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SPATIAL DISTRIBUTION OF OVERSTORY RETENTION INFLUENCES RESOURCES AND GROWTH OF LONGLEAF PINE SEEDLINGS

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Abstract. Increasingly, overstory retention is being used in forests traditionally managed for single-cohort structure. One rationale for retention is that residual stand structure better resembles the complex structure of forests after natural disturbance, helping to perpetuate ecosystem functions dependent on that structure. The benefits of retention come at the cost of reduced survival and growth of regeneration because of competition with residual trees. We argue that inhibition of regeneration depends not only on the number and size of residual trees, but also on their spatial arrangement, which ranges from dispersed to aggregated. We use a model of competition at the scale of seedlings to hypothesize that maximum stand-level resource availability, seedling growth, and seedling survival occur with aggregate retention, rather than dispersed retention, even with constant residual basal area. We test our hypotheses with a silvicultural experiment in longleaf pine (*Pinus palustris*) in Georgia, USA. Replicated treatments included an uncut control, dispersed retention, small-aggregate retention, and large-aggregate retention. We measured light, soil nitrogen, soil moisture, and growth of longleaf pine seedlings across the full range of overstory conditions in each treatment. Postharvest basal areas in the cut treatments were similar. Gap light index increased from the control to large-aggregate retention, as did nitrogen availability, measured on exchange resins. Nitrogen mineralization did not differ among treatments, nor did soil moisture or temperature. Seedling biomass increment increased significantly from the control to large-aggregate retention. Survival did not differ among treatments. We argue that these results are a consequence of exponential relationships between overstory competition intensity, resource availability, and seedling growth. Given this relationship, resources and seedling growth are low across a wide range of decreasing overstory competitor abundance but increase exponentially only at very low competitor abundance. This seedling-scale model translates into maximum stand scale resource availability and seedling growth with large-aggregate retention, compared to dispersed retention, because the probability of a seedling occupying a site free of overstory competition is greater with the former. Our research shows that one can improve competitive environments for regeneration by manipulating spatial distribution of residual trees without sacrificing the ecological benefits of overstory retention.

Key words: *dispersed vs. aggregate retention; forest regeneration; longleaf pine; overstory retention;* Pinus palustris; *plant competition; two-cohort stands.*

INTRODUCTION

Forest managers increasingly incorporate overstory retention into silvicultural systems for forests traditionally managed for single-cohort structure. With retention systems, the silvicultural prescription calls for maintaining some overstory trees during a regeneration harvest, through one or more rotations, creating two- or multicohort stands (Seymour 1992, Franklin et al. 1997, Tappeiner et al. 1997, Halpern et al. 1999). For many forest ecosystems, retention systems result in residual stand age structures that more closely resemble the structural outcomes of natural disturbance, than do stands managed for single-cohort structure (Lindenmayer et al. 1991, Hansen et al. 1995, Franklin et al. 1997, Rose and Muir 1997, Seymour and Hunter 1999). In theory, greater continuity of mature stand structure across rotations results in greater biological diversity and perpetuation of ecosystem functions dependent on that structure (Swanson and Franklin 1992, Franklin 1993, Hansen et al. 1995, Franklin et al. 1997).

The ecological benefits of overstory retention may come at the cost of reduced survival and growth of tree regeneration because of competition with residual trees (Birch and Johnson 1992, Seymour and Hunter 1992, Hansen et al. 1995). This may be true particularly for species intolerant of competition. For example, we have found that as little as 6 m^2/ha of overstory basal area reduces above- and belowground biomass increment of regenerating longleaf pine (*Pinus palustris* Mill.) by up to 50%, relative to an open-canopy condition (Palik et al. 1997). Others report similar results

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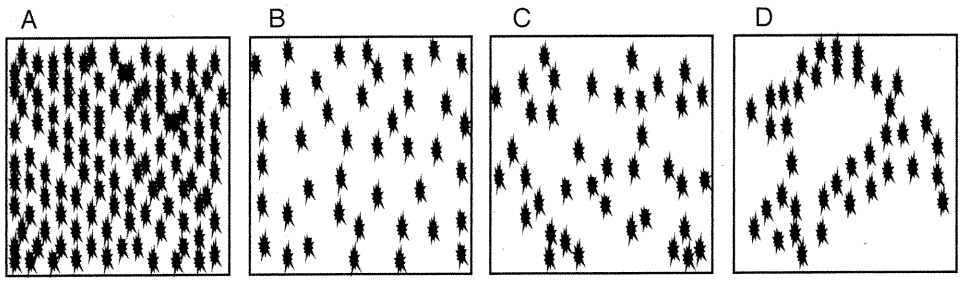

FIG. 1. Conceptual representation of overstory retention treatments that differ in spatial pattern of residual trees: (A) undisturbed forest, (B) dispersed retention, (C) small-aggregate retention, (D) large-aggregate retention. Treatments (B–D) have the same residual overstory basal area.

for longleaf pine (Boyer 1993, McGuire et al. 2001) and other intolerant species (e.g., Perala 1977, Dignan et al. 1998, Zenner et al. 1998, Huffman et al. 1999).

With a retention system, the silviculturist can leave residual trees in various spatial distributions, ranging from dispersed to aggregate. There is continued debate over the merits of dispersed and aggregate retention (Franklin et al. 1997, Palik et al. 1997, Acker et al. 1998, Halpern et al. 1999, Halpern and McKenzie 2001). Under traditional retention systems, e.g., irregular shelterwood (Smith 1986, Matthews 1989), the silviculturist typically disperses residual trees uniformly across the stand (e.g., Boyer 1963, 1993 for longleaf pine). More recently, at least in some regions, the trend has shifted towards greater use of aggregate retention (Acker et al. 1998), as well as variable retention, which combines dispersed and aggregate trees in different combinations in a harvest unit (Franklin et al. 1997).

Much of the debate over dispersed versus aggregate retention focuses on the effects of retention pattern on plant species diversity, stand structural diversity, wildlife habitat, microclimate, and soil and logging disturbance (e.g., Franklin et al. 1997, Halpern et al. 1999, Halpern and McKenzie 2001). However, spatial distribution of retention also may affect growth and survival of regeneration by altering stand-wide competitive environments. We suggest elsewhere (Palik et al. 1997) that dispersed retention distributes the inhibitory effects of overstory trees uniformly across a stand, such that few individual seedlings are free of overstory competition, even at low residual basal area. For instance, with longleaf pine, the inhibitory influences of overstory trees on growth and survival of seedlings can extend to at least 15 m from the crown of the competitor (Smith 1955, Farrar and Boyer 1990, Grace and Platt 1995, McGuire et al. 2001). In stands cut to a low residual basal area (e.g., <15 m^2/ha) using dispersed retention (Fig. 1), few seedlings will be far enough away from residual trees to be free from competition (>15 m in longleaf pine). However, one can aggregate the same amount of residual basal area in space, such that fewer but larger openings occur in the stand (Fig. 1). With aggregate retention, a much greater proportion of the stand will be free of overstory competition, even while holding residual basal area constant, because more seedlings are beyond the range of competitive inhibition from overstory trees (Palik et al. 1997).

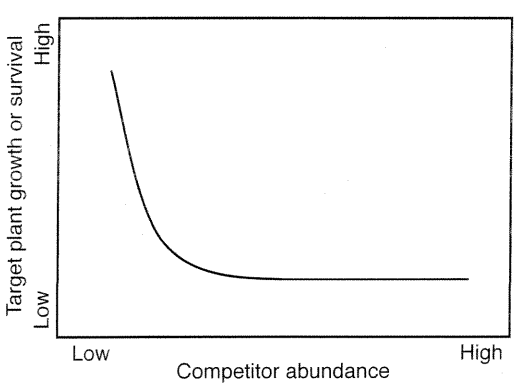

FIG. 2. Conceptual relationship between competitor abundance and target plant growth and survival.

Our hypothesized response of regeneration to spatial patterns of retention, that is dispersed to large aggregate, is a consequence of nonlinear competitive relationships between regeneration and overstory trees at the scale of individual seedlings (Fig. 2). Given this relationship, which is common in the plant competition literature (Silander and Pacala 1985, Goldberg 1987, Sharinsky and Radosevich 1991, Perry et al. 1993, Palik et al. 1997, Acker et al. 1998), growth or survival of target plants is low across a wide range of decreasing competitor abundance and increases, often exponentially, only below some threshold level of low competitor abundance. In the exponentially increasing leg of the curve, target plants are responding to increases in multiple limiting resources (Mitchell et al. 1999).

We predict that in stands managed with dispersed retention, particularly where regeneration consists of species sensitive to a modest amount of competition, most regeneration neighborhoods (i.e., the area around a seedling influenced by overstory competitors) fall to the right on the interaction curve, where growth and survival of target plants are low across a wide range of competitor abundance (Fig. 2). In contrast, with ag-

gregate retention, a larger proportion of regeneration neighborhoods fall to the far left on the interaction curve, where growth and survival increase exponentially because resource competition with the overstory is minimal or nonexistent for many seedling neighborhoods (Fig. 2).

In this paper, we report on an experiment using longleaf pine that tests ideas about spatial distributions of residual trees and their effects on resource availability and survival and growth of seedlings. While others are experimenting in various ways on the influence of retention on regeneration (e.g., Arnott et al. 1995, Coates and Burton 1997, Halpern et al. 1999), we are aware of no studies grounded in the mechanistic framework of plant competition outlined here, nor that make predictions based on such a framework. A better understanding of the effects of residual tree distribution on regeneration dynamics is necessary if we are to develop clear expectations about ecological and productivity trade offs associated with retention systems.

Specifically, we test four hypotheses: (1) resource availability at the seedling scale increases slowly across a wide range of decreasing overstory abundance, increasing exponentially at low overstory abundance; (2) aggregate overstory retention, rather than dispersed retention, maximizes stand-level resource availability, relative to the uncut condition; (3) survival and growth of longleaf pine seedlings increase slowly across a wide range of decreasing overstory abundance, but increase exponentially at low overstory competitor abundance; and (4) at the stand scale, aggregate retention, rather than dispersed retention, maximizes survival and growth of seedlings, relative to the uncut condition.

Methods

Study area

We conducted our experiment at Ichauway, an 11 000-ha reserve of the Jones Ecological Research Center located in southwestern Georgia, USA. The climate of the region is characterized as humid subtropical (Christensen 1981), with a mean annual precipitation of 131 cm evenly distributed throughout the year. Mean daily temperatures range from 21 to 34°C in summer and 5 to 17°C in winter (National Climate Data Center, Asheville, North Carolina). Ichauway is located within the Plains and Wiregrass Plains subsections of the Lower Coastal Plain and Flatwoods section (McNab and Avers 1994). Ichauway has one of the most extensive tracts of second-growth longleaf pine in the southeastern USA and has been managed with low-intensity, dormant-season, prescribed fires for at least 60 years, at a frequency of one fire every one to three years.

Experimental design

Our experiment consisted of a randomized block design with three blocks (replicates) and four treatments within each block. Each block consisted of four 2.0 to 2.5-ha stands, that were prescribed burned before treatment installation in the summer of 1997 and again in winter 2000. Within blocks, the stands themselves were separated by at least 50 m and often were delineated by established roads or trails. The blocks were located in four different locations around the Jones Research Center property.

All blocks, and treatment stands within the blocks, occurred on similar sites and in similar ecosystems, as defined by a multifactor ecosystem classification of the study area (Goebel et al. 2001). Specifically, each block occurred in Ecosystem 11, which is characterized by level to mildly undulating topography and well-drained soils (loamy sand over sandy loam or sandy clay loam) occurring on ancient marine terraces. The overstory is dominated by longleaf pine, with a minor component of oaks (*Quercus falcata* Michx. and *Q. margaretta* Ashe). The understory is dominated by *Aristida stricta* Michx., a perennial bunch grass, along with many other less abundant species of perennial grasses and forbs (Goebel et al. 2001). Each block was located in 60 to 70-yr-old single-cohort stands of naturally regenerated longleaf pine. The stands established after logging of the primary forest early in the 20th century. Since that time, there has been no disturbance in the forest except for occasional removal of trees killed by lightning strikes and windthrow (Palik and Pederson 1996).

We assigned retention treatments randomly to the stands within each block. Treatments consisted of (1) an uncut control, (2) dispersed retention, (3) small-aggregate retention, and (4) large-aggregate retention. We did not include a clearcut treatment for comparison because this management practice is not used on the Jones Research Center property. Basal areas were reduced by ~30% in all three retention treatments (see *Results*), but we altered the spatial distribution of residual trees by cutting progressively larger and fewer openings (defined as areas free of tree crowns) from dispersed retention (single tree selection cutting) to small and large-aggregate retention (~0.1- and 0.2-ha openings and ~0.25- to 0.75-ha aggregates, respectively). A 30% reduction in stand basal area may seem small for a regeneration harvest, but stocking in longleaf pine woodlands on similar sites is low naturally, ranging from 16–20 m^2/ha (Palik and Pederson 1996, Palik et al. 1997, McGuire 2001), due to reductions in regeneration recruitment into the overstory with frequent fire (Platt et al. 1988). Thus, a 30% reduction in basal area resulted in low overstory stocking (see *Results*).

Treatments were harvested in early autumn 1997 using a whole-tree harvesting system. The operator cut trees using a feller-buncher and removed them from the stands using a grapple skidder. The trees were limbed outside of the treatment stands to eliminate the potential inhibitory effects of deep slash on seedling growth and survival.

Planting and sampling design

After harvest, we established 25 8-m^2 (4 × 2 m) plots within each stand. The plots served as locations for seedling planting and resource measurements. We used a stratified locating procedure to ensure that measurement plots covered the full range of overstory conditions in a stand, from open canopy to fully stocked. First, we mapped the geographic locations of all overstory trees (diameter ≥10 cm at 1.4 m height) in a stand using a laser transit and GIS. Next, we overlaid each tree map with a 5 × 5 m grid. The number of grid points varied with stand size and shape, ranging from 444 to 533. At all grid points, ≥15 m from a stand boundary, we calculated a weighted measure of overstory competitor abundance (following Stroll et al. 1994) within a 15-m radius (706 m^2) circle:

$$\mathrm{OAI} = \sum_{i=1}^{n} (A/d) \qquad (1)$$

where OAI = overstory abundance index (typically expressed as a dimensionless value), A = cross-sectional area of tree i (cm^2), d = distance (m) of tree i from the grid point. The point to tree distance (d) was constrained to be no less than 1 m to prevent giving undue weight to trees in close proximity (i.e., ≪1 m) to the sample point. OAI is a better index of overstory competitor abundance than basal area because it gives greatest weight to trees most likely to preempt resources from a target plant, that is, larger trees and trees closest to the measurement point. Conversely, small trees located far from a target plant will contribute very little to OAI, reflecting their limited ability to preempt resources from the target plant. We chose 15 m as our distance from stand boundaries and the radius for calculating OAI because past research on longleaf pine has shown that competitive effects of overstory trees on seedling growth extends approximately to this distance (Farrar and Boyer 1990, Grace and Platt 1995, McGuire et al. 2001).

In each stand, we divided the range of OAI into five equal-class widths (i.e., 0–20%, 21–40%, etc.). Within each OAI class, we chose five grid points randomly using the GIS, for a total of 25 points in each stand. These points served as loci for locating the 25 measurement plots.

Several weeks before planting, we eliminated the herbaceous and woody ground layer in each 8-m^2 plot using a 4% glyphosate solution. Over the course of the experiment, the plots were hand weeded as needed or treated with spot-applied glyphosate while covering seedlings under protective plastic shields. By eliminating herbaceous and small woody vegetation, we were better able to isolate the influence of overstory retention treatments on resources and seedling performance.

In February 1999, we planted 10 one-year-old containerized longleaf pine seedlings in the central 4-m^2 portion of each 8-m^2 measurement plot, distributing them evenly to reduce interseedling competition. Only apparently healthy seedlings with root-collar diameters of 8–12 mm were planted. This grading procedure helped to reduce mortality from out-planting shock and decreased variability in initial seedling sizes.

Resource measurements

We used hemispherical photographs to measure canopy openness and calculate light availability at all 25 measurement plots in each stand. Photographs were taken after full extension of current-years needles, in July and August 1998, on calm, cloudless mornings just before sunrise. For these photos, the camera lens was situated 1.5 m above the ground on a tripod. This height was picked for convenience of camera operation; however in all cases, there was never a lower lying vegetation layer that would have warranted a lower camera height.

To reduce costs, we measured soil resources (nitrogen, water, temperature) on a subsample of six of the 25 measurement plots in each stand. The six plots were selected randomly, stratified within the five OAI classes. Two plots were located in the 0–20% OAI class and one plot in each 20% class thereafter. We measured soil resources in the 2-m^2 portions of a measurement plot, immediately adjacent to either side of the seedling planting areas (nitrogen measurements on one side and soil moisture and temperature on the other side).

In each soil resource plot, nitrogen mineralization (NO_3^- and NH_4^+) was measured using in situ buried-bag incubations (Eno 1960). For the incubations, we extracted soil cores (2 cm diameter by 10 cm depth) from each plot and removed a subsample of soil for estimation of initial inorganic nitrogen pools, placing the remaining samples into gas-permeable plastic bags and burying them in their respective plots. The bags were retrieved at the end of 30- to 60-d incubations, at which time we rinsed them with deionized water and extracted the nitrogen with 25 mL of 2 mol/L KCl per bag. This matrix allowed us to quantify ammonium and nitrate levels simultaneously. Extract solutions were analyzed using a Lachat autoanalyzer (Lachat Corporation, Milwaukee, Wisconsin). Nitrogen mineralization was calculated as the sum of the difference between the initial and final nitrogen concentrations for $NO_3^- + NH_4^+$, standardized to a 30-d period. We conducted seven incubations in 1998 (April through November), five in 1999 (April through December), and three in 2000 (February through June).

Nitrogen (NO_3^- and NH_4^+) availability was measured using ion exchange membranes (Binkley and Matson 1983). The membranes consisted of sturdy surgical cloth impregnated with one layer of either cation or anion beads. We cut the membranes to a standard 5 × 5 cm size and tied a colored cable tie into a corner to distinguish between cation and anion membranes. The membranes were prepared by shaking them in 0.5 mol/

L $NaHCO_3$ for three 20-min periods, followed by a rinsing in deionized water after each charging. We installed two cation and two anion membranes in each nitrogen measurement plot, burying them at a depth of 5 cm. The membranes were retrieved after about seven days, rinsed with deionized water, extracted with 25 mL of 2 mol/L KCl per membrane, and analyzed for nitrogen using a Lachat autoanalyzer. We measured nitrogen availability six times in 1998 (June through October), four times in 1999 (May through November), and three times in 2000 (February through May).

We measured volumetric soil moisture using time-domain reflectometry (Topp et al. 1980), across 0–30 cm and 30–90 cm depths. For each depth, one pair of stainless steel rods was placed vertically in the soil, within the 2-m^2 measurement area adjacent to the planted seedlings. Moisture readings were collected every two weeks, from March 1998 to December 2000 using a cable tester (Tektronix-2A; Tektronix, Beaverton, Oregon). We measured soil temperature at 5 cm depth, at the same time as the TDR readings, using a thermocouple probe (OMEGA Engineering, Stamford, Connecticut), except in 2000 when temperatures were measured only through September.

Seedling measurements

Root-collar diameters of all surviving seedlings were measured in October 2000. In December 2000, we selected a subset of plots in each stand for destructive harvest of seedlings. Not all seedlings were harvested at this time because we needed to leave some for a later comparison with seedling growth in plots that have an intact ground layer. Plots were chosen for the seedling harvest so that they spanned the full range of canopy conditions in the study. This subsample of 276 seedlings was used to estimate biomass increment of seedlings in all plots (see *Methods: Analysis*). On these plots, we measured root-collar diameters of harvested seedlings, clipped their tops for determination of aboveground biomass increment, and excavated and collected their root systems, retrieving all structural roots and as many medium to fine roots as possible. The seedling parts were dried for 48 h at 70°C and weighed.

Analyses

We scanned hemispherical photographs and analyzed the images using HemiView software (Delta-T, Cambridge, UK) to estimate direct and diffuse beam radiation above each plot on a daily basis over a 12-mo period. With this analysis, we calculated gap light index (Canham 1988) for each plot as cumulative seasonal light availability, relative to light availability in the open. In other work, we have found that gap light index and light transmittance measured with light diodes are highly correlated ($r^2 = 0.78$, $P < 0.0001$; Battaglia 2001).

Nitrogen availability (resin membrane) data were averaged into two periods, including 1998 and 1999–2000. We pooled the 1999 and 2000 data because determinations in 2000 were restricted to the early growing season. Nitrogen mineralization data were averaged by year (1998 to 2000). The TDR measurements were converted to volumetric soil moisture following Topp et al. (1980), and the biweekly measurements were averaged by year (1998 to 2000) and depth. We summarized soil temperature over time in the same way as moisture.

Seedling biomass increment over the period of observation (663 d) was estimated by subtracting initial above- and belowground masses from final mass of surviving seedlings. We estimated initial biomass by sampling 50 seedlings at the time of planting and averaging their weights for a single determination of each component (aboveground, 3.8 ± 0.7 g [mean ± 1 SD]; belowground, 3.2 ± 0.5 g). We found that initial biomass variation was minimal and poorly related to diameter, reflecting the uniformity of seedling sizes at the time of planting, thus justifying the use of single mean estimates for initial above- and belowground biomass.

Above- and belowground biomass at the time of harvest was predicted for all surviving seedlings in the 25 plots in each stand:

$$\log(\text{aboveground biomass}) = -0.8577 + 0.3664 \times \text{diameter}^{0.6151} \quad (2)$$

$$\log(\text{belowground biomass}) = -0.7216 + 0.3160 \times \text{diameter}^{0.6242} \quad (3)$$

where diameter is root-collar diameter (aboveground, $r^2 = 0.83$, $P < 0.0001$; belowground, $r^2 = 0.87$, $P < 0.0001$; $n = 276$). We used the models, developed from diameter and biomass data from the harvested seedlings, to predict biomass from diameter data collected on all seedlings.

We used nonlinear regression to relate gap light index, soil resources, and seedling above- and belowground biomass increment (as predicted from Eqs. 2 and 3) to OAI using pooled measurements from the six plots (soil resources) or 25 plots (GLI, seedling response) in each stand. Regression models were selected based on our expectations of resource and seedling responses to changing overstory abundance (e.g., exponential decay and power functions), examination of residual plots, and statistical significance of model coefficients. Examination of residual plots indicated that we met distributional assumptions of the residuals for the regressions. We ran all regressions using the least-squares parameter estimation procedure for nonlinear regression in SigmaPlot 7.0 (SPSS, Evanston, Illinois, USA).

Randomized-block ANOVA was used to test for overstory treatment effects on the suite of measurement

variables including basal area, OAI, gap light index, soil resources, and seedling growth and survival. Prior to analyses, we used a weighting procedure to improve the estimate of stand means based on the six plots (soil resources) or 25 plots (OAI, GLI, and seedling responses) in each stand. Although these plots spanned the range of OAI conditions in each stand (i.e., at least one plot in each OAI class), the OAI classes themselves did not occur with equal frequency. Simply averaging data for the 6 or 25 measurement plots could potentially over- or underrepresent a particular OAI class. To account for this, we weighted each plot measurement to reflect the importance of that particular plot's OAI class in the stand. The weights consisted of the proportions of grid points (see *Methods: Planting and sampling design*) falling in each of the five OAI classes, calculated separately for each stand. Also prior to analysis, we sometimes transformed the data (log or arcsine) to better meet distributional assumptions of the residuals from the ANOVA. If the overall test was significant, a set of orthogonal contrasts was used to test the following statistical comparisons that address the effects of retention pattern on resources and seedling response (see *Results: Hypotheses 2: Aggregate overstory retention maximizes stand-level resource availability* and *Results: Hypothesis 4: Aggregate retention maximizes stand-scale survival and growth of seedlings*): (1) pooled retention vs. control (testing whether overstory treatment had an effect); (2) pooled small- and large-aggregate retention vs. dispersed retention (testing whether aggregation had a greater effect than dispersed retention); and (3) small-aggregate retention vs. large-aggregate retention (testing whether responses differed with level of aggregation).

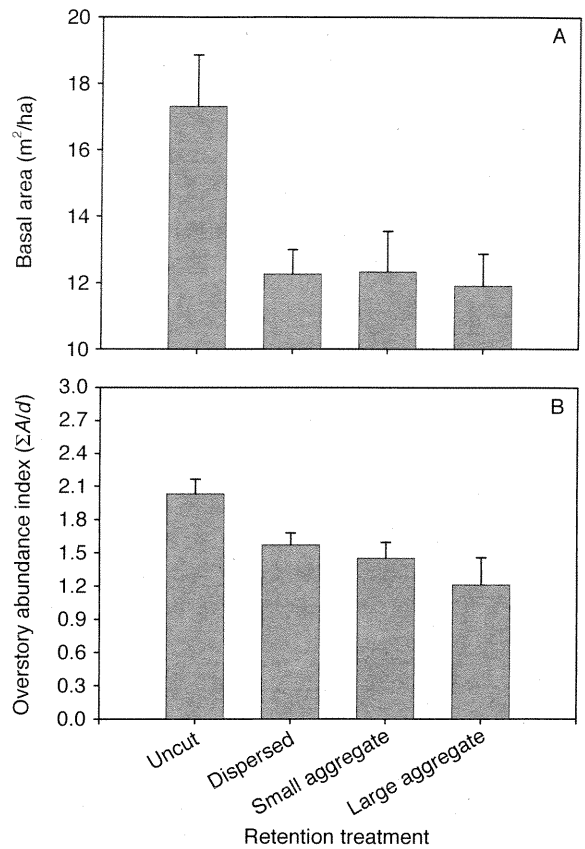

FIG. 3. (A) Overstory basal area and (B) overstory abundance index in four retention treatments in a longleaf pine woodland. Values are means + 1 SE of three replicates.

RESULTS

Changes in overstory structure

Mean (±1 SE) preharvest basal area of the 12 treatment stands was 15.5 ± 1.3 m²/ha. Harvesting significantly lowered basal areas in the three retention treatments ($P = 0.010$). Postharvest basal areas in the retention treatments were similar at ~12 m²/ha, compared to a mean of 17.2 ± 1.5 m²/ha in the control (Fig. 3A). Postharvest basal areas in the pooled retention treatments were all significantly less than the control ($P = 0.002$), while the treatments themselves did not differ (dispersed vs. pooled aggregate retention, $P = 0.900$; small-aggregate vs. large-aggregate retention, $P = 0.736$).

Mean overstory abundance index (OAI) declined significantly ($P = 0.002$) from a high of 2.03 ± 0.13 in the control to a low of 1.21 ± 0.24 with large-aggregate retention (Fig. 3B). OAI in the pooled retention treatments differed significantly from the control ($P = 0.0006$), as did dispersed retention and the pooled aggregate retention treatments ($P = 0.050$). Differences in OAI for the two aggregate retention treatments themselves were marginally significant ($P = 0.085$).

Hypothesis 1: Resource availability at the seedling-scale increases exponentially at low overstory abundance

Gap light index (GLI) increased significantly ($r^2 = 0.53$, $P < 0.0001$, $n = 300$) and nonlinearly with decreasing OAI (Fig. 4A). GLI increased minimally from an OAI of 4.9 down to an OAI of 1.5, but increased more rapidly below this level.

Nitrogen availability ($NO_3^- + NH_4^+$), as measured on resin membranes, was significantly related to OAI in both 1998 ($r^2 = 0.59$, $P < 0.0001$, $n = 72$) and 1999–2000 ($r^2 = 0.36$, $P < 0.0001$, $n = 72$). For example, in 1998, nitrogen availability increased minimally from an OAI of 4.9 down to 0.50, increasing exponentially below this threshold (Fig. 4B). The trend was similar in 1999–2000 although not as strongly related to OAI (data not shown). In contrast, nitrogen mineralization was poorly predicted by OAI (data not shown). Although the regressions were marginally significant each year, the percent variation explained was always very low (1998, $r^2 = 0.039$, $P = 0.096$; 1999,

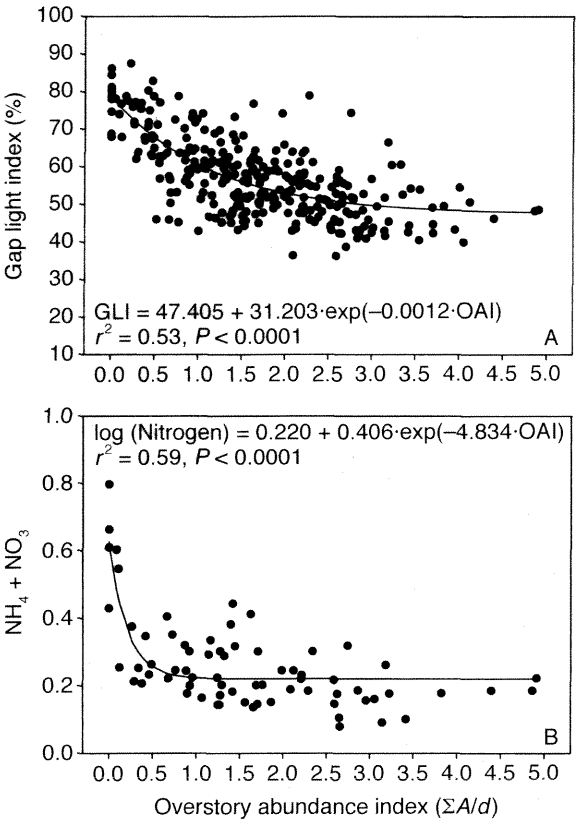

FIG. 4. The response of (A) gap light index and (B) nitrogen availability in 1998 to overstory abundance index in a longleaf pine woodland. Prior to log transformation, nitrogen availability units were measured in μg $[NH_4 + NO_3]$·membrane^{-1}·7 d^{-1}.

r^2 = 0.053, P = 0.053; 2000, r^2 = 0.045, P = 0.075; n = 72 for each year).

Soil moisture did not vary strongly with OAI at either depth or in any year of measurement (data not shown; r^2 = 0.001–0.131). Only one of the six regressions (three years × two depths) was statistically significant (1999, 0–30 cm, r^2 = 0.131, P = 0.002, n = 72), but the biological significance of this was minimal because of the low variance explained. Near-surface soil temperature increased linearly with decreasing OAI in all years (1998, r^2 = 0.22, P < 0.0001; 1999 and 2000, r^2 = 0.10, P = 0.007; n = 72 for each year), but the variation across the range of OAI was small, averaging around a 1–2°C difference between low and high OAI (data not shown).

Hypothesis 2: Aggregate overstory retention maximizes stand-level resource availability

Gap light index (percentage of an open condition) increased significantly (P = 0.005) from the control (49.7 ± 1.0%) through dispersed retention (56.2 ± 1.0%), small-aggregate retention (60.9 ± 1.0%), and large-aggregate retention (64.8 ± 1.1%; Fig. 5). The difference between the control and the pooled retention treatments was significant (P = 0.002), indicating that overstory treatment had an effect. The difference between dispersed and pooled aggregate retention was significant as well (P = 0.025), indicating that aggregation resulted in greater light than in dispersed retention. The difference between small and large-aggregate retention was not significant (P = 0.167), indicating that light environments were similar for both levels of aggregation.

Nitrogen availability at the stand scale differed significantly among treatments (Fig. 6) in both 1998 and 1999–2000 (1998, P = 0.003; 1999–2000, P = 0.001). For both periods, nitrogen availability was higher in the pooled retention treatments compared to the control (1998, P = 0.006; 1999–2000, P = 0.005). Availability was higher with pooled aggregate retention compared to dispersed retention in 1998 (P = 0.012) and marginally so in 1999–2000 (P = 0.079). Availability was significantly higher with large-aggregate retention compared to small-aggregate retention in both 1998 (P = 0.006) and 1999–2000 (P = 0.001).

On average, nitrogen mineralization at the stand scale increased across the retention gradient. For example, in 1998, mineralization increased from 1.2 ± 0.8 kg·ha^{-1}·30 d^{-1} in the control to 1.3 ± 1.0 kg·ha^{-1}·30 d^{-1} with dispersed retention to 1.5 ± 0.2 and 2.5 ± 0.4 kg·ha^{-1}·30 d^{-1} with small and large-aggregate retention, respectively. The patterns were similar in all years (data not shown). However, variability among treatments was large, with only two of the three replicates in any year following the same trend, thus the differences were not significant (1998, P = 0.498; 1999, P = 0.683; 2000, P = 0.754).

Soil moisture averaged ~10% at 0–30 cm and 7% at 30–90 cm in each treatment in all years. There were

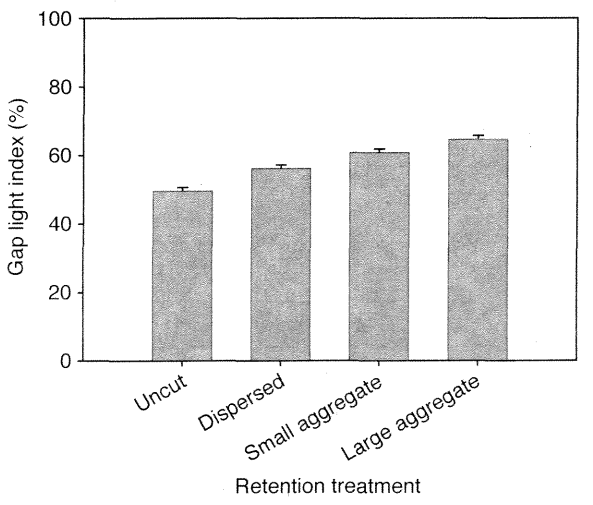

FIG. 5. Gap light index in four retention treatments in a longleaf pine woodland. Values are means + 1 SE of three replicates.

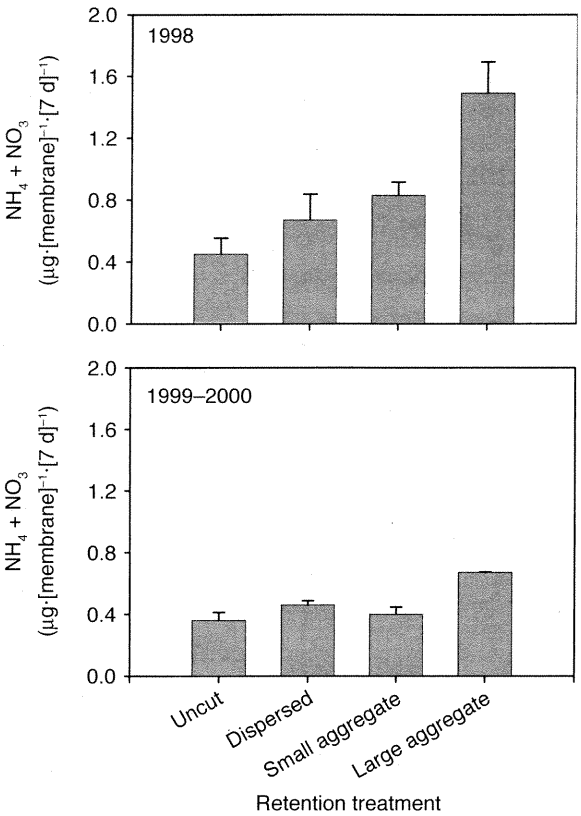

FIG. 6. Soil nitrogen availability in 1998 and 1999–2000 in four retention treatments in a longleaf woodland. Values are means + 1 SE of three replicates.

no significant differences among treatments at either depth for any year (P = 0.175–0.758). Soil temperatures averaged ~23°C in 1998, 18°C in 1999, and 19°C in 2000 in all treatments. Differences among treatments were not significant in any year (1998, P = 0.143; 1999, P = 0.426; 2000, P = 0.264).

Hypothesis 3: Survival and growth of longleaf pine seedlings increase exponentially only at low overstory abundance

A decay function best explained the relationship between overstory competitor abundance, as measured by OAI, and above- and belowground seedling biomass increment (of surviving seedlings), 663 d after planting (Fig. 7). Biomass increment was largely constant across a wide range of decreasing OAI, but increased exponentially below an OAI of ~1.0. Both regression relationships were significant (aboveground and belowground, r^2 = 0.55, P < 0.0001; n = 285). Seedling survival, which ranged from 0% to 100% among plots over the 663-d period, was poorly predicted by OAI (data not shown; r^2 = 0.005, P = 0.215; n = 300).

Hypothesis 4: Aggregate retention maximizes stand-scale survival and growth of seedlings

At the stand scale, both above- and belowground biomass of surviving seedlings increased significantly from the control through dispersed and small-aggregate retention to large-aggregate retention (aboveground, P = 0.019; belowground, P = 0.019; Fig. 8). Biomass increment differences between the pooled retention treatments and the control were only marginally significant (aboveground, P = 0.060; belowground, P = 0.070) because low growth in the dispersed and small-aggregate treatments lessened the influence of high growth in the large-aggregate treatment (Fig. 8). Both above- and belowground growth biomass increment were significantly higher in the pooled aggregate retention treatments compared to dispersed retention (aboveground, P = 0.047; belowground, P = 0.044), indicating that dispersed retention was not effective at reducing competitive inhibition from overstory trees. Finally, large-aggregate retention had significantly greater growth than small-aggregate retention (aboveground, P = 0.016; belowground, P = 0.016).

Seedling survival did not differ significantly among retention treatments (data not shown; P = 0.099). Mean

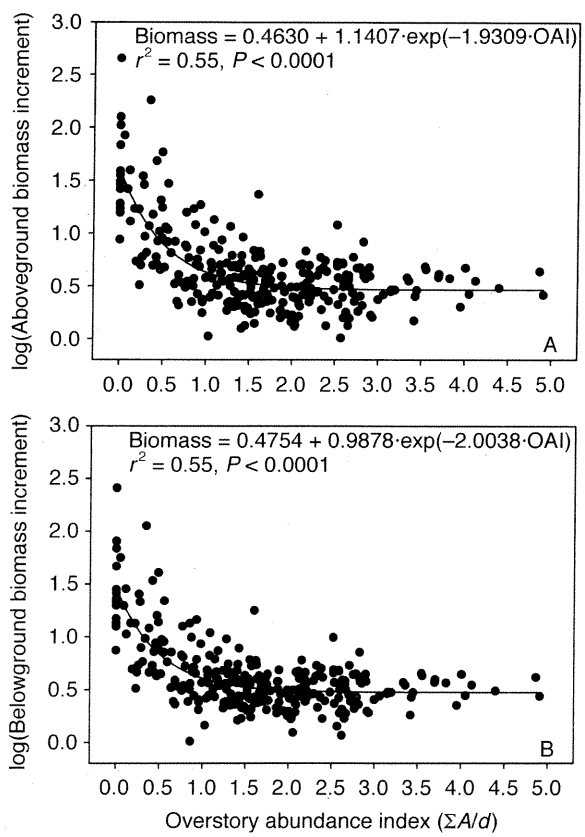

FIG. 7. The response of (A) aboveground and (B) belowground longleaf pine seedling biomass increment to overstory abundance index in a longleaf pine woodland. Units for biomass increment are log(g biomass/663 d).

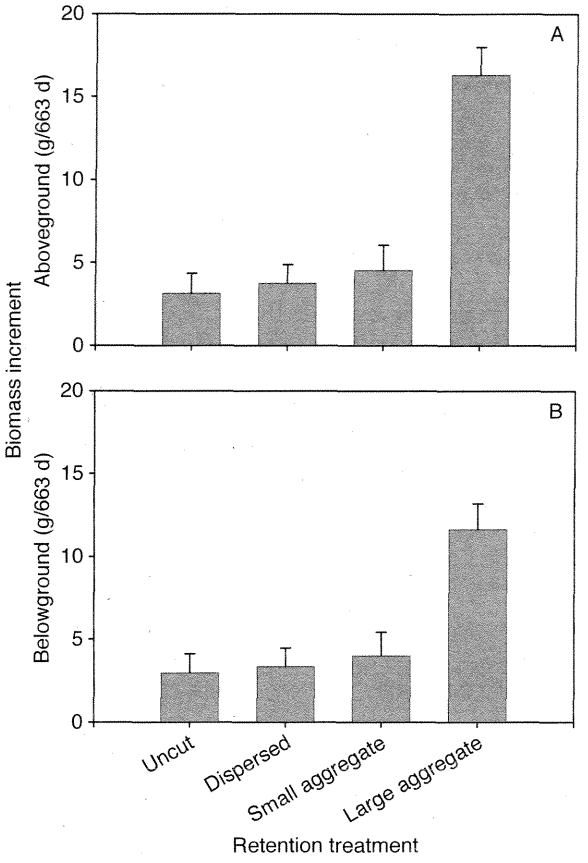

FIG. 8. (A) Aboveground and (B) belowground longleaf pine seedling biomass increment in four retention treatments in a longleaf pine woodland. Values are means + 1 SE of three replicates.

(±1 SE) survival, 633 d after planting, decreased from 51.3 ± 4.9% in the control to 48.7 ± 4.4% with dispersed retention to 46.9 ± 6.9% with small-aggregate retention to 34.2 ± 4.8% with large-aggregate retention. However, variation was high, and trends across the retention gradient (control to large aggregate) were not consistent among blocks.

DISCUSSION

From a purely ecological standpoint, there is little debate over the merits of overstory retention. Many people agree that retaining some overstory trees during a regeneration harvest reduces structural disparity between late-successional conditions and stands managed for single-cohort structure (Zenner 2000, Palik et al. 2002). Greater structural carryover across rotations increases the potential for sustaining functions, habitat, and organisms from the preharvest stand (Franklin et al. 1997, Merrill et al. 1998).

However, there are unresolved questions over appropriate amounts of residual trees and spatial distribution of retention (Franklin et al. 1997, Halpern et al. 1999, Halpern and McKenzie 2001, Palik et al. 2002). Questions over amount of retention often focus on inhibition of regeneration by overstory trees (Palik et al. 1997, Acker et al. 1998, Dignan 1998, Zenner et al. 1998). Debates over spatial distribution of retention often focus on the merits of dispersed vs. aggregate retention for amelioration of microclimate extremes, sustainability of plant and wildlife habitat, and potential for forest floor disturbance (Franklin et al. 1997, Halpern et al. 1999, Halpern and McKenzie 2001).

Our research shows clearly that spatial distribution of retention also is important when considering the effects of a residual overstory on plant competitive environments and regeneration dynamics. Moreover, we show that stand-scale responses to retention pattern are a consequence of cumulative competitive environments at the scale of individual seedlings.

Specifically, as we predicted, light and nitrogen availability at the scale of individual seedlings increased slowly across a wide range of decreasing overstory abundance (starting with a fully stocked overstory), increasing exponentially below a threshold level of very low overstory competitor abundance (hypothesis 1). This seedling scale effect of competitors translated into maximum resource availability at the stand scale (relative to the uncut condition) occurring with large-aggregate retention, rather than dispersed retention (hypothesis 2). Our results on overstory competitor abundance (OAI) across the retention gradient support this interpretation because OAI declined from dispersed to large-aggregate retention, despite uniform residual basal area in the treatments. This suggests that traditional stand-level measures of competitive environment (e.g., density, crown cover, basal area) do not accurately reflect the true competitive environment of a stand. Operationally, these results show that with aggregate retention, a greater proportion of regeneration neighborhoods in the postharvest stand are free of resource preemption from the overstory.

As predicted, growth of longleaf pine seedlings increased gradually across a wide range of decreasing overstory abundance (beginning with a fully stocked overstory) and then increased exponentially as overstory competitor abundance, measured by OAI, decreased below a threshold level of around 1.0 (hypothesis 3). The nonlinear form of this interaction is common in the plant competition literature (Silander and Pacala 1985, Goldberg 1987, Sharinsky and Radosevich 1991, Perry et al. 1993, Palik et al. 1997, Acker et al. 1998). It arises because it is only at low competitor abundance, below the threshold level, that multiple limiting resources start to become available (Mitchell et al. 1999). In our case, availability of light, but especially nitrogen, increased exponentially at low competitor abundance.

There was significant variability in seedling growth, as well as light and nitrogen, around any given level of OAI (Figs. 4 and 7), reflecting heterogeneity in soil conditions or stand structure not fully captured by our

measure of overstory competitor abundance. However, the percent of variation in longleaf pine seedling biomass explained by overstory competitor abundance was substantially higher than values typically reported from similar field experiments (e.g., Goldberg 1987), indicating that OAI is a reasonably inclusive measure of overstory competition intensity.

The resource responses we document translated into significantly greater seedling growth with large-aggregate retention, because the probability of a seedling occupying a "safe site" for regeneration increased exponentially from the uncut stand to large-aggregate retention, even while holding residual basal area constant (hypothesis 4). To illustrate, we estimated probability of safe site occurrence for seedlings across the different stand treatments, using OAI determinations made on the complete series of grid points used to locate resource and seedling measurement plots (see *Methods: Sampling design*). Using an OAI of 1.0 as the competition threshold below which seedling growth rates begin to increase exponentially (Fig. 7), we estimate that, on average, only 16% of understory neighborhoods in uncut stands are safe sites for regeneration, that is, they have an OAI below 1.0. This proportion increases to 30% with dispersed retention, 36% with small-aggregate retention, and 40% with large-aggregate retention.

The exact probability of safe site occurrence and seedling success with different spatial patterns of retention depend on the ecosystem in question, the species involved, and the specifics of growing conditions, such as levels of rainfall. Spatial scale, as it affects level of aggregation, is also an important consideration. Our results are derived from competitive interactions in 2.0- to 2.5-ha stands. We felt that this size was sufficient to include a wide range of regeneration conditions after harvest, given the physical size of overstory competitive neighborhoods for longleaf pine (~15 m radius circle or 700 m^2) and the size of both the harvest openings (0.1 ha and 0.2 ha) and the leave tree patches (0.25 and 0.75 ha) in the small and large-aggregate retention treatments, respectively. For similar ecosystems, canopy conditions in stands smaller than 2 ha will start to be biased towards either openings or residual patches of trees and stands smaller than 1 ha are likely to consist of only a single overstory competitive neighborhood.

Our results on seedling growth contradict the prediction made by Halpern et al. (1999), for coniferous ecosystems in the Pacific Northwest, USA, that growth rates of regenerating trees will be higher with dispersed retention than with aggregate retention. They restrict their prediction to a comparison of only the harvested portions of the aggregate retention treatments vs. dispersed retention, thus excluding seedlings that may be growing within residual patches themselves. Our results reflect competitive conditions throughout the stands, including conditions within retained patches of trees. Comparison of conditions in only the harvested portions of stands in our study would only amplify the growth differences we observed between dispersed and aggregate retention treatments. Our results do support Franklin et al.'s (1997) prediction that inhibition of regeneration will be greater with dispersed retention because overstory competition occurs over the entire harvest unit rather than in discrete patches.

These two predictions may not be mutually exclusive for several reasons. First, growth responses to retention pattern may vary among species depending on their competitive abilities. It may be that species more tolerant of competition than longleaf pine will have maximal growth with dispersed or small-aggregate retention rather than large-aggregate retention. Moreover, the influence of understory competitors, which we eliminated in our study, may alter competitive responses to overstory condition. Even species intolerant of competition may achieve highest growth with dispersed retention if understory competition is suppressed to a greater degree than with aggregate retention. Finally, resource availability and seedling growth may respond much differently to spatial pattern of residual trees if retention levels are lower than used in our study. For instance, low levels of dispersed overstory retention may facilitate seedling growth by ameliorating microclimatic extremes relative to a clearcut.

Unlike growth, seedling survival was weakly related to retention pattern, although there was the suggestion that survival decreased across from the control to large-aggregate retention. Others suggest that overstory shade may facilitate early longleaf pine seedling survival, at least during drought years (Allen 1954, McGuire et al. 2001), which occurred during 1999 and 2000. Over time, we predict increased mortality of shaded seedlings because of greatly reduced early growth compared to the open-canopy condition and thus survival patterns will more closely relate to overstory competitor abundance and retention distribution.

While patterns of early survival across overstory treatments may not be typical of survival during years with higher rainfall, we believe that the growth of surviving seedlings does reflect typical responses to overstory competitors, regardless of early mortality rates. For instance, in an earlier study during a nondrought year, we had 97% survival of planted longleaf pine seedlings, but similar exponential growth responses to declining overstory competitor abundance (Palik et al. 1997). Moreover, the pattern of exponentially increasing growth from the uncut control to large-aggregate retention (Fig. 8) was the same, although of lower magnitude, even when we included dead seedlings (zero net growth) in the analysis.

We found that nitrogen mineralization, as well as soil moisture and temperature, were not well predicted by overstory competitor abundance and consequently by spatial distribution of overstory retention. McGuire et al. (2001) report similar results when comparing ni-

trogen mineralization and soil moisture in experimental gaps to values in intact longleaf pine woodland. These results contrast with those of Parsons et al. (1994) who found that nitrogen mineralization in lodgepole pine forest was generally higher in large openings (where 30 trees were cut) compared to smaller openings and the uncut forest. They also found that mineralization rates increased substantially with the addition of water to the incubation cores. It may be that in the sandy, well-drained soils of our study area, nitrogen mineralization is limited more by moisture than by overstory structure. Regardless, our current results, along with those from other studies (Palik et al. 1997, McGuire et al. 2001), suggest that reduction in longleaf pine overstory competitor abundance largely affects nitrogen availability through reduced uptake, but that nonuptake effects (e.g., increased potential for mineralization) do not change consistently with reduction in overstory abundance.

Management application

Overstory retention after a regeneration harvest often will reduce growth of a new cohort of trees below that occurring in a newly regenerated single-cohort stand (e.g., Palik et al. 1997, Dignan et al. 1998, Zenner et al. 1998, Huffman et al. 1999, McGuire et al. 2001). This may be true particularly for species intolerant of competition. If growth reductions exceed acceptable limits, one proposed solution is to decrease retention levels and thereby relieve some competitive pressure on regeneration (Dignan et al. 1998, Zenner et al. 1998). Our results show clearly that altering the spatial distribution of retention may accomplish the same goal. At least in the initial post-establishment years, growth of regeneration increases substantially as spatial distribution of retention changes from dispersed through small-aggregate to large-aggregate retention, even while holding residual basal area constant. The ecological implications of these growth differences are obvious; one can improve competitive environments for regeneration of intolerant trees without sacrificing all of the ecological benefits of a retained overstory.

Eventually, some of the growing space and resources liberated by partial harvesting will be reoccupied through in-growth from residual trees, even with large-aggregate retention. As such, the magnitude of seedling growth response we document is likely transient. The extent and rate at which resource and growth declines occur will depend on the sensitivity of seedling species to overstory competition, the size of openings and distances of seedlings to residual trees, as well as the size and vigor of the residual trees. Additionally, in an operational setting where a large number of seedlings are planted, competition among individuals within the regenerating cohort will likely occur, reducing competitive gains resulting from aggregation of residual overstory trees.

We do not advocate use of large-aggregate retention to the exclusion of other retention patterns. In fact, there are many variables to consider, in addition to regeneration success, when debating the merits of dispersed and aggregate retention. For example, dispersed retention may result in significantly less soil disturbance during logging than aggregate retention (Halpern and McKenzie 2001), potentially affecting successional pathways and plant diversity. Moreover, in systems that are nitrogen limited, wood production by the residual overstory should be greater with dispersed retention because, as we have shown, more nitrogen is preempted by this cohort than with aggregate retention, even while holding residual basal area constant. Finally, dispersed retention may prove more conducive for regenerating species tolerant of competition, thus providing opportunities for establishing a different suit of species than might be possible using aggregate retention alone.

Competing benefits of different spatial distributions of retention argue for use of spatially variable overstory retention, which could include dispersed residual trees, as well as different levels of aggregation, within a single harvest unit (Franklin et al. 1997). Even with this approach, as with any silvicultural system, regeneration of trees is an important measure of management success. We provide some compelling evidence based on regeneration success of a species intolerant of competition that argues for inclusion of at least some large-aggregate retention in the variable retention mixture.

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