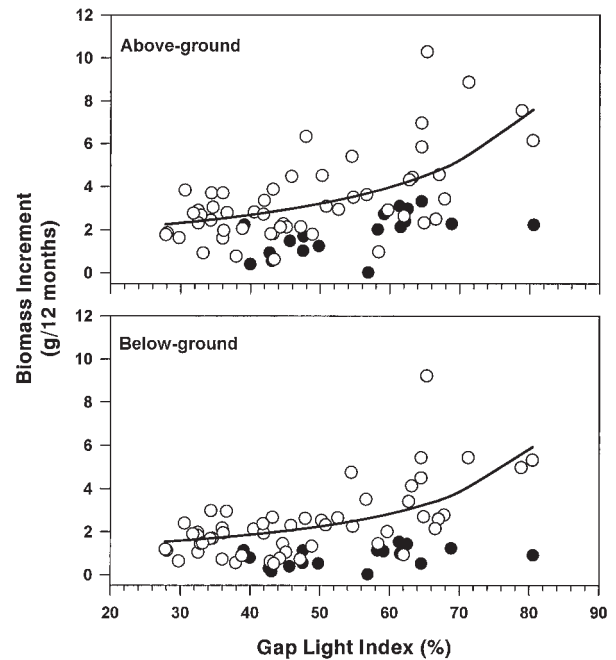


Fig. 4. Longleaf pine seedling biomass increment as a function of gap light index. Open circles are unflooded quadrats, solid circles are flooded quadrats, and solid lines are regression functions fitted to unflooded quadrats only.



Discussion

Overstory competitive effects and longleaf pine seedling responses

Overstory longleaf pines appeared to influence growth of planted pine seedlings through competition for light and nitrogen. Both competitive effects on resources and seedling growth in relation to resource availability were significant and of the proper direction for competition with overstory trees to be invoked as a mechanism controlling seedling development (Goldberg 1990). Several past studies have reported similar net competitive

interactions between the overstory and growth of seedling longleaf pines (Platt et al. 1988; Boyer 1993; Grace and Platt 1994, 1995). However, we are aware of no published studies that have actually addressed the mechanisms behind the patterns, i.e., the effects of competition on resource availability and the correlation between seedling growth and resource levels.

In contrast with growth, survival of planted seedlings was unrelated to abundance of overstory competitors. However, 12 months is probably insufficient time for patterns in survival related to competition to develop. We expect that mortality of seedlings in low-resource microsites will increase over time, as reduced growth results in decreasing rates of resource acquisition and photosynthesis.

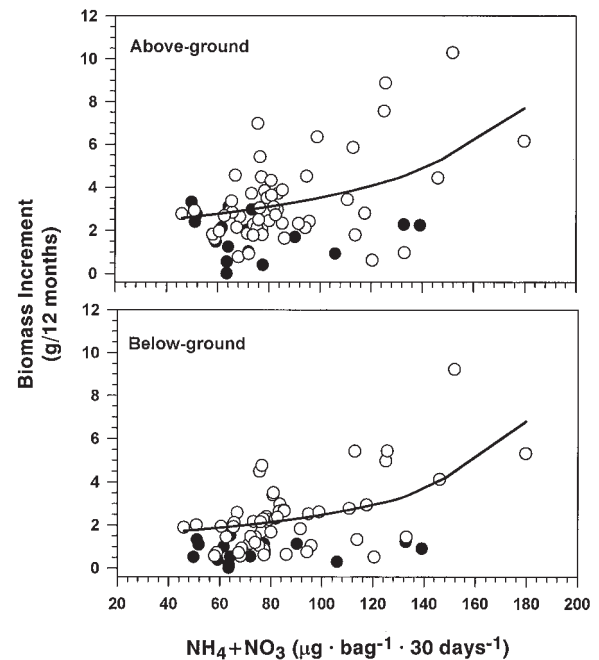
In our study, light availability was high even prior to canopy disturbance and the range of increase was modest compared to increases with disturbance in closed-canopy forests (Minckler and Woerheide 1965; Skeen 1976; Canham 1988a, 1988b; Canham et al. 1990). Still, biomass increment of longleaf pine seedlings was positively correlated with the range of light increases we measured. Nitrogen availability also increased with decreasing overstory abundance, but the increase was modest across a wide range of basal area, increasing substantially only at low overstory abundance, in the center of large gaps. This is similar to findings from lodgepole pine (*Pinus contorta* Dougl. ex Laws) forests where increases in net nitrogen mineralization and nitrification only occurred in openings that exceeded 30 trees in size (Parsons et al. 1994). As with light, longleaf pine seedling growth was positively correlated with changes in nitrogen availability, suggesting that nitrogen competition plays a role in regeneration response in overstory disturbances, but only if the disturbance is large, with few or no live trees remaining.

The growth responses of seedlings to both light and nitrogen levels were curvilinear upward, a shape that contrasts with the decreasing asymptotic resource response curves found in many competition studies (Pacala et al. 1994; Goldberg 1996). The concave upward relationships may result from a multiplicative (rather than additive) combined influence of light and nitrogen on seedling growth, i.e., response to changes in availability of one resource will differ depending on level of availability of the other resource (Peace and Grubb 1982; Pacala et al. 1993).

Elimination of herbaceous competitors in our study may have amplified the increase in nitrogen that occurred at low overstory abundance (and perhaps the other soil resources as well, although they were not related to overstory abundance as was nitrogen). Increased uptake of soil resources by herbaceous competitors may be one reason that not all studies of canopy gaps have demonstrated increased resource availability with reduced overstory abundance (Minckler and Woerheide 1965; Parker 1985; Vitousek and Denslow 1986). Determining the precise mechanism of increased nitrogen with reduced overstory abundance requires additional study, as either uptake or nonuptake mechanisms may be involved (Goldberg 1996).

Effects of overstory abundance on volumetric soil moisture were weaker than we expected and seedling responses were not correlated with moisture. However, volumetric water content may not be the most precise measure of subtle water deficits that can affect seedlings. If practical, measurements of soil water potential, or more importantly, plant water potential, may be useful when measured in concert with water volume.

Fig. 5. Longleaf pine seedling biomass increment as a function of nitrogen availability. Open circles are unflooded quadrats, solid circles are flooded quadrats, and solid lines are regression functions fitted to unflooded quadrats only.



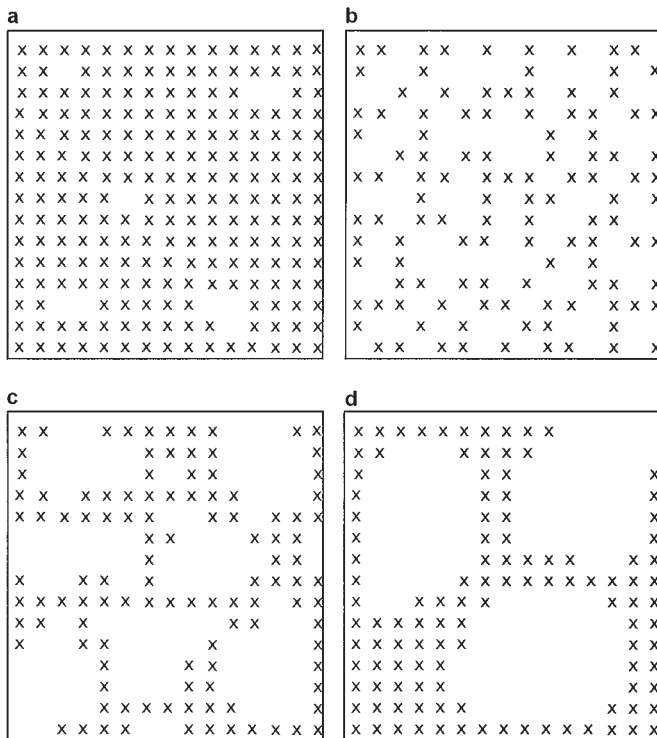
At any rate, rainfall during the sampling period (May 1994 to March 1995) was higher than the long-term average in the region. The influence of canopy competition on soil moisture, and seedling responses to moisture, may be greater during periods of extended drought.

Silvicultural application

Green tree retention is advocated as an important component of silvicultural systems for ecosystem management because of the ecological benefits of maintaining mature trees across rotations (Hansen et al. 1991; Swanson and Franklin 1992). These benefits may come at a cost to survival and growth of regeneration because of competition with residual trees (Birch and Johnson 1992; Seymour and Hunter 1992; Hansen et al. 1995). For example, root collar diameters of longleaf pine seedlings decreased an average of 65–100% as residual basal area increased from no overstory to 21 m²/ha (Boyer 1963, 1993). Volume of regeneration after 35 years was reduced >85% under 4 m²/ha residual basal area, compared with volumes in even-aged stands (Boyer 1993). Growth of the residuals did not compensate for growth losses of regeneration.

We suggest that growth losses of regeneration with green tree retention can be minimized by controlling the distribution of residual trees in a way that capitalizes on the nonlinear relationship between overstory competitor abundance and seedling growth (Fig. 1). Our data show that seedling growth increased substantially only in the center of gaps that averaged about 1400 m² in size and at residual basal areas below 6 m²/ha. In a normally stocked mature longleaf pine stand (Fig. 6a), most individual competitive neighborhoods in the stand will have overstory basal areas >6 m²/ha, i.e., they will fall somewhere to the right on the net interaction curve (Fig. 1), where

Fig. 6. Conceptual model of silvicultural manipulations to alter stand-level competitive environments. All stands begin with the same initial basal area. Stand *a* is an uncut control. In stands *b–d*, 50% of basal area is removed using three different cutting patterns. While each cutting pattern retains the same residual basal area, mean opening size increases from stand *b* to stand *d* (i.e., clumping of residuals increases from stand *b* to stand *d*). In this example, stand *d* contains the greatest number of competitive neighborhoods where growth of regeneration is maximized because both nitrogen and light are maximized.



growth of regeneration is minimal across a wide range of basal areas. Even in a stand cut to a low residual basal area, e.g., 8–10 m²/ha, and where residuals are dispersed uniformly across the stand (as in Boyer 1963, 1993), few openings will exceed 1400 m² in size and few individual competitive neighborhoods will have overstory basal areas below 6 m²/ha (Fig. 6b). However, the same residual basal area can be retained differently in space such that fewer but larger openings (exceeding 1400 m²) are formed (Figs. 6c and 6d). Stand-wide growth of regeneration will be maximized when large gap area in a stand is maximized, i.e., clumping residuals, even while holding residual basal area constant (Fig. 6d). Clumping residuals increases the percentage of competitive neighborhoods in the stand that are shifted to the extreme left on the seedling growth curve (Fig. 1), presumably because both light and nitrogen availability are maximized in these environments (Figs. 2 and 3).

Our silvicultural model needs to be verified using experiments that alter the amount and distribution of residual overstory basal area in whole stands. Should this approach prove effective at minimizing competitive inhibition of regeneration in two-cohort stands, it could facilitate managing for both timber production and maintenance of mature structural elements over time.

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