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SPATIAL PATTERNS OF LONGLEAF PINE (*PINUS PALUSTRIS*) SEEDLING ESTABLISHMENT ON THE CROATAN NATIONAL FOREST, NORTH CAROLINA

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Abstract: Ecological research aimed at determining optimal conditions for longleaf pine regeneration has become increasingly important in efforts to restore the longleaf pine ecosystem. Numerous authors have concluded that a negative relationship exists between the occurrence of seedlings and the occurrence of mature trees; however, observed field conditions in several North Carolina Coastal Plain sites suggested otherwise. Second-growth stands in the Croatan National Forest, North Carolina were examined to further elucidate spatial relationships between longleaf pine seedlings and mature trees. Specific questions addressed were 1) Does the spatial pattern of stems depart from random for either mature trees or seedlings, 2) Is there a spatial association between mature trees and seedlings, and 3) Does a relationship exist between the occurrence of mature trees and underground or surface resources (i.e., carbon and nitrogen content and litter biomass) or root biomass. Ripley's univariate L(t)-statistic was used to test whether the spatial pattern of stems departed from random. Ripley's second order statistic was used to determine whether a significant relationship existed between mature trees and seedlings. Generally, seedlings were found to be aggregated, but no significant spatial relationship was found between seedlings and mature trees. The most significant influence of mature trees on seedlings may be increased litter accumulation in close proximity to trees, which can adversely affect seedling survival by increasing fire intensity.

Key Words: Longleaf pine; regeneration; Ripley statistic; North Carolina; Coastal Plain.

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INTRODUCTION

The longleaf pine (*Pinus palustris* Miller) ecosystem, which once dominated the southeastern U.S. Coastal Plain from Virginia to Texas, has been reduced to a fraction of its pre-settlement area. This loss in area is the result of logging, agriculture, site conversion, the introduction of more vigorous pine species (e.g., loblolly pine, *Pinus taeda* L.), and fire suppression (Wahlenberg, 1946). Less than 3% of the original ecosystem remains, mostly in the form of protected areas and research sites, with a very small amount being used for commercial timber applications (Outcalt and Sheffield, 1996). Ecological research aimed at determining optimal conditions for longleaf regeneration has become increasingly important in efforts to restore the ecosystem. Research of particular interest to the current study has emphasized the importance of fire (Varner et al., 2000) and the spatial relationships between longleaf pine seedling establishment and mature trees, particularly beneath openings in the overstory canopy (Brockway and Outcalt, 1998; McGuire et al., 2001).

Numerous authors have concluded that a negative relationship exists between the occurrence of mature longleaf pine trees and longleaf seedlings. Palik et al. (1997) described a negative relationship between the basal area of mature trees and seedling growth because of decreasing available light and nitrogen levels with increasing basal area. Similarly, McGuire et al. (2001) reported increases in survival and growth of seedlings corresponding to increased levels of available light. Natural seedling occurrence in close proximity to adult trees, however, could not be assessed by either Palik et al. (1997) or McGuire et al. (2001) because seedlings were planted. Brockway and Outcalt (1998) described a "seedling exclusionary zone" along the edges of canopy gaps where seedlings were absent. They attributed this pattern to intraspecific competition between seedlings and the fine root biomass of mature trees. Grace and Platt (1995a,b) also found that the location of seedlings was negatively associated with mature trees as early as the first year of seedling growth. The negative association between seedlings and adult trees was attributed to increased needle litter depth around mature trees, which increases adverse effects of higher fire intensity on young seedlings (Grace and Platt, 1995a).

The above findings and observations suggest that more work is necessary to clarify the relationship between mature trees and seedling establishment. The above research was conducted in the well-drained soils of either northern Florida (Brockway and Outcalt, 1998) or southern Georgia (Grace and Platt, 1995a; Palik et al., 1997; McGuire et al., 2001). Field observations on several moderately to poorly drained longleaf pine stands on the outer Coastal Plain of North Carolina, however, suggested seedling patterns contrary to the above findings.

This study examined spatial relationships between longleaf pine seedlings and mature trees in second–growth stands on the Croatan National Forest (NF), North Carolina. We hypothesized that no single variable is solely or even primarily responsible for the spatial pattern of seedlings. Additionally we hypothesized that, in contrast to the findings of Grace and Platt (1995a), the impact of neighboring trees on seedling survival is negligible in the early stages of seedling growth in the absence of fire. Specifically, we asked these questions: 1) Does the spatial pattern of stems depart from random for either mature trees or seedlings, 2) Is there a spatial association between mature trees and seedlings and, if so, is it related to seedling survival and 3) Does a relationship exist between the occurrence of mature trees and underground or surface resources (i.e., nitrogen and carbon content and litter biomass) or root biomass? Finally, the spatial distribution of seedlings within the study plots was examined qualitatively within the context of these relationships.

METHODS

Study Area

Study sites are located on the Croatan NF, Carteret County, North Carolina. Soils here are generally more poorly drained and nutrient limiting than soils in previous research studies located in the southern portion of longleaf pine's range. All plots are located on the Onslow soil series, a moderately to somewhat poorly drained, loamy sand (fine-loamy, siliceous, thermic Spodic Paleudults). It is highly acidic and generally nutrient-poor. Annual precipitation in the region averages 131 cm with extended droughts often occurring during the growing season. Mean annual air temperature is 17.3°C, with temperature minimums in January (7.4°C) and maximums in July (26.4°C) (Goodwin, 1987).

Sites for this study were chosen based on similar history, age, soil type, management regime, and presence of an intact understory. Additionally, sites were chosen irrespective of canopy openness so that samples would not be biased toward open areas. The study sites have a longleaf pine flatwoods/savanna vegetation structure, with a mature uneven-aged overstory dominated by longleaf pine, no midstory, and a mix of low–growing woody and herbaceous vegetation in the understory. Dominant plants include *Aristida stricta* Michaux (wiregrass), *Vaccinium crassifolium* Andrews (creeping blueberry), *Vaccinium tenellum* Aiton (low bush blueberry), and *Ilex glabra* Gray (inkberry). Average stand age ranges from 70 to 100 yr, and basal area of all tree species ranged from 9 to 21 m^2/hectare. The contribution of species other than longleaf pine was negligible. These sites have been winter–burned every two to four years, for the past two decades, and all sites have been burned within the last three years. Site 1 plots were burned in February 2002, after the initial survey, thus offering a comparison of seedling survival in recently burned and less recently burned plots.

Field Methods

Three circular measurement plots were randomly located on each of three sites, for a total of nine plots. Each plot was 30 m in diameter (0.07 ha) and did not overlap any other plot. One-half of each plot was chosen randomly and all longleaf seedlings in this half were mapped by distance and azimuth from the center point of the plots in January 2001. Ages of seedlings cannot be ascertained with non destructive methods and all longleaf pine trees <5 cm diameter breast height (DBH) were considered seedlings. Seedlings were resurveyed in May 2002 to assess mortality after the prescribed burn in February 2002. Additionally, all mature longleaf pines (DBH ≥ 5 cm) within 40 m of the plot centers were mapped by distance and azimuth from the center point of the plots. DBH and species were also recorded for each tree.

A 30 m transect was established in each plot and went through the plot center. Transect orientation was in the E–W cardinal direction. Litter biomass was measured using eight 0.25 m^2 litter traps placed along the transect of each plot. Litter was collected from each trap monthly from February to May 2001, separated into needles and non-needles, oven dried and weighed.

Two sets of soil cores were collected at three meter intervals along the east–west transect in January and July 2002. Soil cores were separated into three depths in January: 0 to 10 cm, 10 to 20 cm, and 20 to 30 cm. Only the 0 to10 cm and 10 to 20 cm soil cores were collected in July. Cores were analyzed at each depth for nitrogen (N), carbon (C), and organic matter content and root type and content. Samples were analyzed for C/N using a Thermo Finnigan Flash 1112 (Thermo-Finnigan, Italy). Organic matter content was determined using standard loss on ignition procedures. Roots were sorted and categorized as longleaf pine; non-longleaf pine woody; and herbaceous.

Data Analysis

Data analyses were divided into four main groups. The first was a spatial pattern analysis, based on the January 2001 survey, to determine whether longleaf seedlings and/or trees exist in a random, aggregated, or regular dispersion. The hypothesis that a random (Poisson) distribution exists was tested with Ripley's (1977) univariate L(t)-statistic given by:

$$L_i(t) = \left[A \sum k_{ij}/\pi(n-1)\right]^{1/2}$$

where $\sum k_{ij}$ is the summation over all points within distance t of point i, including a boundary correction where required, A is the plot area, and $n - 1$ is all possible pairs of points with i as a pair member (Getis and Franklin, 1987). This statistic is capable of evaluating spatial dispersion at multiple scales (Ripley, 1977). This is beneficial because observed spatial patterns may be a function of the scale of the analysis (Getis and Franklin, 1987). An additional benefit of the Ripley test is an incorporated edge–correction factor that permits extrapolation outside of the actual study plot (Ohser and Stoyan, 1981). The Ripley analysis is performed by creating a series of concentric circles of increasing radii around each point in the dataset (Getis and Franklin, 1987). The variation of interplant distances is then tested for randomness with confidence intervals set at the 5% and 1% highest and lowest values determined by performing 199 Monte Carlo simulations of an expected Poisson distribution.

The second set of analyses examined the nature of the spatial association between mature trees and seedlings. Ripley's bivariate spatial statistic [L(t)-statistic] was used to assess the degree to which seedlings were (or were not) clustered around mature trees (Ripley, 1976). This bivariate analysis provided the same benefits of multiple–scale analysis and edge–correction described above for the univariate test (Getis and Franklin, 1987).

A logistic regression was performed with seedling survival as the dependent variable and potential influence of mature trees as the independent variable in order to address the statistical significance of potential influence of mature trees on the survival of seedlings. The potential influence of mature trees was estimated with the following equation:

$$g_s = \sum (DBH_k/distance_{ik})$$

where g_s indicates the potential effects of neighboring trees on seedlings, DBH_k is the DBH of the kth tree around seedling i, and $distance_{ik}$ is the distance between the ith seedling and the kth mature tree. The seedling survival variable was a binary, categorical variable where dead seedlings were assigned a value of 0 and surviving seedlings were assigned a value of 1. Dummy variables coded for the nine different plots were included in the regression analysis to determine whether plots differed in the relationship between mature tree influence and seedling survival. Dummy variables permitted the incorporation of qualitative variables into a regression model through binary coding where a 1 indicated membership in a group (i.e., plot) and a 0 indicated that the observation was not a member of that group (Hardy, 1993). The plot variable, in this instance, may help to refine the model because it served as a surrogate for various unmeasured plot–specific factors as well as unmeasured factors embedded within the sample itself and the sampling design. Plot 1–3 was chosen as the reference category because it contained the largest number of observations, which is one of several guidelines that can be used in reference group selection, although the choice of reference group was arbitrary and no choice can be incorrect (Hardy, 1993). When interpreting dummy variable coefficients and calculating predicted probabilities they are interpreted individually and relative to the reference group. The predicted probabilities for each plot were first calculated and then averaged across all plots to obtain the average predicted probability of seedling survival for all plots. Logistic regression, which models the probability of an event rather than the predicted value of the dependent variable, was determined to be the optimal estimator in this instance because of its ability to handle effectively seedling survival and the dummy variables coded for the different plots, which are all categorical variables. Ordinary least squares (OLS) regression would have been a poor choice in this instance because the binary nature of the dependent variable would violate the OLS assumption of homoscedasticity in the error term and erroneous predictions would result at extreme x-values (Liao, 1994).

The third set of analyses generated an index to determine relationships between resource levels and occurrence of mature trees. The distance decay function used to this end was:

$$g_r = \sum (\mathrm{DBH}_k / \mathrm{distance}_{jk})$$

where g_r is an index indicating the potential influence of neighboring trees on resource data collection points, DBH_k is the DBH of the kth tree around resource data collection point j, and $\mathrm{distance}_{jk}$ is the distance between the jth data collection point and the kth mature tree. The associations between individual resource levels and the potential influence of mature trees (g_r) were examined for strength, direction, and significance with Pearson's correlation.

The fourth group of analyses compared relationships between resource levels and seedling occurrence. These relationships are difficult to address directly with statistical tests because, in addition to differences in units of observation (i.e., both individual seedlings and soil core locations have been used as sample points), measured variables differ between data collection points. Determining the potential influence of mature trees on local resource levels and the spatial associations between mature trees and seedling occurrence and survival permits qualitative interpretation about the influence of resource levels on the occurrence of seedlings.

RESULTS

Spatial Patterns of Seedlings and Mature Stems

The univariate Ripley statistic revealed that seedlings exhibited clumped dispersions at all distances in seven of the nine sampled plots ($p < 0.01$). L(t) continued to increase with increasing interplant distance in most plots indicating that clustering occurred at interplant distances of 1.3 to 5.3 m. The small plot size used to sample seedlings precluded assessment of spatial pattern of seedlings at broader spatial scales. A random dispersion was observed at all distances in the remaining two plots. These two plots (4–1 and 4–2) had the smallest number of seedlings of all sampled plots ($n = 7$ and $n = 14$, respectively) and should be interpreted cautiously (Table 1).

Mature trees, in contrast to seedlings, had random dispersion at most interplant distances up to 32 m in most plots. Some significant hyperdispersion was observed, though none at

Table 1. Sample sizes for plots used in each of the Ripley analyses.

Plot	Univariate Analysis (Number of Seedlings)	Univariate Analysis (Number of Trees)	Bivariate Analysis (Number of Trees*)
1–1	308	111	9
1–2	248	127	5
1–3	255	63	5
3–1	84	53	N/A
3–2	23	44	5
3–3	87	53	5
4–1	7	46	5
4–2	14	45	2
4–3	58	52	5

* The number of seedlings for each plot was the same as for the bivariate analysis.

interplant distances greater than approximately 6 m; this may be a critical distance at which competition between individuals substantially decreases. A noteworthy exception to the general pattern was plot 1–1, which revealed an aggregated dispersion at all distances examined, although no obvious structural, age-class, or edaphic feature account for its unique pattern.

Spatial Associations Between Mature Trees and Seedlings

Seedlings were randomly associated with mature trees at most interplant distances in most plots (Fig. 1). Lack of a significant association between mature trees and seedlings implied that no relationship, competitive or facilitative, existed. Note, however, that the number of observations used in this analysis is small; consequently, spatial associations might exist without detection because of the low power of the test. Nonetheless, a random association between mature trees and seedlings was evident from the stem map of plot 4–1 (Fig. 1), which shows seedlings clustering around some adults, but not others. Plot 4–1 had the lowest number of observations of all plots, and thus the lowest testing power to distinguish existing patterns.

Relationship of Seedling Survival to the Occurrence of Mature Trees

The logistic regression model used to predict the probability of seedling survival after the winter fire in 2002 was statistically significant ($p < 0.01$) (Table 2). Potential influence of mature trees was significantly negative in relation to seedling survival ($p < 0.01$) (Table 3). The exponential parameter estimate ($e^{(B)}$) indicated that each unit increase in potential influence of mature trees (g_s) decreased the odds of seedling survival by a factor of 0.968 (a 3.2% decrease). Therefore, seedling mortality rates after a winter fire were greater for seedlings occurring in proximity to large trees or a large number of trees, either of which could cause a large g_s value (Fig. 2). A log likelihood test indicated that the model fit the data better when dummy variables representing specific plots were included. The negative relationship between the potential influence of mature trees and the probability of seedling survival was apparent on the plot of predicted values.

Relationships Between the Potential Influence of Mature Trees and Underground or Surface Resources

All resource variables, with the exception of needle litter mass (Fig. 3), were negatively correlated with the potential influence of mature trees (g_r) at all depths both in January and

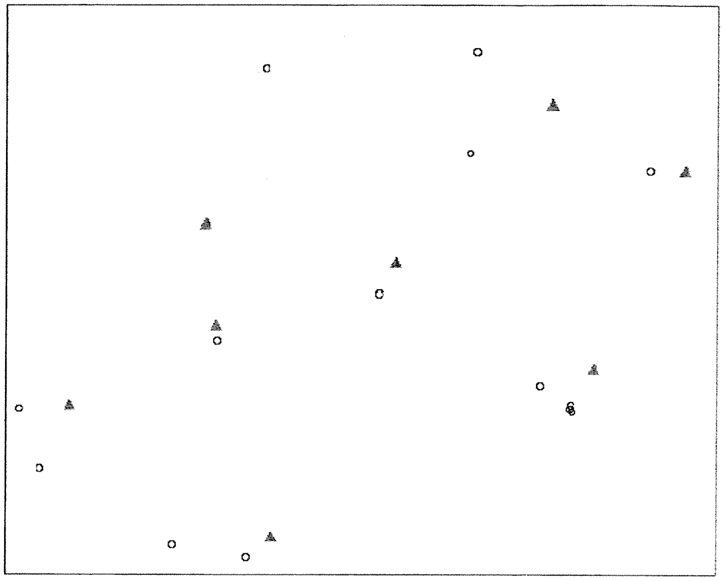

FIG. 1. Plot 4–1, stem map showing a random association between live seedlings and mature trees. Triangles represent mature trees while circles represent seedlings.

in July (Table 4). Nitrogen, carbon, and organic matter content values were all lower at sample points occurring in close proximity to large longleaf pine trees than at more open points. Furthermore, all of these associations were significant, with the exception of organic matter content in the shallowest soil layer in January. The significance of the association varied by season, most likely because the vegetation was actively utilizing soil resources during the growing season (July).

Relationships Between the Potential Influences of Mature Trees and Root Mass by Type

The direction of association between potential influence of mature trees and the biomass of the various root types was inconsistent both by season and by depth. The only significant association was between potential tree influence and herbaceous root biomass in the deepest sampled layer in January (Table 5).

Table 2. Descriptive statistics for the logistic regression of seedling survival onto potential influence of mature trees and plot. The logistic regression model used to predict the probability of seedling survival after the winter burn in 2002, was statistically significant ($p < 0.01$).

		Predicted				
Observed	N	Mortality	Survival	%Correct	X^2	Df
Mortality (coded 0)	1002	987	15	98.5	—	—
Survival (coded 1)	782	365	417	53.3	—	—
Overall				78.7	751.272	9

Table 3. Results from regressing the dependent variable, seedling survival, onto the independent variables, potential influence of mature trees (g_s) and the plot in which seedlings occur (eight dummy variables representing the nine study plots with plot 1–3 as the reference category) (significant at $p < 0.01$). B is the parameter estimate, and $e^{(B)}$ is the exponential parameter estimate.

Dependent Variable	B	Sig.	$e^{(B)}$
g_s	−0.032	0.000	0.968
Plot 1–1	1.314	0.000	3.723
Plot 1–2	0.287	0.172	1.332
Plot 3–1	4.284	0.000	72.545
Plot 3–2	8.565	0.648	5246.059
Plot 3–3	9.316	0.268	11111.258
Plot 4–1	10.363	0.687	31653.325
Plot 4–2	2.411	0.022	11.143
Plot 4–3	4.134	0.000	62.441
Constant	4.189	0.000	65.989

DISCUSSION

Spatial Patterns of Seedlings and Mature Stems

Seedlings were characterized by an aggregated spatial dispersion in most of the longleaf pine plots examined. This type of clumped seedling dispersion conformed to previous findings that have discussed longleaf pine seedling establishment within a patch dynamic framework (Platt et al., 1988). Thus, when a canopy opening is formed, the forest floor beneath the newly opened space is colonized by juveniles responding to decreased competition for light and other nutrients from individuals in the overstory. However this failed to completely account for seedling dispersion because of the open nature of the longleaf pine ecosystem. The magnitude of resource variation (e.g., light availability) in longleaf pine stands is less pronounced with events such as treefall than in closed-canopy

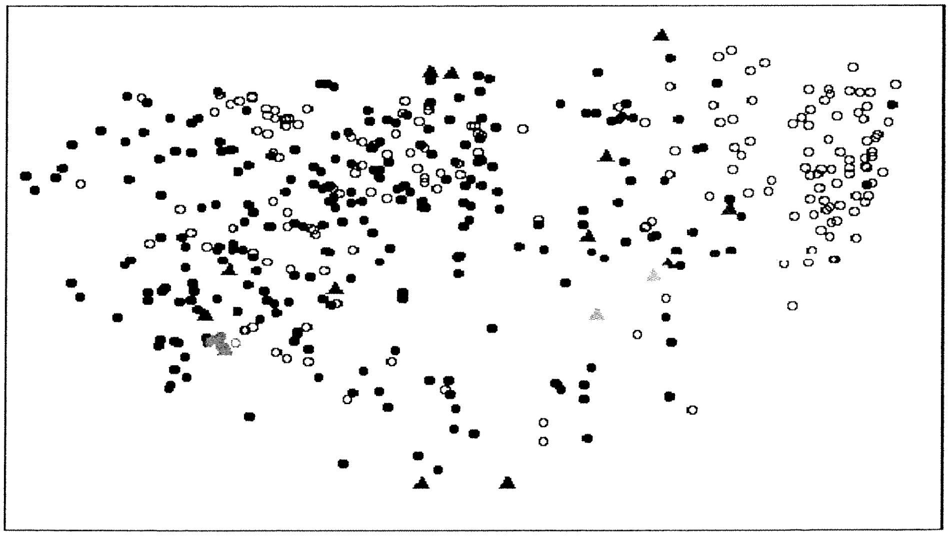

FIG. 2. Plot 1–1 stem map. Triangles represent mature trees, open circles represent surviving seedlings, and closed circles represent dead seedlings.

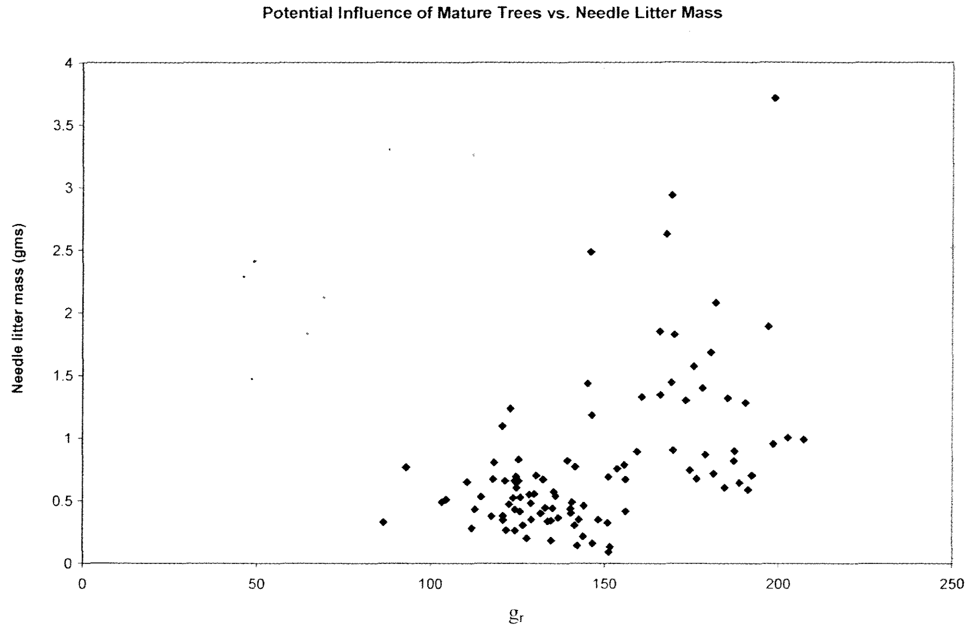

FIG. 3. Bivariate scatter plot for the potential influence of mature trees (g_r) and the average needle litter mass collected from litter traps in all plots.

forests (McGuire et al., 2001) for which the patch dynamic model was developed (Watt, 1947). Others have interpreted dense clumps of seedlings combined with a randomly dispersed tree layer as the result of limited seed dispersal, followed by competitive thinning as most seedlings in a clump fail to survive to adulthood [Parker et al. (2001) for sand pine, Berg and Hamrick (1995) for turkey oak]. Competitive thinning as trees age likely accounts for the change from aggregated distribution among seedlings to a predominantly random distribution among adults observed in our study, provided that the current seedlings are also representative of the adults when they were in the seedling stage. Limited dispersal of seeds away from the maternal plant can also contribute to an aggregated dispersion (Hamrick and Nason, 1996; Parker et al., 2001).

Table 4. Pearson's correlation coefficients for each measured resource variable by depth and the potential influence of mature trees (g_r). Needle litter mass is the mean value of multiple litterfall collections.

Resource Variable (depth in cm)	January r	July r
Needle litter mass	0.505*	
Organic matter content (0–10)	−0.148	−0.302*
Organic matter content (10–20)	−0.382*	−0.343*
Nitrogen content (0–10)	−0.297*	0.000
Nitrogen content (10–20)	−0.360*	0.000
Nitrogen content (20–30)	−0.586*	N/A
Carbon content (0–10)	−0.312*	−0.314*
Carbon content (10–20)	−0.369*	−0.179
Carbon content (20–30)	−0.444*	N/A

* Significant at $p < 0.01$.

Table 5. Pearson's correlation coefficients for each root type by depth and the potential influence of mature trees (g_r).

Root Type (depth)	January r	July r
Non-woody root mass (0–10 cm)	−0.080	0.164
Non-woody root mass (10–20 cm)	0.112	0.109
Non-woody root mass (20–30 cm)	−0.263*	N/A
Woody, non-longleaf root mass (0–10 cm)	0.010	0.095
Woody, non-longleaf root mass (10–20 cm)	0.037	0.165
Woody, non-longleaf root mass (20–30 cm)	−0.048	N/A
Longleaf root mass (0–10 cm)	0.047	0.000
Longleaf root mass (10–20 cm)	−0.026	−0.089
Longleaf root mass (20–30 cm)	−0.212	N/A

* Significant at $p < 0.01$.

Spatial Association Between Mature Trees and Seedling Occurrence/Survival

Seedlings and mature trees were not significantly associated with each other in most of the plots examined in this study. Both competitive and facilitative relationships have been suggested as the potential nature of the relationship between mature trees and seedlings. A facilitative relationship could result from mature trees acting as "nutrient pumps," thus making resources more readily available to the shallow–rooted seedlings (Reich, 2001). Conversely, a competitive relationship could result from mature trees utilizing resources that are available in those shallow layers on which seedlings depend for resource availability (Brockway and Outcalt, 1998). The fact that neither type of spatial association was observed in this study may be the result of several factors. Site management and environmental characteristics may differ between this study and those where competitive or facilitative relationships have been previously observed. A negative spatial relationship between mature trees and seedlings may develop as evidenced by the decreased probability of seedling survival with increased potential influence of mature trees.

No significant relationship was detected between the occurrence of mature trees and longleaf root biomass, in addition to no association between mature trees and seedling occurrence. These findings complement one another because a significant association between mature tree influence and root biomass could potentially lead to a dearth of seedlings within the zone where tree root biomass is prominent, with trees utilizing vital nutrient and moisture resources required by seedlings in shallow soil layers. Such a zone was described by Brockway and Outcalt (1998), who found that the fine root biomass of mature trees surrounding large openings in the canopy was the most significant determinant of seedling proximity to parent trees. Many of these inconsistencies in research findings could be explained by differences in the age of seedlings sampled, as well as differences in research design. Our study has focused exclusively on seedling "establishment" defined as newly germinated seedlings. Brockway and Outcalt (1998) included seedling growth over a period of time into their analysis. Likewise, failure to sort roots by type (i.e., woody vs. herbaceous) by Brockway and Outcalt (1998) most likely inflated the estimate of fine root biomass of parent trees in that study.

Relationships Between the Potential Influence of Mature Trees, Underground or Surface Resources, and Root Biomass

The negative correlation between mature tree influence and resource availability is consistent with previous research reporting that those resources, specifically nitrogen, were related to patterns of seedling establishment (Palik et al., 1997). Negative relationships suggested that soil resources may be utilized by mature trees to the detriment of competing vegetation. The potential for mature trees to negatively influence seedling establishment and growth through competition for soil nutrients has also been concluded in previous studies (Palik et al., 1997; Brockway and Outcalt, 1998). The lack of a significant association between mature tree influence and woody root biomass in this study, however, suggested that non-woody, understory vegetation, which was negatively associated with trees, may have more influence on resource availability than nearby mature trees at the 0–20 cm soil depths.

An important effect of mature trees on seedlings may be the potential for increased litter accumulation in the proximity of trees (Fig. 3), which can adversely affect seedling survival by increasing fire intensity (Grace and Platt, 1995a). Support for this includes the lack of a significant spatial association between mature trees and seedlings prior to fire, the decreased probability of seedling survival with increasing potential mature tree influence, the significant positive relationship between mature trees and needle litter mass (Fig. 3), clustering of dead seedlings around mature trees following fire, and the lack of a significant association between mature trees and root biomass (Table 5). Thus, seedlings with a high g_s value may be at greater risk of mortality in the event of fire than seedlings with a lower value, which could eventually create a negative spatial association between mature tree influence and the occurrence of seedlings. These, and other, edaphic factors may influence root habits, nutrient and moisture characteristics, and a host of other variables important to seedling establishment.

CONCLUSION

Site specific variables produce different patterns of seedling establishment, which will have implications for land managers who seek to maximize seedling establishment. Differences in management objectives or regimes can also produce a substantial difference in forest patterns and processes.

The various sites on which our studies have been conducted have differed markedly in management objectives. For example, when the goal has been to reduce fuel and hardwood competition, early winter burns have been utilized because they will have a less profound impact on longleaf pine seedlings during the growing season (Wade and Johansen, 1986). Conversely, if the objective is to create suitable habitat for quail, as is the case in many areas of the Jones Ecological Research Center (Palik et al., 1997) and the Wade Tact (Grace and Platt, 1995a) in Georgia, winter burns may be too early for quail habitat because they may over–expose the birds to predators. These research sites have different management regimes, including fire season, which can produce significantly different forest patterns and processes. Consequently, land managers should carefully choose the management regime that best meets their objectives and is appropriate to the area in which they are working. Putting a management regime into place in one area based on patterns observed in another area, where site conditions and management differ, may be inappropriate and detrimental to the land manager's objectives.

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