SPATIAL PATTERNS OF LONGLEAF PINE SEEDLING ESTABLISHMENT ON THE NORTH CAROLINA COASTAL PLAIN

by

CHADWICK R. AVERY

(Under the Direction of KATHLEEN C. PARKER)

ABSTRACT

Spatial relationships between longleaf pine seedlings and mature trees were examined in second-growth stands in coastal North Carolina. 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? 3) Does a relationship exist between the occurrence of mature trees and underground or surface resources (i.e. nitrogen content, carbon content, and litter biomass) or root mass? 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 next to trees, which can adversely affect seedling survival by increasing fire intensity.

INDEX WORDS: longleaf pine, regeneration, Ripley statistic

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CHADWICK R. AVERY

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CHADWICK R. AVERY

Major Professor:	Kathleen C. Parker
Committee:	Albert J. Parker Steven R. Holloway

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
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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 has been the result of logging, agriculture, site conversion, the introduction of more vigorous pine species (e.g. loblolly pine), 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 seedling establishment and mature trees, particularly 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 seedlings and the occurrence of mature trees. Grace and Platt (1995a) found that mature trees were negatively associated with seedling location as early as the first year of growth. Palik et al. (1997) described a negative relationship between the basal area of mature trees and seedling growth, due to increased available light and nitrogen levels with decreasing basal area. Similarly, McGuire et al. (2001) reported an increase in survival and growth of seedlings corresponding to increased levels of available light. Brockway and Outcalt (1998) described a "seedling exclusionary zone," along the edges of canopy gaps, wherein seedlings were absent. They attributed this pattern to intraspecific competition between seedlings and the fine root biomass of mature trees. Grace and Platt (1995b) also attributed the negative association between seedlings and adult trees to increased needle litter depth around mature trees, which increases adverse effects of fire on young seedlings. Although Grace and Platt (1995a) hypothesized that increased litter accumulation and shading associated with mature trees could increase lethal pathogens and adversely affect juvenile establishment in the first year of growth in the absence of fire, their data do not fully support this presupposition (e.g. "densities of juveniles remained higher in areas of high than low adult tree density and survival was higher in areas of high versus low adult tree densities" (p. 80)). Additionally, seedling occurrence in close proximity to adult trees could not be assessed by either Palik et al. (1997) or McGuire et al. (2001) because measured seedlings were planted. Furthermore, personal observation has demonstrated that seedlings can occur in very close proximity to adult trees in the first years of growth, contrary to the conclusions of previous studies. These findings and observations suggest that more work is necessary to clarify the relationship between mature individuals and seedling establishment.

The purpose of this study is to examine spatial relationships between seedlings and mature trees in second-growth stands of longleaf pine on the North Carolina Coastal Plain. Specific questions to be addressed are: 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, does it vary with seedling survival? 3) Does a relationship exist between the occurrence of mature trees and underground or surface resources (i.e. nitrogen content, carbon content, and litter biomass) or root mass?

Finally, the spatial distribution of seedlings within the study plots is examined qualitatively within the context of these relationships. I hypothesize that no single variable is solely, or even primarily, responsible for the occurrence of seedlings. Furthermore, I hypothesize 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.

Methods

Study area

Study sites are located on the Croatan National Forest, Carteret County, North Carolina. These soils are generally more poorly drained and more nutrient poor than previous research sites, which have typically been 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). This soil is highly acidic and generally nutrient-poor. Annual precipitation in the region averages 111 mm, but extended droughts often occur during the growing season. Mean annual temperature is 17.3^{o}C, with the coldest temperatures in January (7.4^{o}C) and the warmest in July (26.4^{o}C) (Goodwin 1987).

The study sites have a longleaf flatwoods/savanna vegetation structure, with a mature uneven-aged overstory dominated by longleaf pine (scattered loblolly and pond pines are also present), no midstory, and a mix of low-growing woody and herbaceous vegetation in the understory. Average stand age ranges from 70 to 100 years. For the past two decades, these sites have been winter-burned every 2 to 4 years. All sites have been burned within the last three years. Site 1 plots were burned since the initial survey, in February 2002, thus offering a comparison of seedling survival in recently burned and less recently burned plots.

Sites for this study were chosen based on similar history, age, soil type, management regime, and presence of an intact understory. Additionally, in contrast to previous studies, sites were chosen irrespective of canopy openness so that samples would not be biased toward open areas.

Field methods

Three circular measurement plots were located on each of three sites, for a total of nine plots (Figure 1). Each plot was 30 m in diameter (0.07 ha) and did not overlap any other plot. All seedlings on one-half of each plot, chosen at random, were mapped by distance and azimuth from the center point of the plots in January 2001. Seedlings were resurveyed in May 2002 to assess mortality after the prescribed burn in February 2002. Additionally, all mature trees within 40 m of the plot centers were mapped by distance

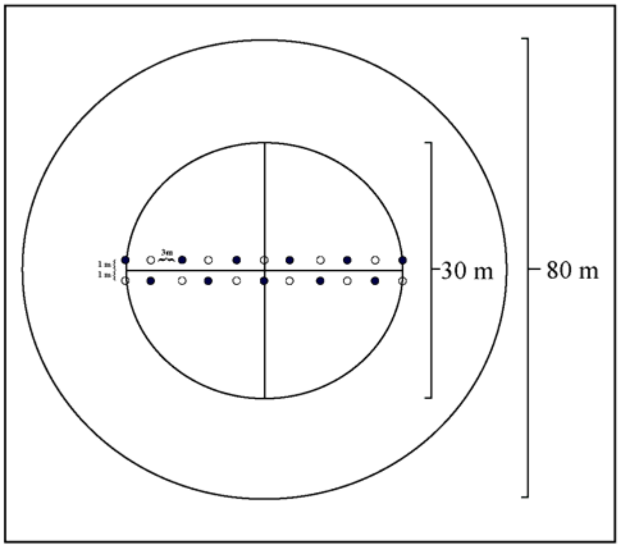

Figure 1. Schematic showing basic layout of a measurement plot (not to scale). Seedlings were mapped only on one half, chosen at random, of the inner circle, while mature trees were mapped within both the inner and outer circles. Open circles represent points at which soil cores were extracted in January and also the locations of litter traps. Closed circles represent points at which soil cores were extracted in July.

and azimuth from the center point of the plots. Diameter at breast height (DBH) and species were also recorded for each tree.

Two 30 m transects, intersecting at plot center, were established in each plot. Transect orientation was intended to be in cardinal directions (N-S and E-W). Due to a compass malfunction, however, the east-west transects in site 3, plots 2 and 3, and site 4 were actually laid out with an orientation of 107^{o} to 287^{o}.

Litter biomass was measured using litter traps placed along the east-west transect of each plot. Litter was collected from each trap, separated into needles and non-needles, dried, and weighed, monthly from February to May 2001.

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 two soil depths were collected in July: 0 to10 cm and 10 to 20 cm. Cores were analyzed at each depth for nitrogen, carbon, and organic matter content. Additionally, cores were analyzed at each depth to determine root type and content. Roots were sorted and categorized as longleaf; woody, non-longleaf; and non-woody.

Data analysis

Data analyses were divided into four main groups. The first was a spatial pattern analysis to determine whether seedlings and/or trees exist in a random, aggregated, or regular distribution. The hypothesis that a random (Poisson) distribution exists was tested with Ripley's univariate L(t)-statistic[1], capable of evaluating spatial dispersion at multiple scales (Ripley 1977). This capability is beneficial because observed spatial

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[1] $L_i(t) = [A \Sigma k_{ij}/\pi(n-1)]^{1/2}$ where Σk_{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).

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, developed by Ohser and Stoyan (1981), that allows for extrapolation outside of the actual study plot. 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 running 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 provides the same benefits of multiple-scale analysis and edge-correction described above for the univariate test (Getis and Franklin 1987). Both the univariate and the bivariate Ripley analyses were performed using a computer program written by S. Rathbun (University of Georgia) and E. Berg (Kenai National Wildlife Refuge, AK), and modified by P. Aldrich (University of Georgia).

In order to address the statistical significance of potential influence of mature trees on the survival of seedlings, a logistic regression was performed with seedling survival as the dependent variable and potential influence of mature trees as the independent variable. The potential influence of mature trees was estimated with an index of the form

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

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 killed 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. 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 homoskedasticity 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 of the form

$$g_r = \Sigma\ (DBH_k/distance_{jk}),$$

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 $distance_{jk}$ 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 the relationship between resource levels and the occurrence of seedlings. 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 showed that seedlings exhibited a clumped distribution at all distances in 7 of the 9 sampled plots ($P<0.01$)[2] (Figure 2). 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 relatively small plot size used to sample seedlings precluded assessment of spatial pattern of seedlings at broader spatial scales. In the remaining two plots, a random distribution was observed at all distances. It is worth noting that 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).

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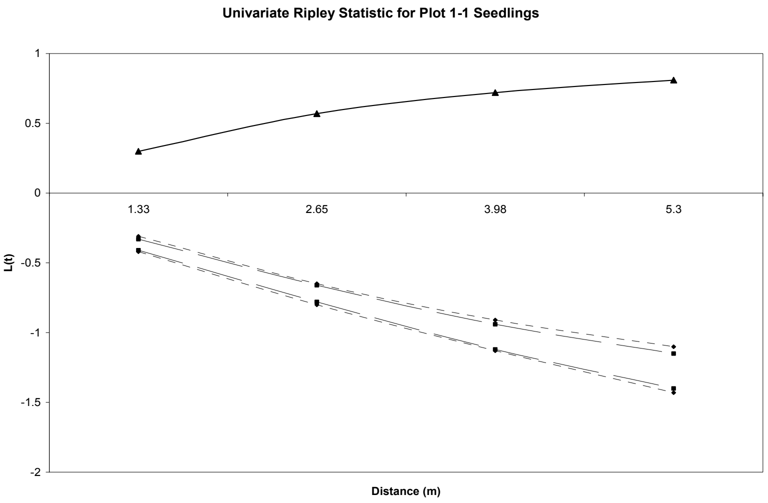
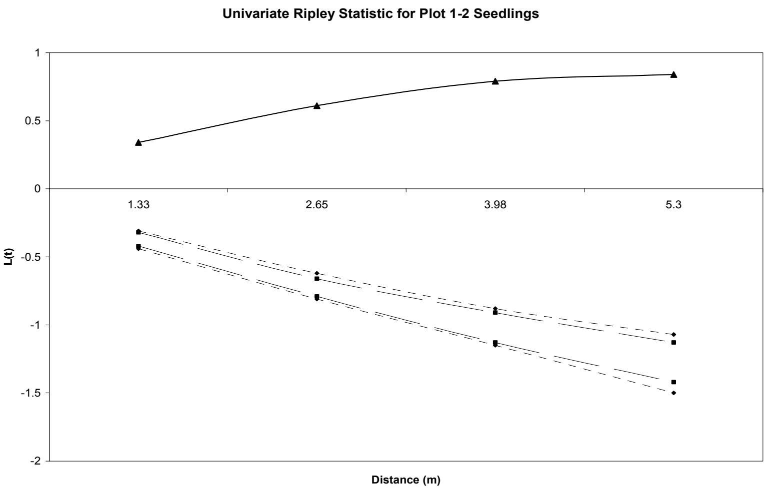
[2] Although the Ripley statistics show significant aggregation in most seedling plots, the upper and lower confidence intervals are negative in most cases. Others have reported this phenomenon in analyses of other species (Precht 1989).





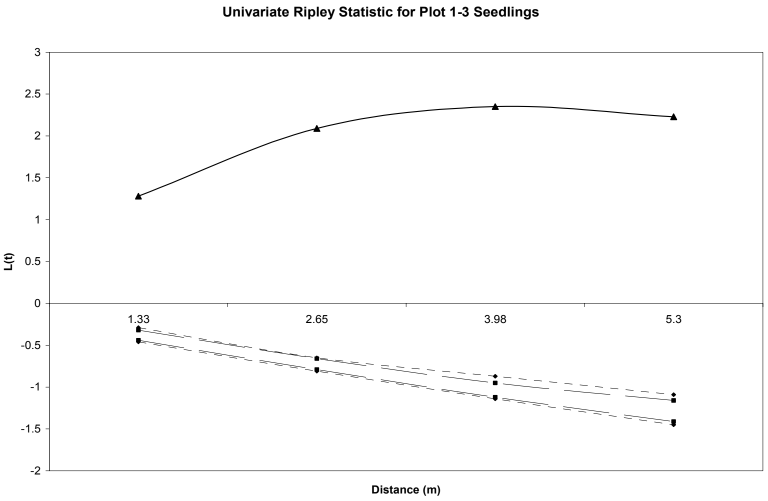


Figure 2. Observed L(t) values for univariate Ripley analysis of seedlings in all plots. The upper and lower 1% and 5% confidence intervals are indicated by the broken lines, while the calculated statistic is represented by a solid line. L(t) values of greater than zero indicate a clumped distribution while values of less than zero indicate a regular distribution.

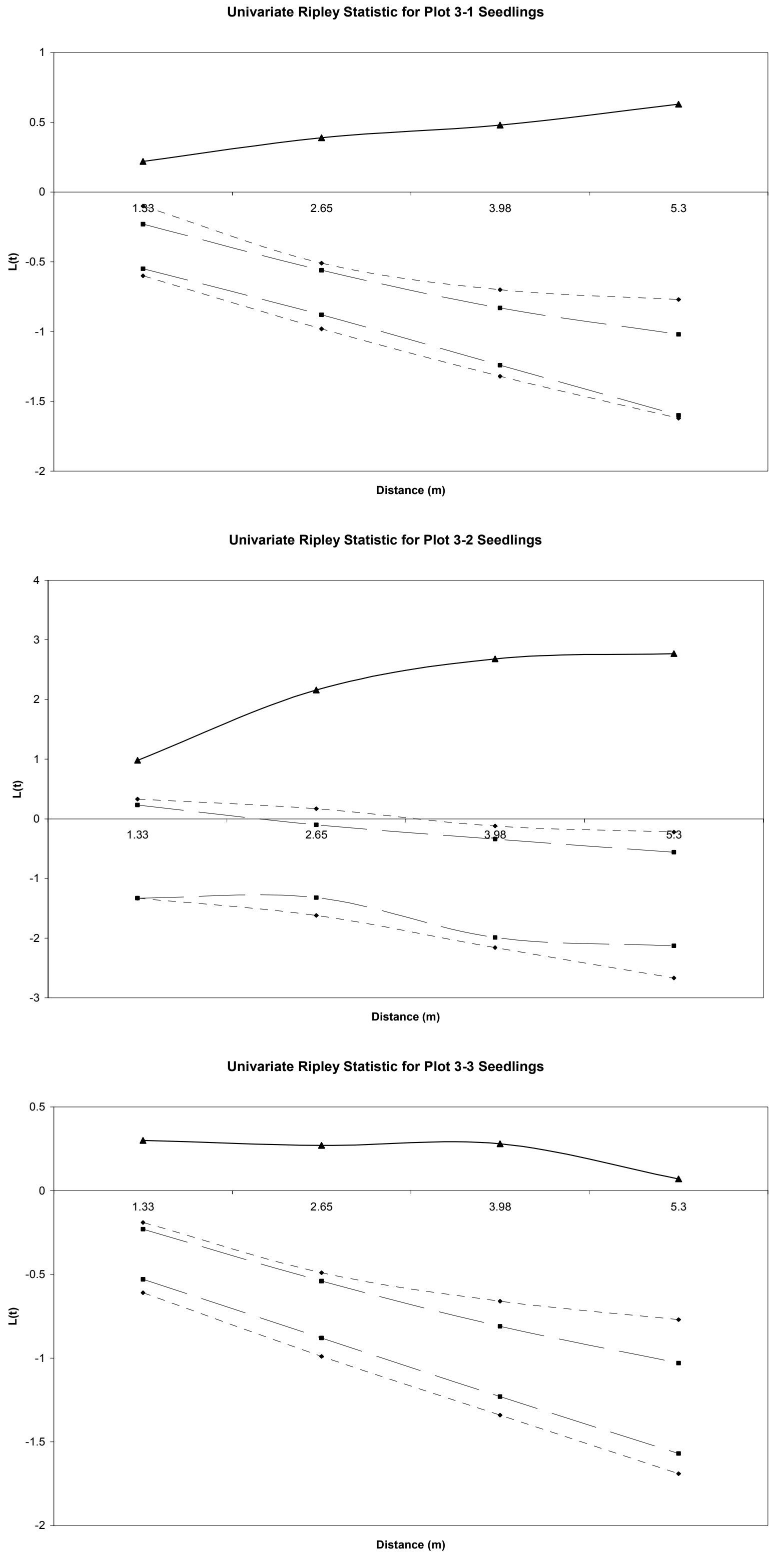
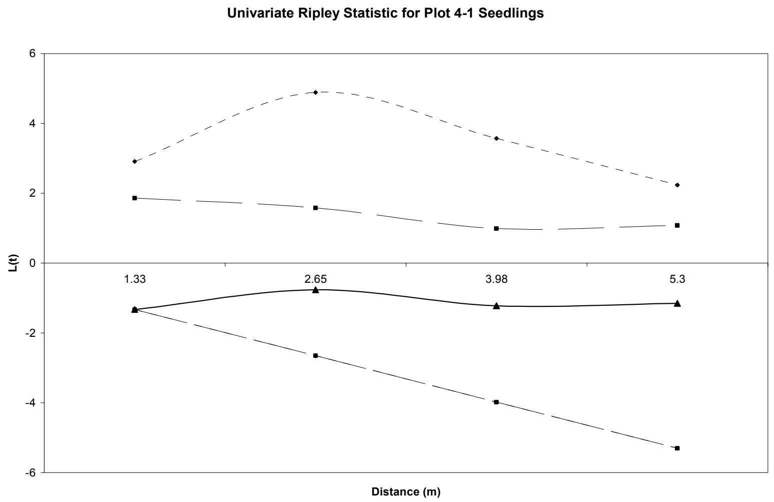
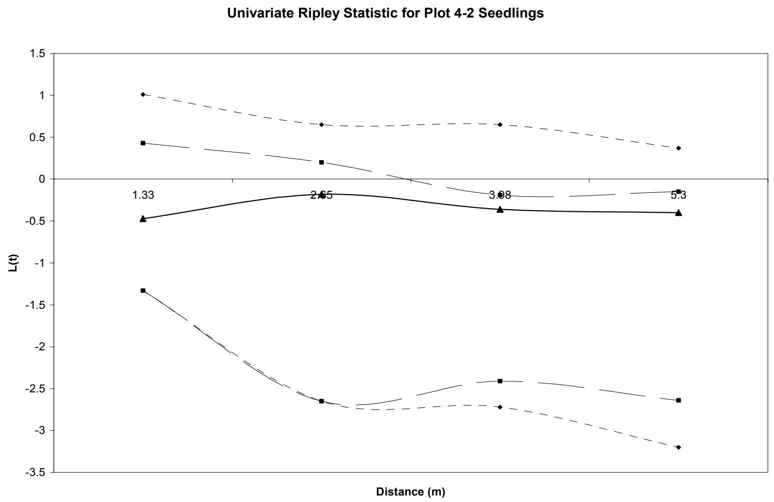


Figure 2 (*cont'd*). Observed L(t) values for univariate Ripley analysis of seedlings in all plots. The upper and lower 1% and 5% confidence intervals are indicated by the broken lines, while the calculated statistic is represented by a solid line. L(t) values of greater than zero indicate a clumped distribution while values of less than zero indicate a regular distribution.





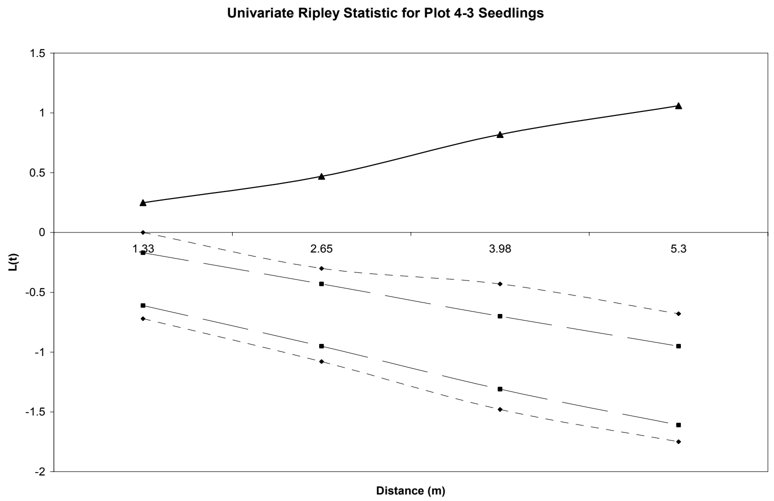


Figure 2 (cont'd). Observed L(t) values for univariate Ripley analysis of seedlings in all plots. The upper and lower 1% and 5% confidence intervals are indicated by the broken lines, while the calculated statistic is represented by a solid line. L(t) values of greater than zero indicate a clumped distribution while values of less than zero indicate a regular distribution.

Table 1. Sample sizes for plots used in each of the Ripley analyses.
*The number of seedlings for each plot was the same as for the bivariate analysis.

Plot	**Univariate analysis (Sdlg.)**	**Univariate analysis (tree)**	**Bivariate analysis (tree)***
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

In contrast to seedlings, mature trees had a random distribution at most interplant distances up to 32 m in most plots (Figure 3). Plots in sites 3 and 4 trended from negative values for the Ripley statistic at close distances to positive values at greater distances, although in most cases these trends were not significantly different from random. Competitive thinning as trees age likely accounts for the change from an aggregated distribution among seedlings to a predominantly random distribution among adults, provided that the current seedlings are also representative of the adults when they were in the seedling stage. A noteworthy exception to the general pattern was plot 1-1, which showed an aggregated distribution at all distances examined, although no obvious structural, age-class, or edaphic features of plot 1-1 account for its unique pattern. Some significant hyperdispersion was observed, though none at interplant distances greater than approximately 6 m; this may be a critical distance at which competition between individuals substantially decreases.

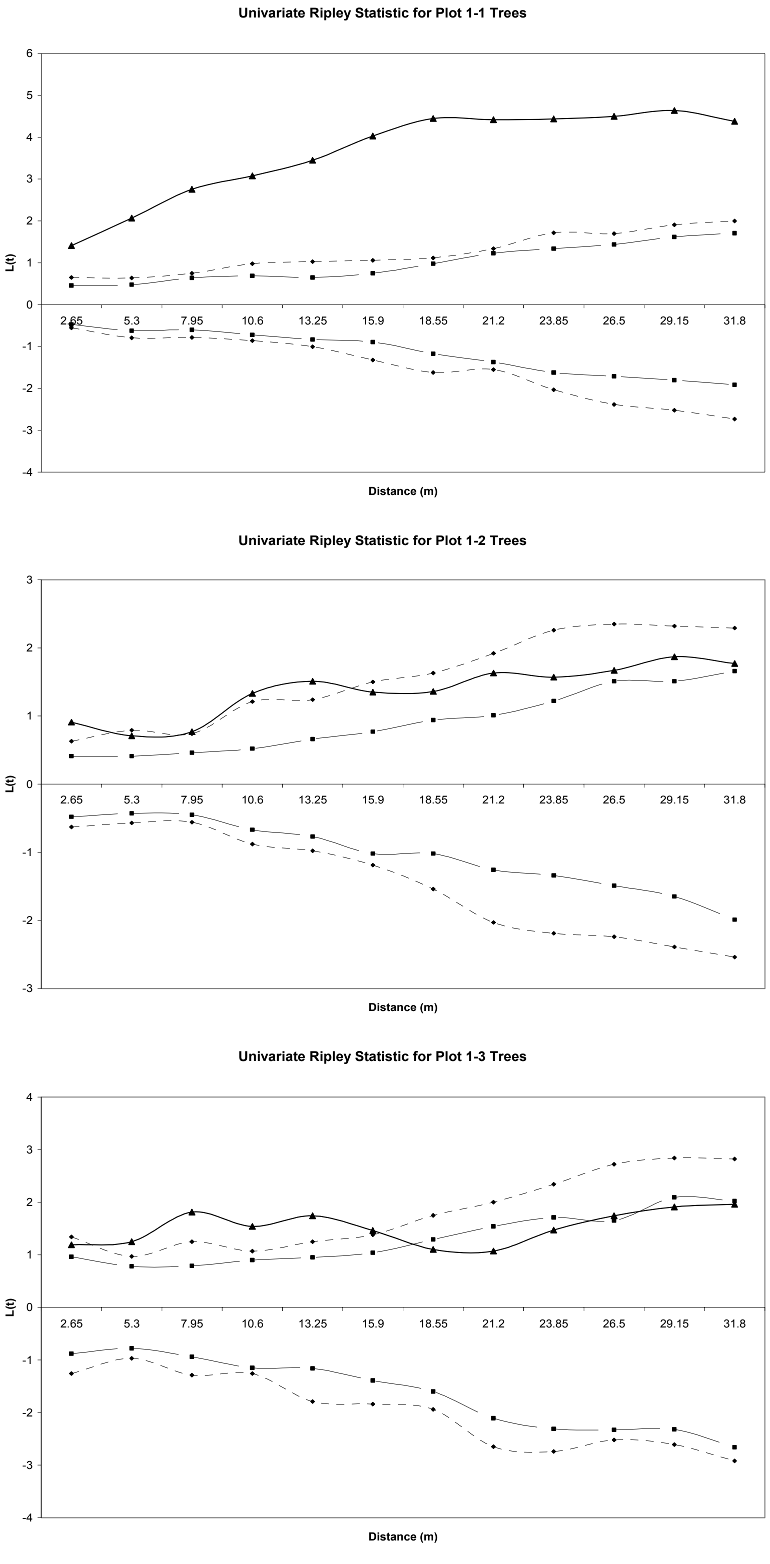
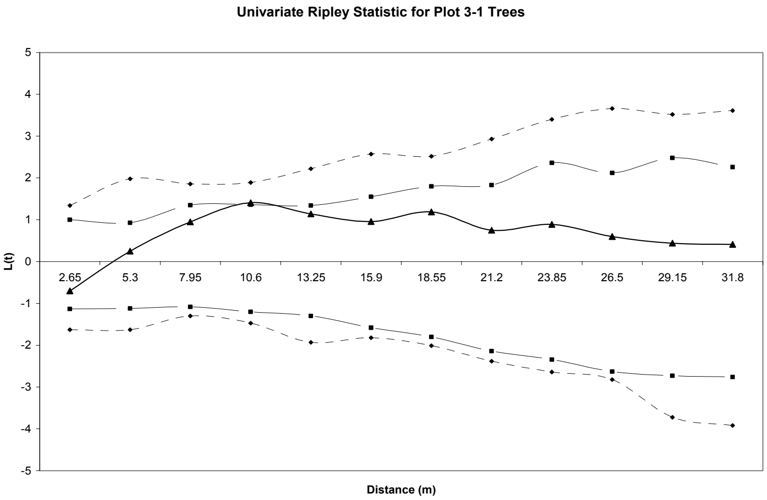
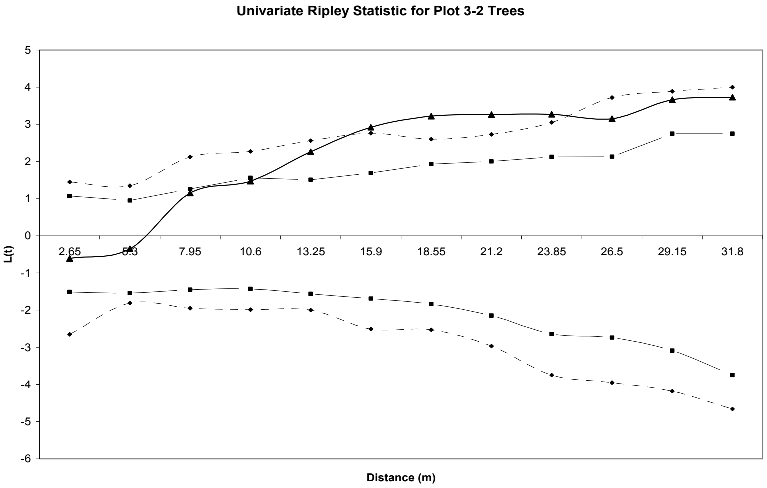


Figure 3. Observed L(t) values for univariate Ripley analysis of mature trees in all plots. The upper and lower 1% and 5% confidence intervals are indicated by the broken lines, while the calculated statistic is represented by a solid line. L(t) values of greater than zero indicate a clumped distribution while values of less than zero indicate a regular distribution.


Univariate Ripley Statistic for Plot 3-1 Trees


Univariate Ripley Statistic for Plot 3-2 Trees

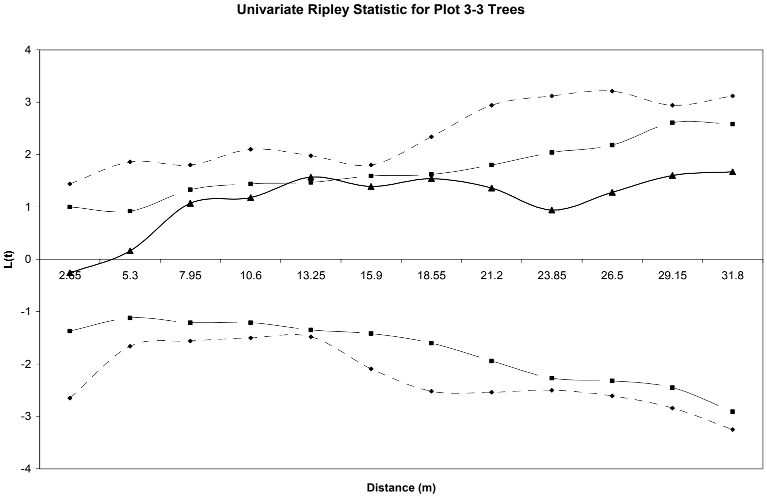
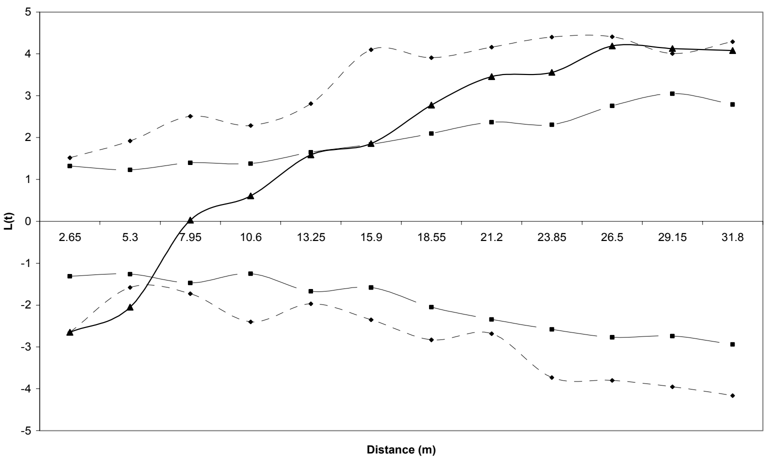
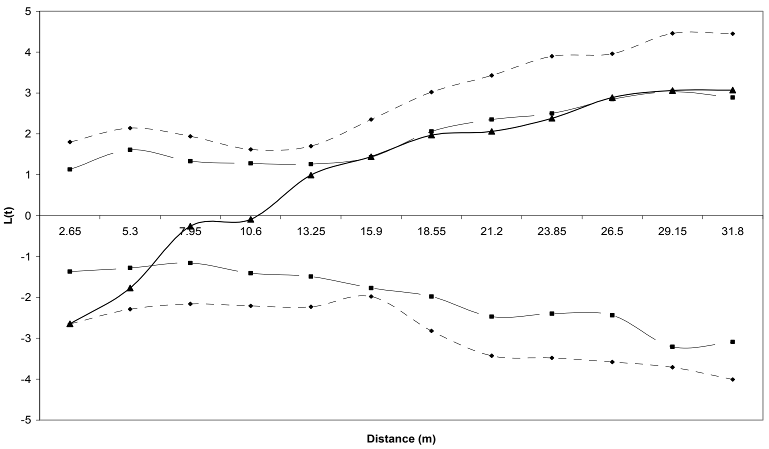

Univariate Ripley Statistic for Plot 3-3 Trees

Figure 3 (cont'd). Observed L(t) values for univariate Ripley analysis of mature trees in all plots. The upper and lower 1% and 5% confidence intervals are indicated by the broken lines, while the calculated statistic is represented by a solid line. L(t) values of greater than zero indicate a clumped distribution while values of less than zero indicate a regular distribution.


Univariate Ripley Statistic for Plot 4-1 Trees


Univariate Ripley Statistic for Plot 4-2 Trees

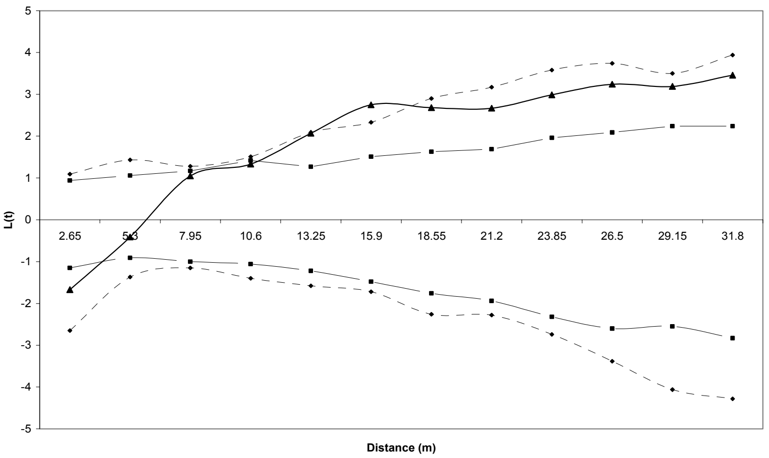

Univariate Ripley Statistic for Plot 4-3 Trees

Figure 3 (cont'd). Observed L(t) values for univariate Ripley analysis of mature trees in all plots. The upper and lower 1% and 5% confidence intervals are indicated by the broken lines, while the calculated statistic is represented by a solid line. L(t) values of greater than zero indicate a clumped distribution while values of less than zero indicate a regular distribution.

Spatial associations between mature trees and seedlings

At most interplant distances in most plots, seedlings were randomly associated with mature trees (Figure 4). This lack of a significant association between mature trees and seedlings implies that no relationship, competitive or facilitative, exists. It is important to note, however, that the number of observations used in this analysis is relatively 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 is somewhat evident from the stem map of plot 4-1 (Figure 5), 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.

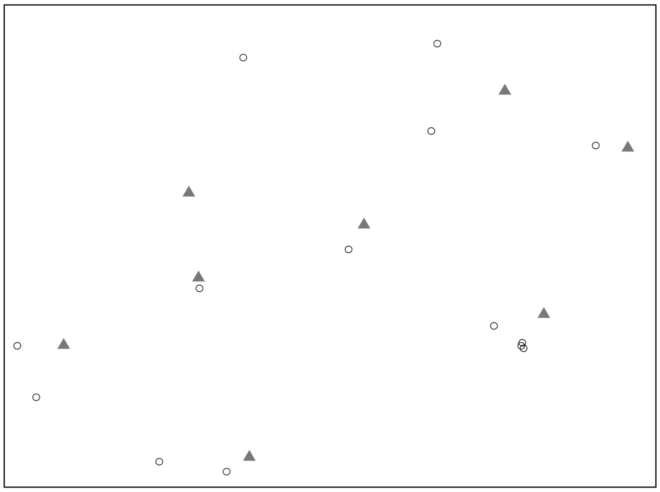


Figure 4. Map of plot 4-1, which provides evidence of the random distribution suggested by the bivariate Ripley analysis. Triangles represent mature trees while circles represent seedlings.

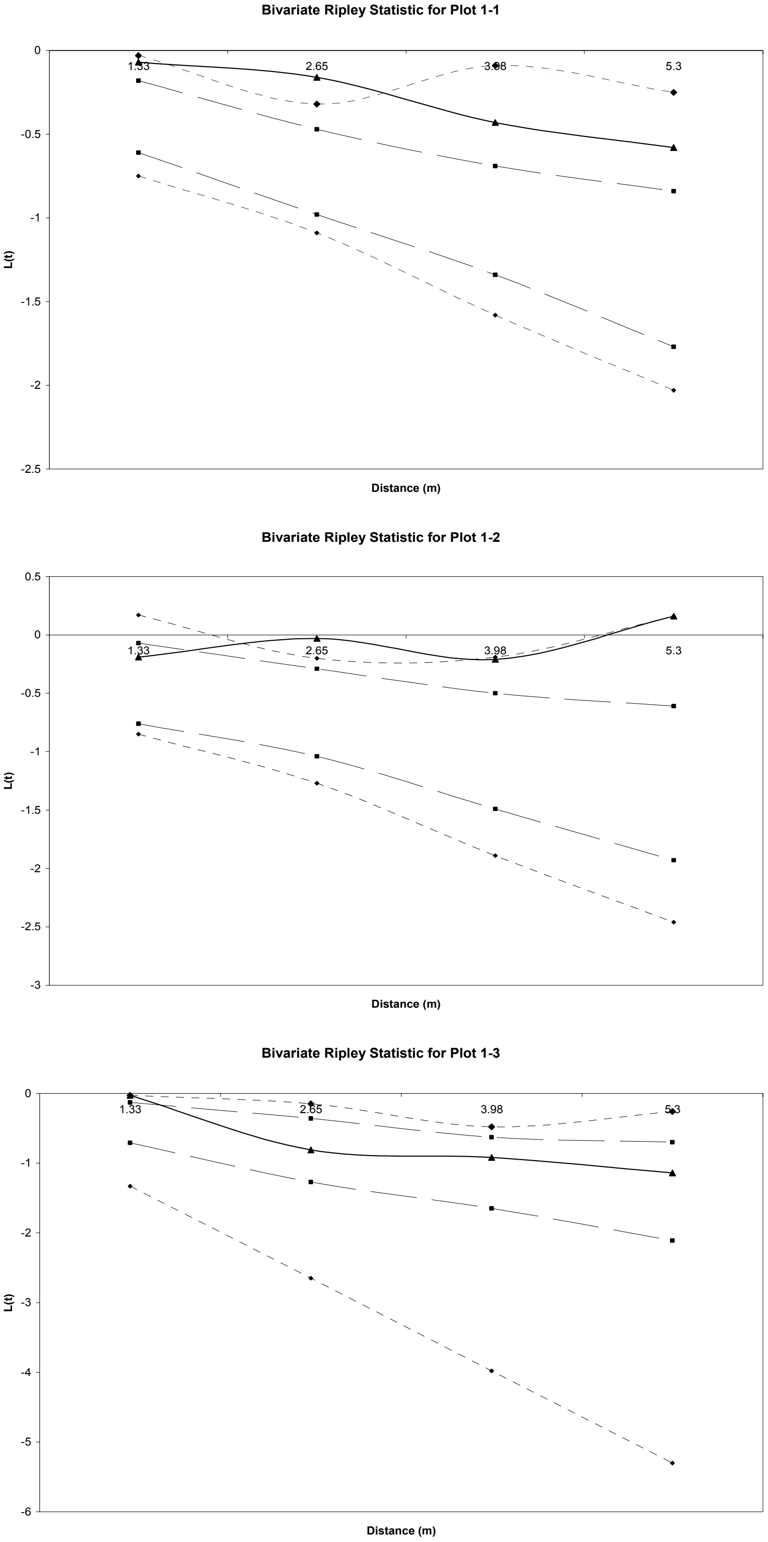
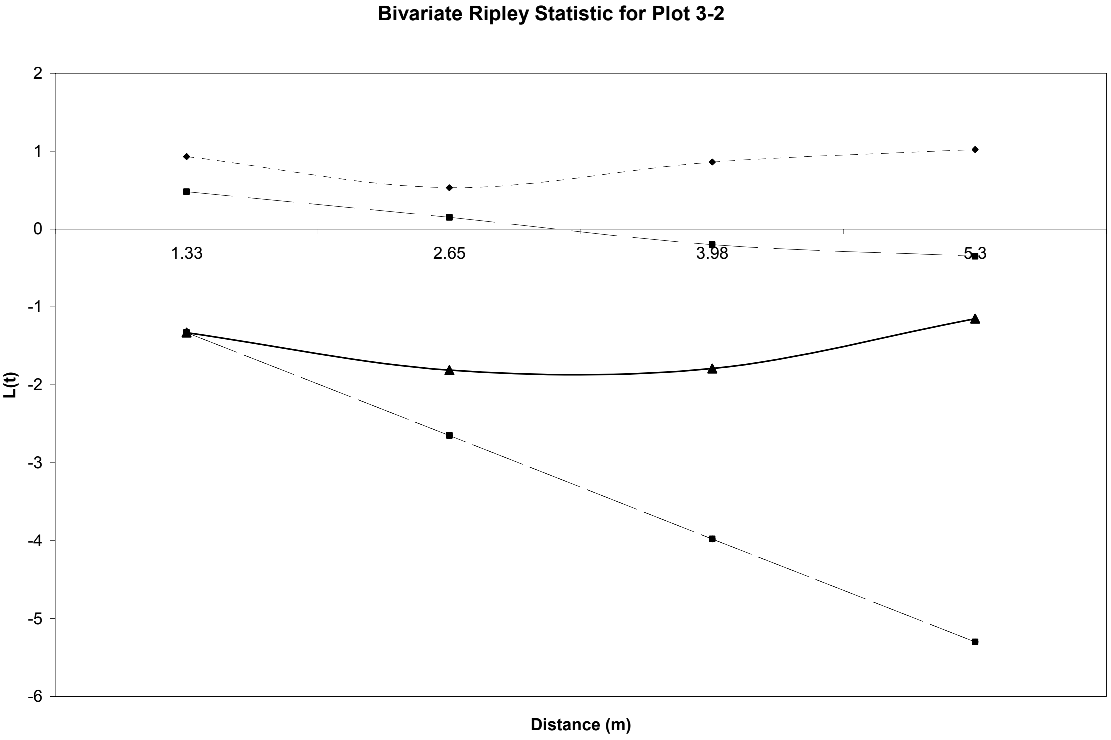


Figure 5. Observed L(t) values for bivariate Ripley analysis of seedlings and mature trees in all plots where both occurred. The upper and lower 1% and 5% confidence intervals are indicated by the broken lines, while the calculated statistic is represented by a solid line. L(t) values of greater than zero indicate a positive association between mature trees and seedlings while values of less than zero indicate a negative relationship.



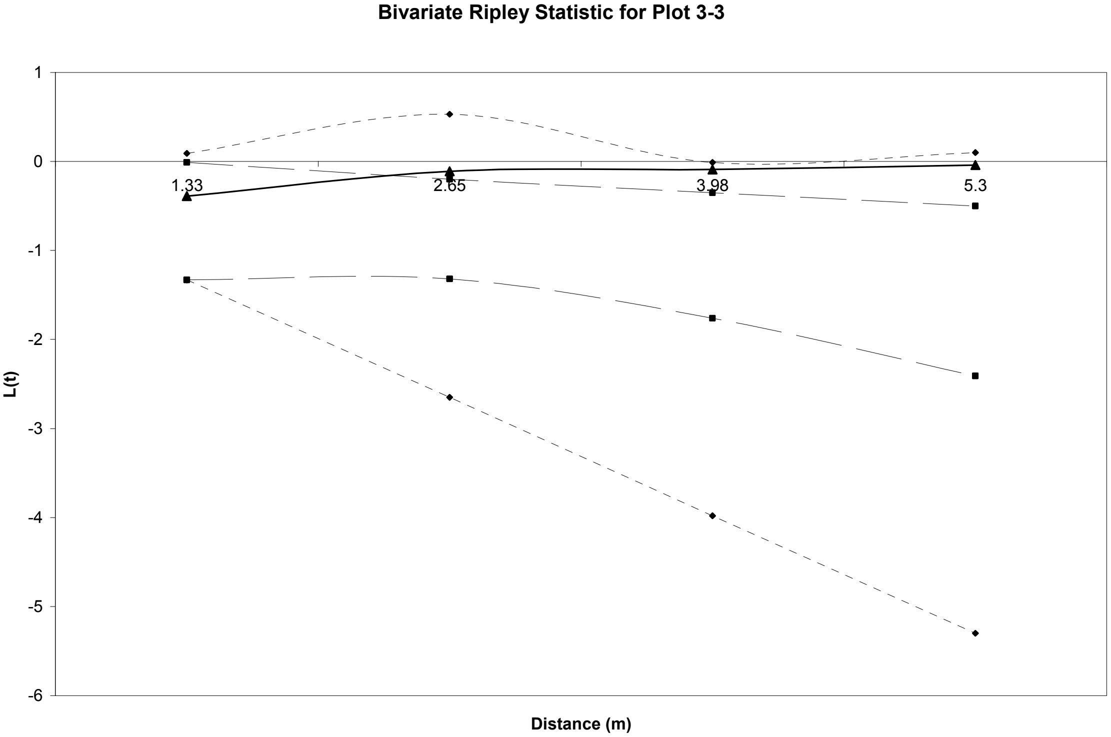
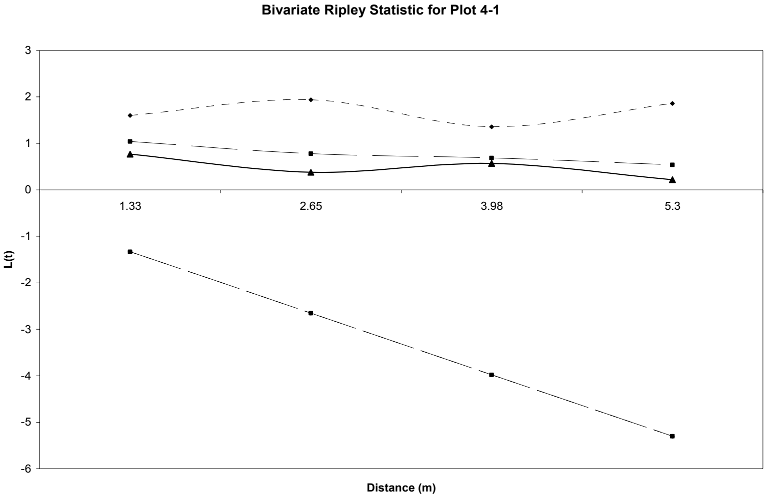
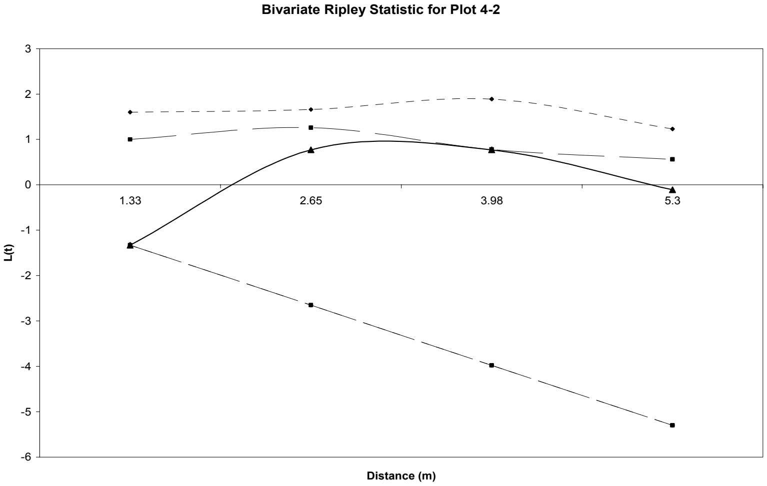


Figure 5 (cont'd). Observed L(t) values for bivariate Ripley analysis of seedlings and mature trees in all plots where both occurred. The upper and lower 1% and 5% confidence intervals are indicated by the broken lines, while the calculated statistic is represented by a solid line. L(t) values of greater than zero indicate a positive association between mature trees and seedlings while values of less than zero indicate a negative relationship.





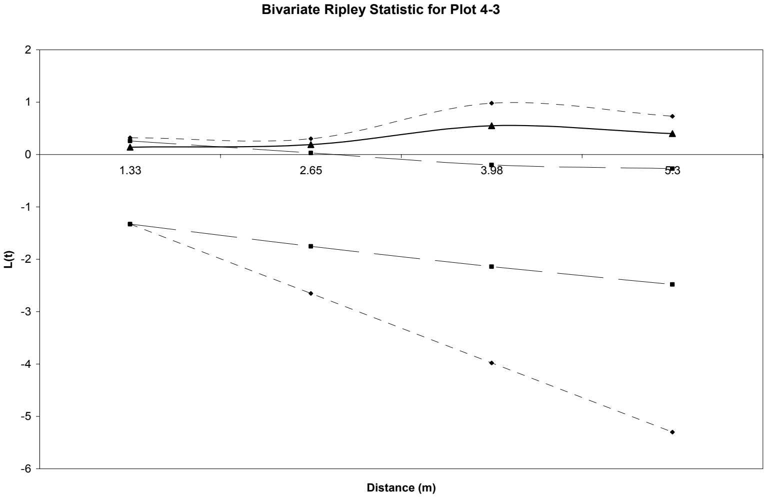


Figure 5 (cont'd). Observed L(t) values for bivariate Ripley analysis of seedlings and mature trees in all plots where both occurred. The upper and lower 1% and 5% confidence intervals are indicated by the broken lines, while the calculated statistic is represented by a solid line. L(t) values of greater than zero indicate a positive association between mature trees and seedlings while values of less than zero indicate a negative relationship.

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 burn in 2002 as a function of potential influence of mature trees (g_s) and the plot in which seedlings occurred was statistically significant ($P<0.01$) (Table 2). Potential influence of mature trees was significantly negatively related to seedling survival ($P<0.01$) (Table 3). The exponentiated parameter estimate ($e^{(B)}$) indicates that each unit increase in potential influence of mature trees (g_s) decreases the odds of seedling survival by a factor of 0.968 (a 3.2% decrease) (Figure 6). Therefore, seedling mortality rates after a winter burn were greater for seedlings occurring in proximity to relatively large trees or a relatively large number of trees, either of which could cause a large g_s value (Figure 7). A log likelihood test indicated that the model fit the data better when dummy variables representing specific plots were included. Dummy variables allow for the incorporation of qualitative variables into a regression model through binary coding where a 1 indicates membership in a group (i.e. plot) and a 0 indicates that the observation is not a member of that group (Hardy 1993). In this instance, the plot variable may help to refine the model because it serves 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 is arbitrary and no choice can be incorrect (Hardy 1993). When interpreting dummy variable coefficients and calculating predicted probabilities, however, they are interpreted individually and relative to the reference group. To obtain the average predicted probability of seedling survival for all plots, the predicted probabilities for each plot were first calculated individually and then averaged across all plots. The negative relationship between the potential influence of mature trees and the probability of seedling survival is apparent on the plot of predicted values (Figure 6).

Table 2. Descriptive statistics for the logistic regression of seedling survival onto potential influence of mature trees and plot.

		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 survivability, 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).

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

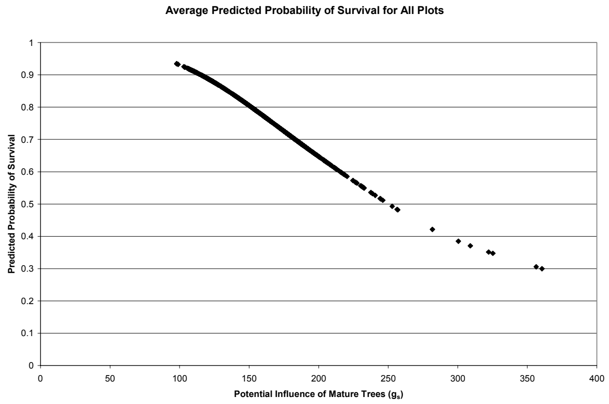


Figure 6. Average predicted probability curve for all plots. Predicted values were generated for the range of actual observations.

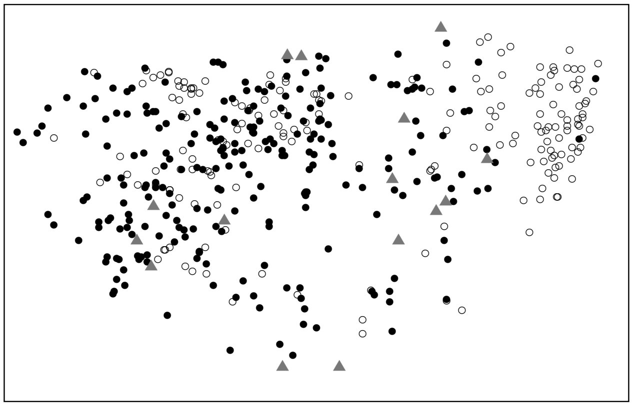


Figure 7. Plot 1-1 stem map. Triangles represent mature trees, open circles represent surviving seedlings, and closed circles represent dead seedlings. Clustering of killed seedlings around mature trees is apparent.

Relationships between the potential influence of mature trees and underground or surface resources

All resource variables, with the exception of needle litter mass (Figure 8), were negatively correlated with the potential influence of mature trees (g_r) at all depths both in January and 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 individuals 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). In January, when resource availability was more readily observed, a consistent trend was observed wherein resource content increased with depth, suggesting that resource competition may be occurring between understory plants in the shallowest depths of the soil where newly germinated seedlings obtain vital resources.

Table 4. Pearson's correlation coefficients for each measured resource variable by depth and the potential influence of mature trees (g_r).
* Significant at P<0.01

Resource Variable (depth)	January r	July r
Needle litter mass (collected from litter traps from 2-5/2002)	0.505*	
Organic matter content (0-10 cm)	-0.148	-0.302*
Organic matter content (10-20 cm)	-0.382*	-0.343*
Nitrogen content (0-10 cm)	-0.297*	0.000
Nitrogen content (10-20 cm)	-0.360*	0.000
Nitrogen content (20-30 cm)	-0.586*	N/A
Carbon content (0-10 cm)	-0.312*	-0.314*
Carbon content (10-20 cm)	-0.369*	-0.179
Carbon content (20-30 cm)	-0.444*	N/A

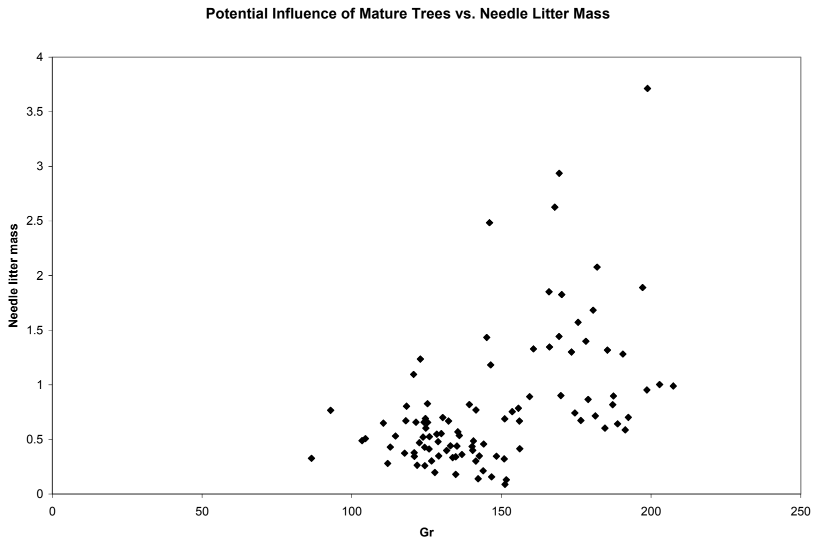


Figure 8. Bivariate scatter plot for the potential influence of mature trees (g_r) and the average needle litter mass collected from litter traps.

Relationships between the potential influence of mature trees and root mass by type

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

Table 5. Pearson's correlation coefficients for each root type by depth and the potential influence of mature trees (g_r).
* Significant at P<0.01

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

Discussion

Spatial Patterns of Seedlings and Mature Stems

In most of the longleaf pine plots examined, seedlings were characterized by an aggregated spatial distribution. A clumped seedling distribution conforms to previous findings that have discussed longleaf pine seedling establishment within a patch dynamic framework (Platt et al. 1988). Within this context, when an opening is formed in the overstory canopy, 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. In the open-canopied longleaf pine forest, however, the magnitude of resource variation (e.g. light availability) is less pronounced with events such as treefall than in the closed-canopy forests (McGuire et al. 2001) for which the patch dynamic model was developed (Watt 1947). Limited dispersal of seeds away from the maternal plant can also lead to an aggregated distribution (Hamrick and Nason 1996, Parker et al. 2001). Others have interpreted dense clumps of seedlings combined with a randomly distributed 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).

Spatial association between mature trees and seedling occurrence / survival

In most of the plots examined in this study, seedlings and mature trees were not significantly associated with each other either positively or negatively. 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). In contrast, 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 site and those where competitive or facilitative relationships have been previously observed. The potential in this study for a negative spatial relationship to become more pronounced between mature trees and seedlings in the future is significant, however, as evidenced by the decreased probability of seedling survival with increased potential influence of mature trees (Figure 6).

In addition to a lack of association between mature trees and seedling occurrence, no significant relationship was found to exist between the occurrence of mature trees and their corresponding root mass in subsurface depths where seedling interactions with vegetative competition are most important. These findings complement one another because a significant association between mature tree influence and corresponding root mass could potentially lead to a dearth of seedlings within the zone where tree root mass 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. These inconsistencies in research findings can likely be explained, at least in part, by differences in the age of seedlings sampled as well as differences in research design. Failure to sort roots by type (i.e. woody vs. non-woody) by Brockway and Outcalt (1998) could have inflated the estimate of fine root biomass of parent trees in that study. Furthermore, the current study has focused exclusively on seedling "establishment" as the sprouting of a seedling from below the soil surface where a seed has germinated. Brockway and Outcalt (1998) and others, however, have also taken seedling growth, monitored over a period of time, into their analysis. In the present study, seedlings may be killed in time as a result of competition for either above or belowground resources with nearby mature trees, thereby producing a clustering of seedlings within large openings in the overstory canopy, as has been reported in previous studies. This may account for some of the inconsistencies between the current study and previously published ones.

Relationships between the potential influence of mature trees, underground or surface resources, and root mass

The negative correlation between mature tree influence and resource availability is consistent with previous research reporting that these resources, specifically nitrogen content, were related to patterns of seedling establishment (Palik et al. 1997). Negative relationships suggest 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 mass in this study, however, suggests that non-woody, understory vegetation may have more influence on resource availability than nearby mature trees at these soil depths.

The most significant influence of mature trees on seedlings may be the potential for increased litter accumulation in the proximity of trees (Figure 8), which can adversely affect seedling survival by increasing fire intensity (Grace and Platt 1995a). Evidence includes the lack of a significant spatial association between potential influence of mature trees and seedlings in the pre-burn survey (Figure 4), the decreased probability of seedling survival with increasing potential mature tree influence (Figure 6), the significantly positive relationship between the potential influence of mature trees and needle litter mass (Figure 8), clustering of fire-killed seedlings around mature trees in the post-burn survey (Figure 7), and the lack of a significant association between potential influence of mature trees and root mass (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.

Conclusion

The primary reason for initiating this study was to compare the spatial patterns of longleaf pine seedling establishment with those described by previous authors. All of the studies heretofore have been conducted in the well-drained soils of either north Florida (Brockway and Outcalt 1998) or south Georgia (Grace and Platt 1995a, Palik et al. 1997, McGuire et al. 2001). The more nutrient-poor and poorly drained soils of the North Carolina Coastal Plain, which was also a part of longleaf pine's pre-settlement range, provide an interesting comparison to previous studies. These, and other, edaphic factors may influence root habits, nutrient and moisture characteristics, and a host of other variables important to seedling establishment. The fact that these findings differ somewhat from those of previous work indicates that site specific variables may, in fact, 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 these 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). On the other hand, 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 regimes, which can produce significantly different forest patterns and processes.

For all of these reasons, 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 regimes differ, may be inappropriate and could be detrimental to the meeting of the land manager’s objectives. Historically, lightning strikes, most frequent during the growing season, were the predominant ignition source in these areas. The evolution of ecosystem species to this burn pattern may be reason to utilize growing season burns to mimic these processes.

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