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Environmental Ramification of the Fire Ecology of Slash Pine (*Pinus elliottii*): A Study of Population Dynamics and Dispersal following a Fire Event

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ENVIRONMENTAL RAMIFICATIONS OF THE FIRE ECOLOGY OF SLASH PINE
(PINUS ELLIOTTII): A STUDY OF POPULATION DYNAMICS AND DISPERSAL
FOLLOWING A FIRE EVENT

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
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Dedication

I dedicate this work to my Lord and Savior, who created all that I hold dear, and to my brothers and sisters in Christ, that we may endeavor to be better stewards of His creation.

*Let the sea and what fills it resound,
the world and those who dwell there.
Let the rivers clap their hands,
the mountains shout with them for joy,
Before the Lord who comes,
who comes to govern the earth,
To govern the world with justice
and the peoples with fairness. Psalm 98: 7-9*

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Environmental ramifications of the fire ecology of slash pine (*Pinus elliottii*): a study of population dynamics and dispersal following a fire event

Kara E. Teague

ABSTRACT

With increasing encroachment on natural communities by anthropogenic activity, it is important to understand the functions of natural ecosystems in an effort to conserve natural areas. A first-hand study of the population dynamics of South Florida Slash Pine (*P. elliottii* Engelm. var. *densa*) following a fire event provided insight to its recovery and dispersal following a fire. A natural fire (lightning-induced) occurred in the spring of 2000 at the T. Mabry Carlton, Jr. Reserve, Sarasota County, providing an opportunity to study aspects of slash pine in relation to fire. One objective of my research was to look at dispersal/recruitment conditions and slash pine dynamics in relation to fire. I looked at the varying degrees of tree mortality due to fire at different stands of slash pines. I also looked at the stands in terms of stand composition and spatial arrangement of surviving adults. Finally, I studied how variable seedling establishment and survival was between stands. Few inferences could be drawn between fire and these individual analyses; however, all analyses revealed that at the scale of this study, pine flatwoods are patchy.

I also looked at the dispersal of slash pines following a fire event. I modeled my research after Ribbens et al. (1994) and Clark et al. (1998), who took a phenomenological

approach to dispersal modeling. This approach involved using distances between adults and seeds/seedlings and fecundity of adults to create dispersal models based on maximum likelihood estimates (MLE). I found that, while I could predict a model within acceptable parameters for most of the stands, more data was needed to predict models that better fit the data. This finding, along with the fact that I recovered no seed data for analysis, suggests factors are contributing to dispersal and recruitment (e.g. cone-crop) that need to be accounted for in the future.

Introduction

Human activity and ecological changes are affecting the Floridian landscape. Remaining natural areas present opportunities to study the mechanisms of Florida's ecosystems, hopefully with the outcome of lessening the impact of human activity. These areas offer insight to the dynamic relationships between climate, vegetation, and natural phenomena (e.g. natural fires) in the Floridian environment. One such ecosystem is the slash pine flatwoods in south Florida. This vegetative regime dominates much of the inland area of south Florida. These pine flatwoods are fire-dependent. Through looking at fire, specifically its importance in Floridian environments, and the biology of the fire-dependent species, *Pinus elliottii* (slash pine), the interaction between the two can be better understood. A first-hand study of the population dynamics of this species following a fire event will provide insight to its recovery and dispersal following fire. Consequently, the importance of fire and spatial mechanisms for ecological systems in Florida's natural settings can be better recognized.

Slash Pine Demography

Pinus elliottii belongs to a group of pines whose ecologic traits include fast growth, strong and heavy wood, long leaves, and moderate shade tolerance (McCune 1998). In the south, slash pine is renowned for its strong wood and fast growth. Indeed, because of this, it is one of the most popular trees to plant for timber in North America.

Two different types of slash pine are recognized in the Florida peninsula. *Pinus*

elliottii Engelm. var. *elliottii* is intermingled with *Pinus palustris* (longleaf pine) throughout much of the northern part of Florida. In this region, *P. elliottii* generally occupies wetter areas, while *P. palustris* dominates the drier upland areas. Consequently, *P. elliottii* communities tend to burn less frequently than *P. palustris* communities in northern Florida. (Lohrey and Kussoth 1990)

Further south in Florida, just north of Lake Okeechobee, a transition zone occurs among the pine species. This zone marks the southern limit of *P. palustris*, and *P. elliottii* begins to dominate the landscape (Stout and Marion 1993). It is along this transition zone that *P. elliottii* Engelm. var. *elliottii* is intermingled with the second recognized slash pine variety, *P. elliottii* Engelm. var. *densa*, also known as South Florida slash pine. The zone also marks a gradual change in the morphological traits between the two varieties (Lohrey and Kussoth 1990). There is much discussion as to the exact width of the transition zone and the gradualness of the changes in traits between the two species.

In general, *P. elliottii* is characterized by thick dark gray bark that is deeply furrowed and broken into irregular rectangular plates (West and Arnold 1956). It has long needles, with two or three needles per fascicle (Lohrey and Kussoth 1990). *P. elliottii* grows in many soil types; however, it requires wet habitats (West and Arnold 1956), and, consequently, is often found along streams and the edges of swamps and bays (Lohrey and Kussoth 1990). Seed fall occurs in the second autumn after pollination, and seeds are dispersed via wind (West and Arnold 1956; Lohrey and Kussoth 1990).

Seeds germinate readily, and seedlings are generally slim in structure (West and Arnold 1956; Lohrey and Kussoth 1990). The seedling stage marks the period in the life

of the slash pine that it is most susceptible to fire. Adequate soil moisture, even standing water, serves as a mechanism to protect the seedlings during the wet-season fire events (Lohrey and Kussoth 1990).

One major morphological difference between the two slash pine varieties involves their seedlings. In the southern parts of the Everglades, *P. elliotii* var. *densa* seedlings exhibit a 'grass stage' similar to that of *P. palustris* (West and Arnold 1956). The seedlings of South Florida slash pines grow a large taproot, but the top of the seedling does not elongate for three to six years. A thick bark also develops during the 'grass stage'; this bark serves as an extra measure in fire protection for the seedling (Tomlinson 1980).

Since *P. elliotii* is a dominant species over much of south Florida, it is important to understand its dynamic relationship with fire. One important aspect of this relationship is the effect of fire on seed dispersal and recruitment for the slash pine. As slash pines are relatively intolerant of competition and shade (Lohrey and Kussoth 1990), fire serves to reduce competition and open the canopy (Platt et al. 1991).

Fire Ecology in Florida

Fire is a prominent characteristic of the Florida landscape. The southeast region of the United States is characterized by adiabatic thunderstorms that occur almost daily during the wet summer season, generally from May to October (Abrahamson and Harnett 1990; Platt 1999). Floridian climatic conditions such as seasonal precipitation present circumstances favorable to lightning-induced fires.

Naturally occurring fires during the summer growing season result in an open landscape dominated by overstory pines and herbaceous groundcover (Platt 1999). The

mesic pine flatwood communities of south Florida benefit from their fire-intensive climate (Little and Dorman 1954). Fire serves to hinder invasion of woody species of plants and prune edges around tree islands in wetlands and prairies. Fire also recycles minerals in pine-dominated ecosystems. (Hofstetter 1984)

Historically, Florida's upland landscape was dominated by open pine flatwoods/savanna prairies (Platt 1999). The area was characterized by clumps of trees that did not form a continuous canopy. The combined effects of seasonal climates, herbivory, and fire maintained the savanna landscape. However, human settlement changed the countryside. Timber harvesting, cattle grazing, and hunting by fire have had their effects on the natural environments of Florida (Crocker 1987, Frost 1993). Fire suppression, which began in the early twentieth century, caused further degradation of the already-changing landscape (Goodman and Christian 1993). Consequently, a small portion of the original continuous pine flatwoods remains (Kelly and Bechtold 1990). Today, the fire-dependent pines, which dominate and define their ecosystems, cover approximately one third of the area of south Florida (Harper 1927).

Due to decades of fire suppression, fuel has accumulated to create potentially dangerous situations in much of this pine area. Moreover, suppression of natural fires and/or non-traditional prescribed burning during the dry season has led to conditions that discourage recruitment of fire-dependent species and facilitate invasion of hardwood species. (Hofstetter 1984).

Objectives

The objectives of my study were a) to look at the demography and spatial dynamics within stands of *P. elliotii* v. *densa*, especially in relation to fire intensity and

stand demography, and b) to develop a dispersal model for *P. elliotii* v. *densa* following a fire event. To accomplish the first objective, the analysis of the demographic and spatial variation of the stands, I looked at percent mortality as a function of fire event, demographic and spatial aspects of the surviving adult populations, and seed and seedling variations among the stands. One interesting outcome from this analysis was the question of the scale on which the analysis becomes statistically significant. In developing a dispersal model for *P. elliotii*, I looked at appropriate models, especially those developed by Clark et al. (1998) and Neubert and Caswell (2000). To accomplish these goals, I sampled ten slash pine stands in Sarasota County one year following a major fire event. The fires effectively consumed most understory growth, including *P. elliotii* juveniles. Thus, new seedlings were assumed to be from post-fire seed fall, and timing effectively allowed for the sampling of surviving trees and seeds responsible for stand replenishment or replacement.

Project Location-The T. Mabry Carlton Reserve

The T. Mabry Carlton Reserve is located in Sarasota County, Florida and encompasses 24,565 acres. It was purchased in 1982 by Sarasota County to provide “potable water, recreation, open space, and environmental education” (Sarasota County Community Services Parks and Recreation). Prior to that, the reserve was used for ranching and other similar uses. While the area may have once been used sparsely for timbering purposes, the pines have been largely left to grow in a natural state for many years. (Weber 2001)

The Carlton Reserve is characterized by microtopographic changes. These slight differences in elevation result in a variety of landscape types. Over 1,000 seasonal

wetlands and marshes mark the landscape of the Reserve. During the wet season, these otherwise dry areas fill with standing water. Hammocks, generally dominated by oak and cabbage palm, occur throughout the reserve, especially along the edges of the wetland areas. Most of the rest of the landscape consists of pine flatwoods, which are dominated by slash pine. The understory of the flatwoods consists of primarily *Serenoa repens* and *Aristida stricta*. (Sarasota County Community Services Parks and Recreation)

A natural fire (lightning-induced) occurred in the spring of 2000 in the Carlton Reserve. The flatwoods areas that were burned by this fire provided excellent research areas for studying slash pine population dynamics and seed dispersal after a potential stand-replacing fire event.

Study Sites

Ten study sites in the 2000 fire event were used. See Appendix A: Map of research area in the T. Mabry Carlton Reserve, Sarasota, Florida. The sites for the 2000 fire event were located no more than three miles apart. At each of these sites, stands of approximately 125 meter radius were established. *Pinus elliottii* provided the majority of the canopy, with *Quercus* and *Serenoa repens* present at varying degrees at the sites. Indeed, saw palmetto was a major understory species present, and the degree of presence varied at each stand. Stands were selected based on the logistics of avoiding disturbances and unsuitable patches (e.g. dense palmetto and wetlands) and on ensuring spatial variation in regards to degree of fire intensity, adult mortality, and understory denseness. They were not, in other words, a random sample.

Analysis of Fire Severity

Introduction

How severe was the 2000 fire, and how did this vary among stands? The wildfire that occurred in spring 2000 at the T. Mabry Carlton Reserve in Sarasota County, Florida, provided an opportunity to study the effects of fire on the population and spatial dynamics of slash pine stands. I was able to study the pre- and post-fire conditions and the severity of fire at each of the study sites. Such information was fundamental for understanding conditions for dispersal and recruitment for the slash pines in the study area. As wildfires, by nature, are patchy (Johnson 1992), and fires in Florida are no exception, this study also provided a glimpse at how the patchiness of the fire played out spatially among the stands in my research area and how the pines themselves contributed to the patchiness of the fire.

Here I use percent mortality per site as an indication of the degree of fire severity. Mortality, from a demographic viewpoint especially as a function of size, is meaningful in measuring the affect of fire on trees. Some stands suffered crown fires, resulting in large tree mortality and loss of future seed sources. Field observations revealed diverse levels of fire severity at the study sites, as discerned by the varying heights of burn scars on the trees and the counts of dead trees. Thus, the data gathered on live and dead trees of different stage classes were examined to determine the degrees of variability in fire in the stands. The main questions addressed for the mortality analysis were whether sites

varied in stand composition size pre-fire or in fire severity (as gauged by the percent of large trees killed. I also asked if pre-fire stand density predict fire severity.

Methods

Data collection

Ten stands were chosen that, based on field observations, covered a range of mortality due to the fire. At each of the ten stands, four transects of 4-meters by 50-meters were sampled, for an area of total 800 square meters per stand. All trees along these transects were identified as live or dead and large or small. The dead trees in the samples were obvious victims of fire; the large trees were dead trees that had succumbed to a crown fire. The cutoff for distinguishing between large and small trees was 5 cm DBH. Since we sampled less than one year after the fire and included all stumps and snags in the tally, we assumed all trees within the transects were accounted for.

Data analysis

To ask whether stands different in pre-fire size structure, all trees were assumed to be alive pre-fire. I examined the data with a χ^2 contingency table to determine whether stands were statistically different from one another in counts of large and small trees. Since stands were selected for apparent burn severity, not pre-fire stand structure, this was an honest test. I compared stands for mortality rate by examining histograms of mortality. Finally, I employed scatter plots to ask whether the fire severity at each stand was predicted by pre-fire tree density.

Results

Did sites vary in size structure before the fire? The χ^2 contingency table is shown in Table 1. The resultant χ^2 value of 119.33, with 9 degrees freedom, far exceeded the

level needed for significance at the 0.01 level (21.67), showing that the values were not independent. Therefore, the stands did vary from one another in terms of pre-fire size structure. Examination of the components of χ^2 (the partial χ^2 in Table 1) reveals the contribution of each cell to the total χ^2 . Figure 1 illustrates the different pre-fire population structures at each stand.

Table 1-- χ^2 contingency table for size structure of the stands pre-fire.

Stand	Large			Small			Totals
	Observed	Expected	Partial χ^2	Observed	Expected	Partial χ^2	
A	24	15.22	5.06	3	11.78	6.55	27
B	15	18.60	0.70	18	14.40	0.90	33
C	26	43.40	6.97	51	33.60	9.01	77
D	14	11.84	0.40	7	9.16	0.51	21
E	53	34.94	9.33	9	27.06	12.05	62
F	26	59.18	18.60	79	45.82	24.02	105
G	36	25.36	4.46	9	19.64	5.76	45
H	36	23.67	6.42	6	18.33	8.30	42
J	14	14.09	0.00	11	10.91	0.00	25
K	44	41.71	0.13	30	32.30	0.16	74
Totals	288			223			511
$\chi^2 = 119.33$, degrees of freedom = 9							

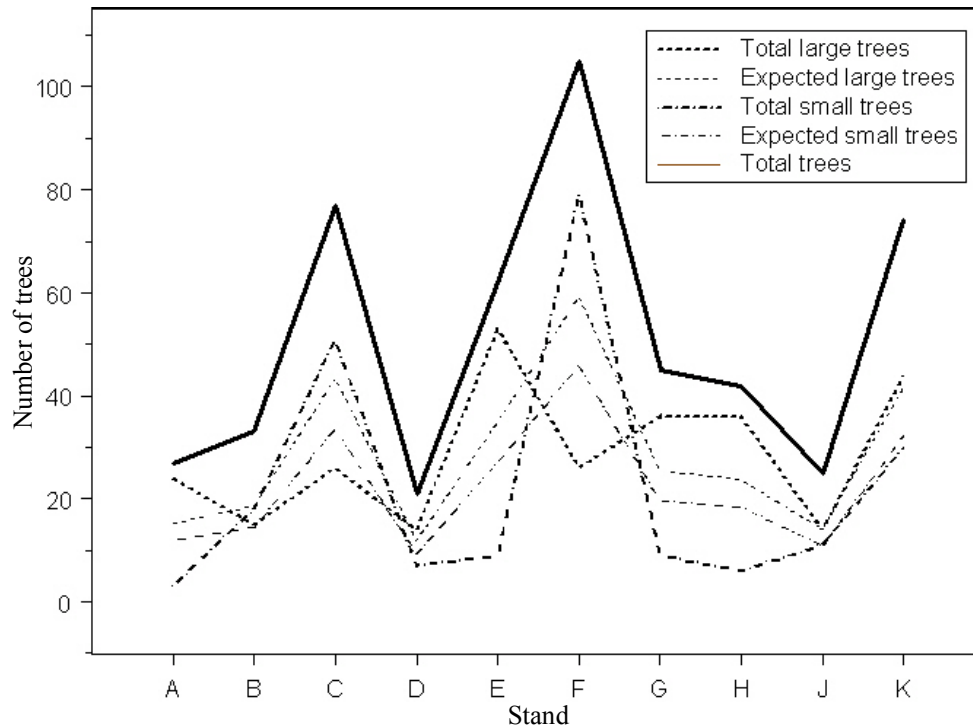


Figure 1--Pre-fire tree counts for each stand: large, small, and total. Expected values based on the χ^2 contingency table are in bold.

Did sites vary in percent large tree mortality after the fire? In other words, did fire severity vary substantially among stands? While field observations suggested that they did indeed vary, graphical visualization and statistical analysis offered a more sound answer. To begin, the data were graphed in histogram form (Figure 2) by percent mortality per stand. The data were distributed in a bimodal shape: large trees experienced either very high or very low mortality in different stands... Since the sites weren't selected randomly, this pattern should be interpreted cautiously.

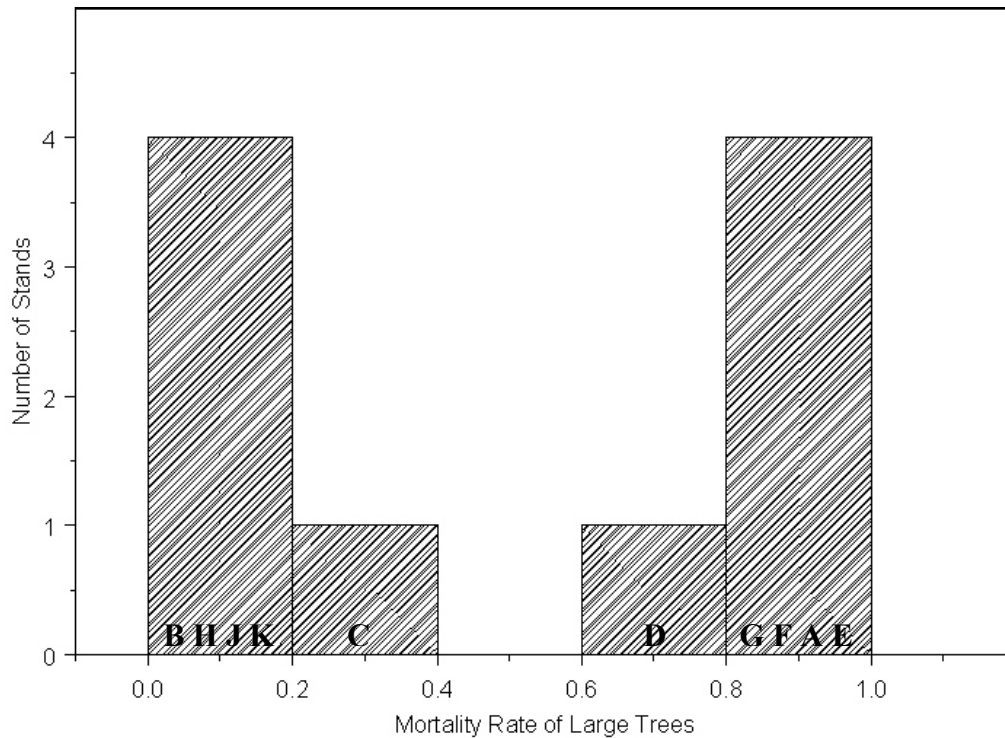


Figure 2--Histogram of the distribution of mortality of large trees for each stand. Stands are labeled in order of mortality.

I used graphical analysis to ask whether stand density before the fire affected mortality. I plotted the percent mortality per stand as a function of large, small, and total tree density per stand (Figures 3a-c). The graphs reveal considerable scatter in mortality rate as a function of density, regardless of whether small, large, or all trees are considered. The correlation between pre-fire density and mortality is positive but low. When looking at large trees, the coefficient was 0.255. For small trees, the coefficient was 0.019, and for the total tree count, it was 0.2.7. Therefore, it seems that mortality was not determined simply by pre-fire tree density in the research area. In Figure 3c, the mortality data reflect the bimodal pattern shown in Figure 2.

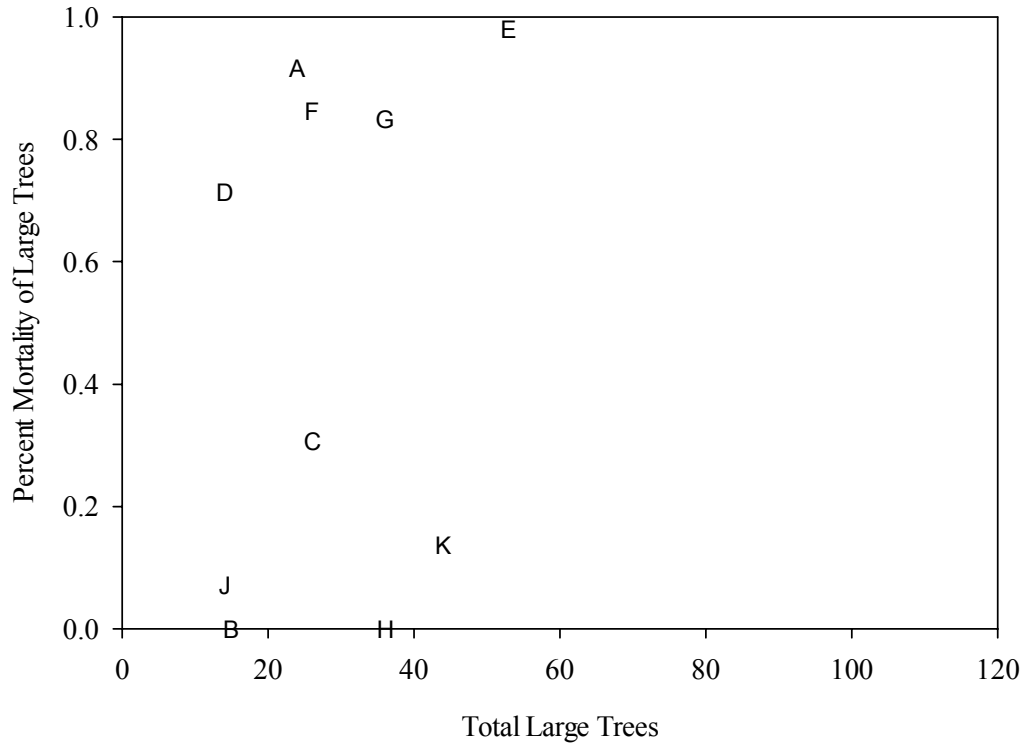


Figure 3a--Large tree mortality per stand as a function of large trees pre-fire.

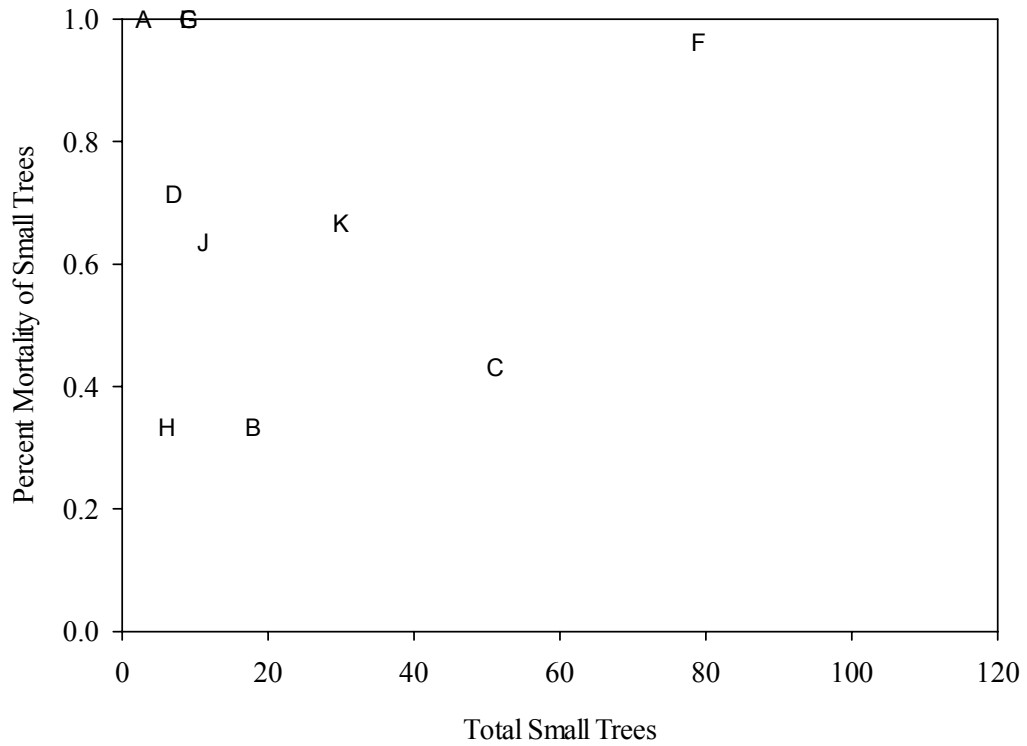


Figure 3b--Small tree mortality per stand as a function of small trees pre-fire.

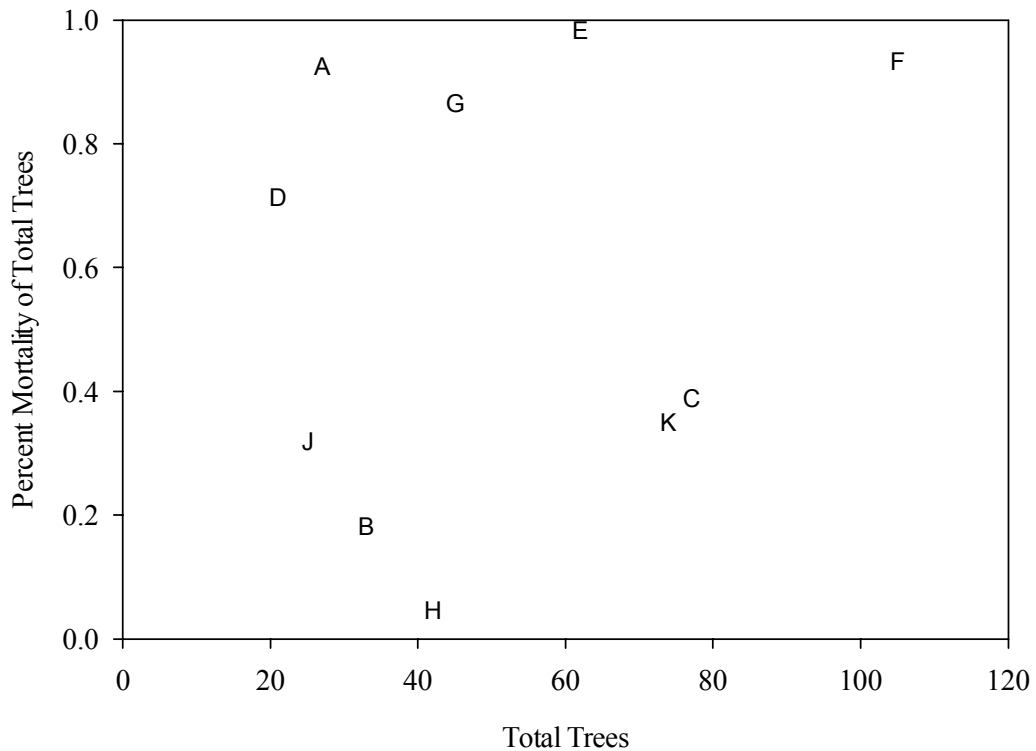


Figure 3c--Total tree mortality per stand as a function of total trees pre-fire.

Discussion

It seems clear that the stands did indeed differ in fire severity. Stands A, E, F, and G suffered high mortality; Stands B, H, J, and K underwent lesser degrees of mortality, and Stands C and D were slightly more intermediate in their mortality rates than the other stands. This is expected, since wildfire is generally patchy. However, as the degree of mortality played a factor in study site selection, these data cannot be used to quantify the patchiness of the fire. To do so, this method for quantifying fire severity could be repeated on a random sample of stands

I could not relate tree mortality to pre-fire density. It may be that there was insufficient variation in pre-fire tree density to do so, although pre-fire density varied over an order of magnitude. Certainly there was great variation in mortality rate. Many

factors could potentially contribute to the patchiness of a fire. Fire presence, intensity, and spread are determined by many factors, including species, density, fuel, and moisture (Bond and van Wilgen 1996). Further study on this topic should address these other factors to gain better understanding on how fire affects the ecology of slash pine flatwoods.

Adult Stand Structure

Introduction

Slash pine seed dispersal and stand recovery after a fire is necessarily dependent on the surviving adult population either in that stand or in stands sufficiently close to provide propagules. The number of reproducing adults post-fire would potentially affect seed production, which would, in turn, have bearing on the resultant seedling population. Obviously, the locations of adults would have effects on seedfall (e.g. location of source and obstruction of wind flow). Also, the spatial dynamics of a stand would affect establishment, nutrient availability, and space. Adults can hinder juvenile establishment and growth through shading and competition for nutrients (Lanner 1998). In fire-prone systems such as that of the longleaf pines- a species similar to slash pines- the adult trees build up a layer of litter around their base to promote low-intensity ground fires. This serves to suppress competition by limiting establishment of hardwood species (Grace and Platt 1995, Platt and Rathbun 1993). Thus, when looking at dispersal and recruitment of slash pine, it was essential to account for the factors of size, count, and spatial arrangement of surviving adult slash pines. The main questions I wanted to address in this section of the analyses were:

1. How did the stands compare in terms of stand composition with each other and with the pooled population?

2. How were the stands arranged spatially, and how did they compare with the rest of the stands? Were the trees arranged in clustered, regular, or random patterns?

I found these last questions more interesting. This aspect of my research was pertinent to dispersal and establishment of seeds as it likely addressed biological issues. If the stands showed a clustering pattern, it was likely that suitable site availability for germination was a major factor present. On the other hand, if I found the stands to be more regular, then intraspecies competition was likely a major contributor to position of individuals. As stands were expected to have a mixture of patterns based on the trees sizes being studied, I further asked whether one size group affected the spatial pattern of another.

Methods

Data Collection

All of the adults within a 125-meter radius of the center of the seedling transects in each of the ten stands were mapped, tagged, and measured for DBH (diameter at breast height). Mapping involved obtaining latitude and longitude readings using a DGPS (differential global positioning system) device for all trees with a DBH of 7.5 cm or greater. The DGPS equipment allowed for accuracy to 3 meters. Adults were tagged with aluminum numbered tags. Information for each adult tree was recorded on site via a Palm Pilot. The area for the adults was chosen to effectively record almost every possible parent for seeds and seedlings in the sampling area, based on the knowledge that most seeds from the closely related species *P. palustris* fall within 75 meters from their

source (Platt 2001) and *P. elliottii* seeds have similar aerodynamic properties (Benkman 1995, McCune 1998).

Data Analysis

The size structures of the stands were compared with density and histogram plots. I used log-linear models to determine the best-fit classification scheme for the histograms. The models have the general form

$$N_{ij} = \mu + \alpha_i + \beta_j + \gamma_{ij}$$

where N_{ij} is the number of trees in the i th bin and j th stand, μ is the average number, α_i and β_j represent the coefficients for the independent variables bin and stand, respectively, and γ_{ij} represents the coefficient for the interaction of bin and stand. The idea here was to use formal model selection criteria, such as the AIC (Akaike Information Criterion), to find the classification scheme that "best fits" the data but also uses few parameters. The AIC combines the log of the likelihood (thus, which model is most likely, given the data) and a penalty for additional parameters:

$$AIC = -2(\log \text{likelihood}) + 2(\text{number of parameters})$$

(Burnham and Anderson 1998). Generally, the model with the lowest AIC value best represents the data. The AIC values decreased significantly with increasing bin size.

I quantified the spatial distribution of the adults with several methods available in S+ Spatial Stats, a module for S-Plus. It was necessary to convert the coordinates from latitude/longitude data to an x/y grid to be read in the S-Plus program; ArcView GIS was used for this conversion. To look at the spatial distribution of the adults, I chose to study how the spatial dependence of the trees varied through space for each stand. In other words, I looked at how trees were arranged in relation to surrounding trees. To

accomplish this task, I used nearest neighbor distances among size classes and applied Ripley's K-function:

$$K(d) = \lambda^{-1} E[\text{number of points} \leq \text{distance } d \text{ of an arbitrary point}]$$

where λ is the mean number of points per unit area (intensity) and $E[\]$ is the expectation (Kaluzny et al. 1998). I performed this analysis using the total population, as well as using schemes dividing the population into five, nine, and fifteen size classes. Using these variable-sized categories provided a way to examine the robustness of the conclusions.

As my field sites were located in an area of pine flatwoods interspersed with wetlands, it was very likely that edge effects were present. Edge effects can result in vague K-function analyses (Kaluzny et al. 1998). When the spatial analysis was not discrete in showing a spatial pattern, I used simulation envelopes and added them to the K-function plots. These graphical envelopes represented the maximum and minimum values from a spatially random simulated data set based on the data. Data that fell outside these envelopes provided evidence against randomness, thus making it possible to discern between clustering and random spatial patterns if edge effects were indeed present. (Kaluzny et al. 1998)

Finally, I used point-to-point nearest neighbor distances for small and large trees for each stand to look for evidence that one size class influenced the spatial pattern of the other. I chose a cutoff DBH of 23.5 cm., which was the average DBH where the spatial pattern of the stands changed from clustering to random, signifying a change from smaller to larger trees (see Results). The empirical distribution function used to determine the point-to-point nearest neighbor distances was:

$$\hat{G}(y) = n^{-1} \sum_{d_i \leq y} 1$$

where n is the number of points (trees) in each stand, d is the distance from the i th point to the nearest other point, and y is the distances of all points (Kaluzny et al. 1998). This analysis was different from the previous in that it included effects from interactions between the size classes (large versus small trees). Again, as there were likely edge effects at the stands, maximum and minimum simulation envelopes were again employed. Graphs that fell to the left of the envelope (less than the minimum values for a random pattern) revealed the data was clustered. If the graph fell to the right of the minimum value line, there was not enough evidence to support the spatial pattern of the dependant variable was indeed determined by the independent. (Kaluzny et al. 1998)

Results

Variation in Stand Composition

I compared individual stands with the pooled population of trees mapped to gain insight as to how the stands varied in terms of tree sizes and counts. To begin, an appropriate classification or binning scheme was derived for the total population. The idea here is simple: since there is no a priori way to tell how the population is structured (that is, what set of size categories are an adequate description of the population or best predict population dynamics), use the AIC values of a series of bin schemes in a log linear model to determine the best set of categories. Table 2 shows different bin schemes and their resultant AIC values. The negative values of AIC for the models including interaction terms are artifacts of the way S-plus calculates AIC (values given are within an additive constant of the true AIC), so comparison of AIC values should simply be based on their values.

The log linear analysis revealed that, when the interaction between stands and bin size was included, the AIC value was drastically reduced across all bin schemes. This suggests the stands did indeed vary structurally since, by adding the stand as a variable, there was no consistent bin scheme which best represented the data. Since the resultant model with the lowest AIC had too many bins to effectively represent the data, it also proved necessary to use less statistically formal, but biologically important, criteria for selecting classification schemes for my data: tree counts, resolution, and bin structure. Bin schemes were rejected if the majority of the stands were left with no trees in bins. On the other hand, the bin scheme had to reflect the measurement resolution of the DBH (observed field error was within 2 cm.). Finally, other than the last bin, which included outliers, all the bins were of equal range in DBH. A bin size of 18 (width 1.8 cm DBH) was ultimately chosen as it had a comparatively low AIC value, yet retained few enough bins to effectually represent the data.

Table 2--Size structure analysis of the stands based on different bin schemes. Smaller values of the AIC represent preferable models.

Number of bins	df	AIC
No interaction between stand and bin size		
3	14	213.0105
4	15	309.5566
8	19	540.2390
13	24	803.9184
18	29	1014.5511
23	34	1228.3134
38	49	2129.2000
50	61	3753.5303
Interaction between stand and bin size		
3	34	-873.8861
4	45	-1132.6167
8	89	-2420.3103
13	144	-3998.1004
18	199	-5301.1395
23	254	-6896.6123
38	419	-9380.1970
50	551	-9745.8105

Histograms of individual stands were next graphed using the 18-bin scheme. This allowed all stands to be compared with a common bin scheme. To view a concise comparison, the density plot of the log DBH of the total population was superimposed over the histogram of log DBH for each stand. Figure 4 reveals that the stands did vary in their relation to the average density plot. Those stands that most closely mirrored the average density plot were Stands D, E, and G. At varying degrees, stands A, F, H, and K are more negatively skewed than the mean of the total population. Stand C was more positively skewed. Stand J was also slightly positively skewed compared to the total population and was more platykurtic than any of the other stands. Table 3 is a summary of the densities of trees at each stand.

Table 3--Summary data of the adult density of each stand

Stand	Mean size	Variance of size	Skewness	Kurtosis
A	28.42	47.69	0.285	-0.668
B	18.06	39.06	1.268	1.7362
C	17.67	80.66	1.175	.0554
D	18.74	44.99	1.082	2.029
E	20.29	24.18	0.438	-0.091
F	22.68	81.84	0.110	-1.108
G	19.11	49.42	1.129	1.215
H	21.12	34.69	0.430	0.142
J	18.57	82.63	1.065	0.932
K	22.14	39.02	0.402	0.650

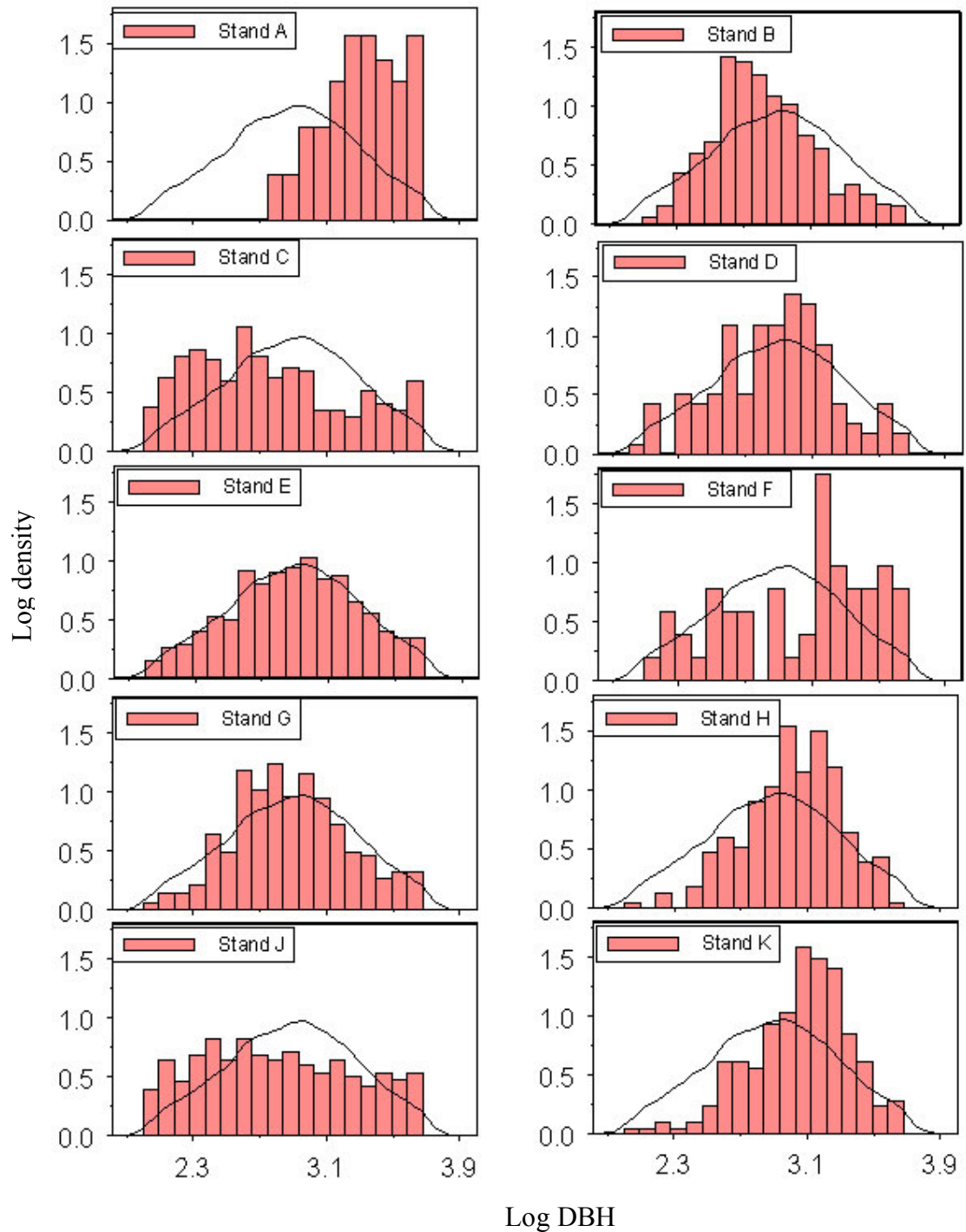


Figure 4--Log density of total population against histogram of log population per stand. The y-axis represents log density and the x-axis represents log bin ranges of DBH.

Spatial Variation

All ten stands exhibited varying degrees of clustering when the entire tree population was analyzed. From graphical analysis based on Ripley's K Function, Stand A showed evidence for only slight clustering. Stand D showed evidence for clustering at short distances, after which evidence for a random pattern was observed. Stand J showed evidence for strong clustering. See Appendix B for table of spatial patterns for all stands at various bin schemes.

Considering such biologic factors as favorable germination sites and competition, it was necessary to look for spatial patterns of trees in different size classes. Evidence was observed for general trends among all three schemes: younger trees (smaller DBH, generally less than 20cm) generally followed a clustered pattern, older trees (larger DBH, generally greater than 26cm) generally followed a regular pattern, and a random pattern was often evident between the two. This trend was best observed in the nine- and fifteen-bin schemes. See Appendix B. However, the five-bin scheme was useful in observing spatial pattern where there were too few post-fire adults to populate the nine- and fifteen-bin schemes. Such was the case for Stands A, D, and F. In addition, stands where the trend of apparent loss of clustering with increasing tree size was not observed were also stands with either few large or small trees.

Stands A and F showed slight clustering. It is likely the low numbers of smaller trees in the two stands affected the clustering pattern. Stand E did not appear to follow the trend of increasingly regular pattern with tree size; there was evidence for clustering in most bins. This is most likely due to the few large trees mapped at Stand E. The same

tendency can be observed in Stand K. Stand J showed evidence for the strong clustering, which was interesting due to the large number of smaller trees mapped.

Finally, each stand was examined to detect any evidence for spatial pattern based on small-scale interactions between small and large trees. The results of this analysis are shown in Figures 6a and 6b. Each subplot in Figures 5a and b is an empirical distribution function plot of point-to-point nearest neighbor distances of the size classed (large or small) with upper and lower simulation envelopes representing the maximum and minimum values. These values were determined by a simulated random data set based on the original data. When looking at the spatial arrangement of small trees, I found evidence that large trees did have an effect on the spatial pattern. In most cases, the graph of small tree distances showed definite clustering (graph was to the left of the simulation envelopes). This concurred with the previous analysis where I found that small trees tended to show evidence for clustering. This analysis demonstrated evidence that large trees do affect the spatial pattern of small trees. The one exception was Stand A; the lack of clustering there was likely due to the low count of trees below 23.5 cm DBH (14 trees). However, the large trees were not found to be clustered; all of the graphs were to the right of the minimum simulation graph. Thus, it could not be concluded that the locations of small tree had any affect on the locations of the large trees. This was expected; biologically speaking, juveniles do not often out-compete adults. The plots of the large trees were included for comparison reasons.

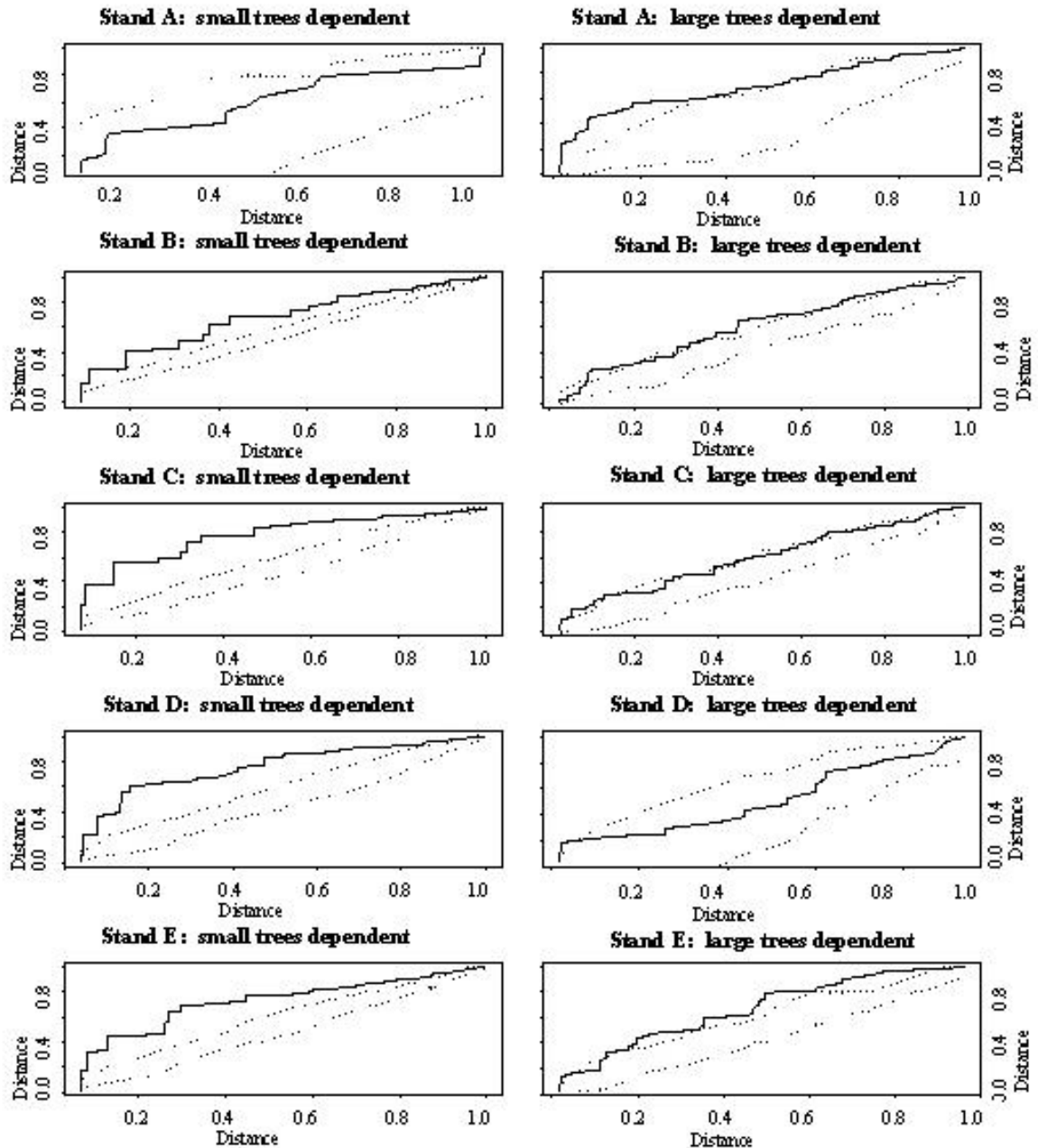


Figure 5a--Evidence of spatial pattern dependence on nearby trees: Stands A-E. Empirical distribution function plots of point-to-point nearest neighbor distances with upper and lower envelopes of complete spatial randomness (dotted lines). Plots include interactions. The left column contains analyses where the small trees were the dependent variable and large trees were the independent variable. In the right column, distance to large trees is the dependent variable, with distance to small trees as the independent variable. Evidence for clustering is present if the plot falls to the left of the envelope.

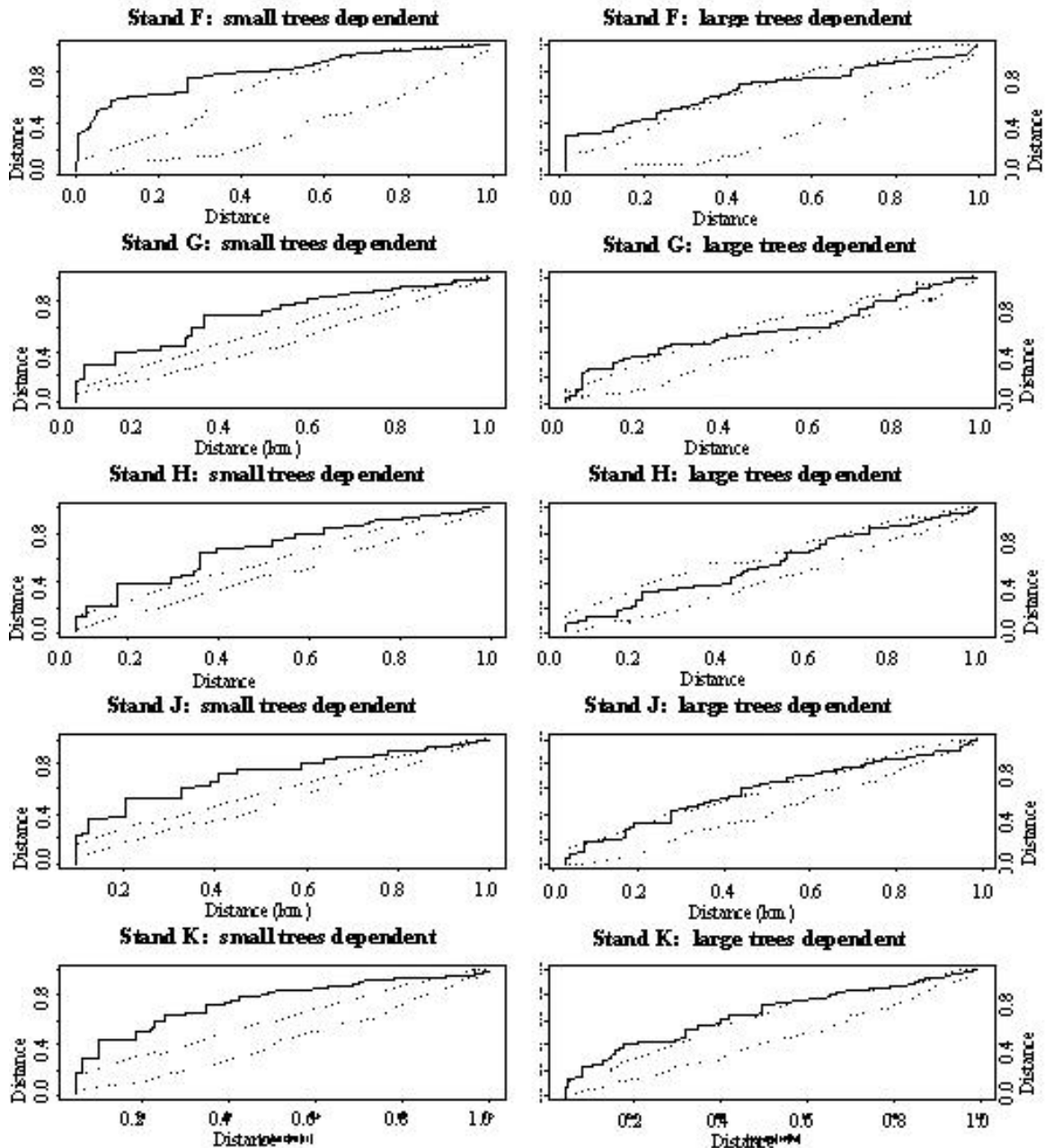


Figure 5b--Evidence of spatial pattern dependence on nearby trees: Stands F-G. Empirical distribution function plots of point-to-point nearest neighbor distances with upper and lower envelopes of complete spatial randomness (dotted lines). Plots include interactions. The left column contains analyses where the small trees were the dependent variable and large trees were the independent variable. In the right column, distance to large trees is the dependent variable, with distance to small trees as the independent variable. Evidence for clustering is present if the plot falls to the left of the envelope.

Discussion

From looking at compositions and spatial patterns, I could determine that the study sites were indeed different from each other. Individual stands varied in comparison to the mean distribution of trees. To further uphold these findings of varying degrees of demographic structures, further study should be done with more numerous and more random replications.

Among the stands, I found general trends of clustering in small trees and increasing loss of clustering with increasing trees size, ultimately reaching a regular pattern. These trends raise interesting ecological questions. Do trees germinate in a clustered pattern? Do they then reach a regular pattern after years of competition and natural selection? Platt and Rathbun (1993) found evidence in longleaf populations supporting the idea that small trees occur in a clustered pattern away from large trees. Indeed, in areas of old-growth longleaf pine, small trees were underrepresented, suggesting direct competition with large trees.

While all the stands showed evidence for clustering, the degree of clustering varied. Further analysis would need to be done to determine if spatial patterns of the stands was a result of the burn intensity or if the two are both determined, in part, by some underlying conditions. One condition could be the interactions among trees, or competition, which is often thought to dominate spatial patterns in conifers (Platt and Rathbun 1993). Another condition could be the health of the pre-fire trees. Under more favorable study conditions (conducive to pre-fire analysis), pre-fire tree health would be a beneficial factor to study. Finally, fire history could explain the spatial pattern; fire contributes to maintaining the open, patchy landscape characteristic of flatwoods in

Florida (Abrahamson and Hartnett 1990). Thus, past fires in the stands likely contributed to the spatial patterns.

When I looked at point-to-point nearest neighbor distances, there did appear to be evidence that adult trees affected the clustering of small trees. This was expected since, as mentioned earlier, interaction with neighboring trees can affect recruitment and establishment (Platt and Rathbun 1993). Further research would be useful to look at whether clustering in my study area was more a product of neighboring large trees or other conditions (e.g. topography, vegetation cover, edge effects, etc.).

Seedling Densities and Survival

Introduction

How much seedling establishment occurred after the fires, and how variable was it between stands? Data on seedling densities and survival made it possible for us to address these questions. Field observations revealed patchy distributions of seedlings, with many stands having relatively few seedlings, and a few stands having many, highly clustered, seedlings. Seedlings that survived a year could offer insight to suitability of the stands in terms of physical conditions, competition, etc. Therefore, a one-year census was conducted of the seedlings that had originally been sampled. The questions in this analysis were:

1. What was the average seedling density following the fires? Did stands vary in terms of seedling densities? What was the pattern of dispersion of seedlings within stands?
2. What was the average chance of a seedling surviving one year? Did stands vary in terms of seedling survival?

Methods

Data Collection

Seedling data were collected on 50-m belt transects, for a total of three transects per stand. Transects were composed of quadrats 4 meters square, totaling seventy-five quadrats per stand. Where physical conditions prohibited three transects, additional, shorter transects were employed to ensure seventy-five sampling quadrats. The center of

each quadrat was mapped utilizing DGPS (see chapter *Analysis of Adult Stand Structure*), and all seedlings within the quadrat were counted and tagged. Tagging involved attaching numbered bird bands to each seedling; the bands allowed the seedlings to be tagged for a few seasons without causing permanent damage as the bands would break off before hindering growth. Seedling survival data for the 2000 burn sites were gathered by returning in the spring of 2002 and noting tagged seedlings still alive. Some arbitrarily chosen seedlings within the stands but not in the quadrats were also tagged and mapped for survival analysis; these were used for survival analyses but not for estimation of density or dispersion patterns.

Data Analysis

The sampling for seedlings involved 75 4-m² quadrats per stand. Analysis of the seedling data included how the seedling counts varied per quadrat within each stand and how the total densities varied among stands. The densities of seedlings were compared among stands with one-way ANOVA. To better match the assumptions of the ANOVA, I used the square roots of density values. I employed multiple comparison tests to compare variables. As my field studies included a follow-up census in the second spring, I looked at survival across stands using a χ^2 independence test. Also, survival was examined with a χ^2 goodness-of-fit test to the total mean survival.

Results

Figure 7 illustrates the variation of seedling counts between quadrats within each stand. Most stands had few seedlings; those stands with greater seedling densities had great variation among quadrat samples. This follows from the fact that many of the quadrats had values of zero seedlings; it also makes it clear that the seedlings were highly

clumped spatially. Table 4 shows the relationship of variance in density of quadrats within the stands compared to the mean density per stand.

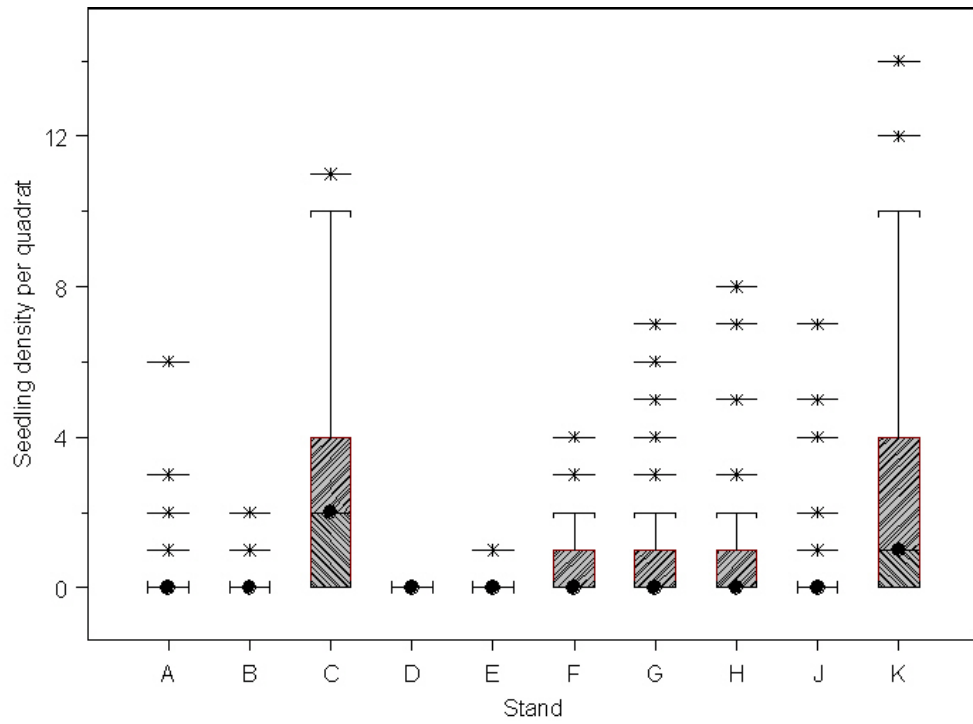


Figure 6--Box plot of seedling density per quadrat per stand. Circles represent median density per stand, and asterisks represent outliers beyond the quartiles.

Table 4--Relationship of variance in density of quadrats within the stands compared to the mean density per stand.

Stand	Mean density of quadrats (m)	Variance of density among quadrats (v)	v/m
A	0.44	1.00	2.30
B	0.09	0.11	1.21
C	2.41	6.81	2.82
D	0.00	0.00	0.00
E	0.08	0.07	0.93
F	0.51	0.96	1.89
G	1.07	2.90	2.72
H	0.76	2.08	2.73
J	0.36	1.26	3.50
K	2.39	10.38	4.35

A one-way ANOVA resulted in rejection of the null hypothesis that stands had the same seedling densities. To further explore how stands differed from one another, I used multiple comparisons tests. Since the sample sizes were equal (75 quadrats per stand), I used Tukey's method.

Results are shown in Figure 7.

There were many stand pairs that show significant differences, the greatest being between Stands C and D. It is also interesting that Stands C and K are significantly different from all stands except each other. Stand G shows a significant difference with seven stands. To check the robustness of these results, I used two other standard multiple comparison, Bonferroni and Scheffe methods. Results from all three were very similar.

To compare the number of surviving seedlings after a one-year interval among stands, I used a χ^2 test for

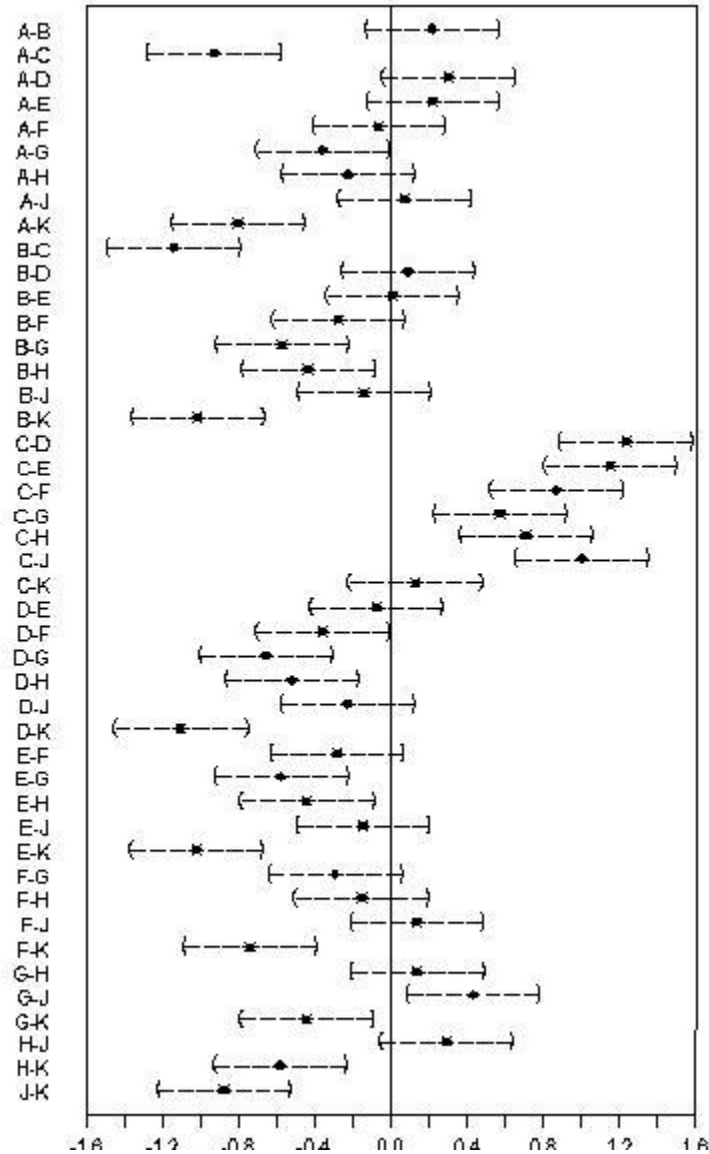


Figure 7--Plot of results of pair-wise comparisons using Tukey's method (95% confidence intervals). Those confidence intervals which do not intersect the zero vertical reference line are statistically different. (S-Plus Guide to Statistics 2001)

independence. The resultant χ^2 value of 26.78, with 8 degrees freedom, exceeded the level needed for significance at the 0.01 level (20.09). See Table 5. Thus, stands differed from one another in survivor counts. I also used a χ^2 goodness-of-fit test to examine departures from the pooled mean survival probability. The resultant χ^2 value of 35.60, with 8 degrees freedom, far exceeded the level needed for significance at the 0.01 level (20.09). See Table 6. Consequently, stands were not only different in their respective counts of survivors, but the pooled mean survival rate is not a good predictor of survival in general. Indeed, Figure 8 shows the difference in variation of seedling survivorship in the stands.

Table 5-- χ^2 contingency table for seedling survival.

Stand	Original count			Survivor count			Totals
	Observed	Expected	Partial	Observed	Expected	Partial	
A	32	30.44	0.08	3	4.56	0.54	35
B	7	6.09	0.14	0	0.91	0.91	7
C	181	185.23	0.10	32	27.77	0.64	213
E	6	6.96	0.13	2	1.04	0.88	8
F	38	40.87	0.20	9	6.13	1.35	47
G	80	88.70	0.85	22	13.30	5.69	102
H	57	60.00	0.15	12	9.00	1.00	69
J	27	26.96	0.00	4	4.04	0.00	31
K	179	161.75	1.84	7	24.25	12.27	186
Totals	607			91			698
$\chi^2 = 26.78$, degrees of freedom = 8							

Table 6-- χ^2 goodness of fit test to the mean survival.

Stand	Dead seedlings			Surviving seedlings		
	Observed	Expected	Partial χ^2	Observed	Expected	Partial χ^2
A	29	27.20	0.12	3	4.80	0.67
B	7	5.95	0.19	0	1.05	1.05
C	149	159.86	0.15	32	27.14	0.87
E	4	5.10	0.24	2	0.90	1.35
F	29	32.30	0.34	9	5.70	1.92
G	58	68.01	1.47	22	11.99	8.35
H	45	48.45	0.25	12	8.55	1.40
J	23	22.95	0.00	4	4.05	0.00
K	172	152.16	2.59	7	26.84	14.66

$\chi^2 = 35.60$, degrees of freedom = 8

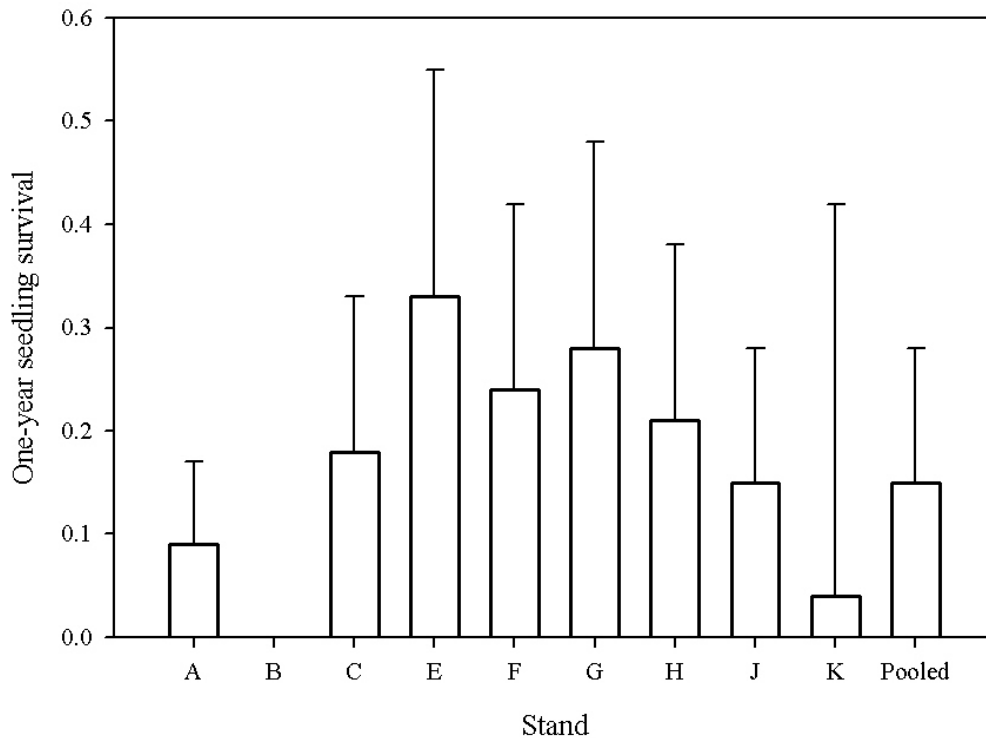


Figure 8--Variation of seedling survivorship with one standard error of the estimate.

Discussion

In conclusion, the stands did indeed differ in terms of seedling densities and one-year survival of those seedlings. To further explore the reasons behind these differences, analyses should be conducted to explore the various conditions affecting establishment and survival. Field observation revealed that sites varied in terms of understory species, understory density, and year-round water retention and flow. The seedlings were found to be clumped spatially. This relates to the clumped patterns of younger large trees observed in this research (refer to chapter *Analysis of Adult Stand Structure*). It is likely that biological factors played a role, including inter- and intra- species competition. Also, long-term study could provide insight to the role climate plays in the area.

Dispersal models for South Florida Slash Pine

Introduction

Dispersal ability in some species has strong effects on population dynamics. The South Florida slash pine (*Pinus elliottii* Engelm. var. *densa*) relies on fire to promote suitable conditions for dispersal and recruitment. *P. elliottii* Engelm. var. *densa* is a dominant feature of the ecosystems in which it is found. Since the landscape is often fragmented by stand-replacing fires, wetlands, and human disturbance, we need to know something about the distances over which dispersal occurs. This is likely to become more important with increasing human population growth because of its effects on fire suppression and fragmentation of flatwoods.

The purpose of this study was to determine the seed/seedling dispersal curve for South Florida slash pine following a fire event. Seed dispersal modeling in ecology generally falls under two types, mechanistic and phenomenological (Nathan and Muller-Landau 2000). Mechanistic studies to quantify seed/seedling distributions are generally done in a controlled setting, such as an isolated tree in an open field with released seeds at specific heights (Green and Johnson 1995, Ribbens et al 1994). Greene and Johnson (1995) have formulated dispersal models for long-distance wind dispersal in trees. They measured the heights of seed release, velocities of seeds in flight, and velocities of wind. These models were intended for long-distance dispersal (greater than 100 meters) and were based on experiments recording the dispersal distances of seeds released from a point source at an open airfield. While this provided excellent testing grounds, the

experiments left out such factors as the effects of turbulence (as is induced by understory and nearby trees) and gusts of wind. Even so, their work is highly respected; given the complexity and assumptions of their experiments, their results nonetheless were compatible with their predictions (Green and Johnson 1995). Accordingly, their work serves as a basis for further testing and model development on seeds that rely on wind dispersal.

The work by Greene and Johnson was based on a known point source in an open area; in natural settings as those found in Florida (e.g. Florida flatwoods), such conditions are uncommon. Thus, it would be difficult to reproduce such an experiment for slash pine populations and measure the necessary parameters. Fortunately, recent work provides an approach that can be utilized in the flatwoods environment. This phenomenological approach uses the spatial distribution of adults, the fecundity of adults, and the spatial distribution of seeds and/or seedlings to estimate a dispersal kernel, the probability distribution at dispersal distances. These variables can be measured in the field with relatively minimal difficulty and can be used to develop models that reflect dispersal.

Ribbens et al. (1994) studied the spatial distribution of seedlings juxtaposed with the distribution of adults. This study addressed the issues of seedling recruits produced by adults as a function of adult fecundity (i.e. adult size) and the spatial distribution of seedlings. Since they used the association of all seedlings with all adults, the issue of conspecific neighbors was addressed. In their experimental design, Ribbens et al. (1994) studied trees with defined growth and reproduction seasons to ensure that seedlings sampled were known to be from one reproductive cycle.

Clark et al. (1998) extended this approach to include seed data. By using seed traps, they were able to estimate dispersal kernels directly, without the complicating factor of seedling survival. Their method also allowed them to account for differences in adult fecundity. By comparing this direct estimate of a dispersal model with information on seedling distribution, the limitation on establishment can be quantified and included in the models on dispersal. Consequently, recruitment can be studied and modeled. The most widely-used phenomenological models for seed dispersal are the exponential model, Gaussian model, and 2Dt model, a two-dimensional variation of the Student's t distribution (Clark, et al. 1999, Nathan and Muller-Landau 2000). These models are summarized in Table 7.

Table 7--General dispersal models.

Model	Equation	Variables
Exponential	$f(r) = \left(\frac{1}{N}\right) \exp\left[-\left(\frac{r}{\alpha}\right)^1\right]$	r=distance $f(r)$ = seed shadow density α =central tendency of distance N=normalizing function*
Gaussian	$f(r) = \left(\frac{1}{N}\right) \exp\left[-\left(\frac{r}{\alpha}\right)^2\right]$	r=distance $f(r)$ = seed shadow density α =central tendency of distance N=normalizing function*
2Dt	$f(r) = \frac{p}{\pi u \left[1 + \left(\frac{r^2}{u}\right)\right]^{p+1}}$	$f(r)$ = seed shadow density p= shape parameter u=scaling parameter

$$* N = \int_0^{\infty} \int_0^{2\pi} \exp\left[-\left(\frac{r}{\alpha}\right)^c\right] d\Phi dr = \frac{2\alpha^2\Gamma(2/c)}{c}$$

Methods

Data Collection

Data for the dispersal analysis included: GPS coordinates for adult trees, seed traps, and seedling quadrats; DBH information for adult trees; and density information

from seed traps and seedling quadrats. See previous chapters for more detailed descriptions of data collection of the adult trees and seedlings. For the seed data, ten seed traps were established at each study site around the quadrats and at least 5 meters apart. The design of the trap mirrored one used in a similar study by Clark et al. 1998. A plastic basket was supported approximately 1.5 feet from the ground in a PVC pipe frame. Netting was suspended in the basket to catch the seeds and allow for drainage. Wire mesh capped the basket to protect the seeds from predation.

Data Analysis

The observed data from each stand were fitted to each of the three mathematical models using S-Plus. I found the best-fitting (i.e., maximum likelihood) parameters for each model. This approach also allowed me to use AIC values to choose among the models. I set limits when determining the maximum likelihood estimates (MLE). These limits allowed MLEs to be determined within expected values for pines (Clark 2001) while guaranteeing the statistical program would not run indefinitely in the event that there were errors in the data or models.

Finally, I used a bootstrapping method to estimate confidence intervals for each of the dispersal kernels. Bootstrapping methods are commonly used to explore the sampling distributions of parameters (Venables and Ripley 1999). Using S-Plus, I ran a bootstrap based on the seedling densities in each quadrat of each stand, which returned an estimate of the probability density of the data. This allowed me to determine maximum likelihood estimates for each of the parameters in a generated larger sample. Thus, I could add confidence intervals to the dispersal kernels at the 0.025 and 0.975 levels.

Results

None of the models consistently proved the best at describing dispersal for the slash pines in the study area. In most cases, the AIC values for all three models were very similar. See Appendix C. Overall, the Gaussian model most often best described the seedling shadow at the stands. However, in six of the ten stands, one or two of the models were rejected because their parameters reached the set limits in analysis before a maximum likelihood estimate could be attained. Consistently, the models which reached the parameter limits did so with the parameter for the central tendency of distance. I set the limit for distance at 500 meters, a distance higher than any expected dispersal distance. These models were excluded from the bootstrapping step. The dispersal curves for all models with fits that are believable (i.e. none of the parameters reached their limits) are included in Appendix D.

For the derived models in Appendix D, most of the estimated seed fall occurred within 20-40 meters of the source tree. Also, in most cases, the confidence intervals around the curves fit better in the tails of the curves, an anomaly (discussed below) suggesting a problem with the underlying model. The exceptions to this were found in the exponential and Gaussian curves for Stand G, which show a more gradual slope and fatter tail. The dispersal curves for Stands C and K were also unusual. The confidence intervals for Stand C were enormous. The curves for Stands C and K fell outside the confidence intervals.

Discussion

Overall, the Gaussian model had the lowest AIC values, suggesting that it is the best model to represent dispersal in slash pines. However, there was not enough

information to correlate between dispersal and other studied differences in the stands (i.e. fire presence/severity and spatial distribution of adults). In three stands, the exponential model actually better described the seedling shadow. These stands, A, F, and G underwent higher degrees of fire. However, Stand E resulted in similar mortality rates from the fire, but its data better fit the Gaussian curve. None of the stands showed similarity in spatial analysis of large trees or seedling density (see previous chapters). Thus, only vague connections can be drawn between dispersal and any factors addressed in this study.

Perhaps the most striking facts of this analysis were that the lowest values of AIC were for the stands with the smallest sample sizes and that the bootstrapped confidence intervals were narrowest in the tails of the estimated dispersal kernels. This combined with the relatively small differences in the AIC values overall and the wide confidence intervals for all the models suggests at the least that there was insufficient power to estimate dispersal kernels (Steidl and Thomas 2001). This inference is supported by the fact that for most stands, the AIC values were suspiciously similar. Those models resulting in very different AICs turned out to be the ones that resulted in parameters that reached maximum range during analysis.

Although the Gaussian model best described seedling shadow overall, more research is needed. Indeed, according to Clark et al. (1999), the 2Dt model should best represent the tree species. However, this model requires a great amount of data to reach a reasonable fit to the model. Moreover, while my research is useful in setting the groundwork for understanding dispersal of slash pine following a fire event, more work is needed. Data collection over a period of years would be beneficial by providing a time

factor to include in the models (Clark 1998). This aspect could show variations in the models based on the numbers of seasons before or after a fire event and on the fluctuations in seed rain due to seasonality. Also, a greater sampling effort is likely necessary. A retrospective power analysis (Steidl and Thomas 2001) could be performed to ascertain the effectiveness of this study. Then, further research at these sites could be conducted to ensure acceptable statistical power. It could be possible to simulate the amount of data necessary to attain sound dispersal models, and then endeavor to achieve that sampling in the field.

It is likely that the problem is much deeper than simply one of small sample size. If this were the only difficulty, then the AIC would tend to improve with sample size and the confidence intervals would not be narrowest in the tail. However, the stands with the greatest counts of seedlings, Stands C and K, had the worst fits. Thus, it seems likely that additional problems exist. One is that it is likely the underlying assumptions for the kernel models did not hold true in my research areas. Indeed, all the models I used involved a normalization constant that assumed rotational symmetry (Clark et al. 1999) and they assume that seedling density is well predicted simply by the distance from a source tree and the strength of that source. At all of my research sites, the seedlings were highly clumped (see chapter *Analysis of Seedling Densities and Survival*). At the scale which I studied, this clumping pattern violated the assumptions of rotational symmetry and of uniformly available establishment sites.

This idea helps explain the unusual results at Stands C and K. Of the ten stands studied, these two had by far the greatest amount of seedlings. They both had lower mortality than other stands, and a substantial number of adult trees. For C and K, the

Gaussian model was chosen since both the other models were rejected due to parameters reaching maximum range during analysis. Also, only for Stands C and K did the dispersal curves lay outside of the bootstrap confidence intervals. It is likely that factors I did not account for in my analysis affected the results from these two stands. As mentioned, it is likely that the highly clumped pattern of the seedlings resulted in poor model fits. Since the seedlings were highly clumped, these stands not only had the greatest amount of seedlings but also the highest variance in quadrat densities. Following this, the other stands, while having lower seeding densities, also had lower variance between quadrats (i.e., there were more zeros), resulting in better estimates.

Moreover, while this study could be used for a preliminary dispersal model of slash pine populations, I did not find strong enough evidence to clearly determine the best model for slash pine dispersal based on seedling information. Seedling data by nature encompasses complicated information. Seedlings underwent dispersal, site selection, competition, and environmental factors, all of which contribute to the clumped spatial pattern.

A better approach to determining dispersal would be to look at seed data, which was one of the objectives of this study. Seed data would provide a simpler, more discrete system as only the factor of dispersal would play into seed trap data. My goal was to retrieve seed data from traps. However, after the traps had been in place for a year, I found virtually no seeds in the traps. Many variables could account for my having found no seeds in the traps. While experiment design is always a factor for error, the seed traps seemed to function properly as I found many other species of seeds in the traps. A more reasonable explanation could be in site conditions. At the time of cone and seed

production, two springs prior to seedfall, my research area was in a long drought season. It is likely the population was under the influence of the drought conditions and fertility was affected. The fact that my field crews observed few pine cones in the canopy or on the ground further supports this idea. Further research could be done at these sites to monitor the recovery of the slash populations from the drought conditions of the past few years.

Discussion

The objectives of this research were to look at the demography and spatial dynamics within stands of slash pine, especially in relation to fire intensity and stand demography, and to develop a dispersal model following a fire event. It seems clear that the processes of fire, mortality, and seed dispersal are complex and highly variable, and they do not relate to one another in any simple fashion. I do believe, though, my findings will serve as a basis for further research in slash pine ecology.

Fire severity at each stand did not depend on pre-fire stand structure. This may seem surprising, because the usual dogma is that dense stands with many small trees lead to severe fires. However, this belief seems clearly to be an oversimplification, because many factors contribute to the scope of fire damage, including weather and climate, fuel, ignition sources, and vegetation type (Bond and van Wilgen 1996). The size and density of the slash pine populations would play a contributing role in terms of fuel contribution, microclimate creation, and vegetation community foundation, but not be the sole (or even major) factor in determining the character of the fire.

There was a strong spatial pattern evident at my study areas. Surviving trees ranged from a clustered pattern in smaller trees to a regular pattern in larger trees. The seedling analysis fit into this scheme as they were also highly clustered. These trends suggest that, at the scale of this study, pine flatwoods are patchy. One feature of almost all the analyses was this patchiness: stands varied in terms of fire severity, stand composition, and seedling density.

One of the main goals of this study was to determine a dispersal model for slash pine. While I did not find enough evidence to support any one model as describing the seedfall of slash pine, my results can be used as a basis for further research. One conclusion from my results was that the clumped pattern of the seedlings violated the central assumption used in trying to estimate the parameters of the dispersal models from seedling dispersion data, namely that dispersion is primarily determined by seed dispersal (or equivalently, that each microsite on which a seed lands is an equally good site for establishment). The result was that the models fit the data more and more poorly as the amount of data available increased. This study should be repeated with data from seed traps, which would result in better fits since seeds are not subjected to the large number of additional processes that seedlings are, such as site selection, competition, and environmental factors.

Overall, this study was an effort to establish groundwork for future study in the area of dispersal and recovery of slash pine populations following a fire event. However, from looking at all the analyses in this study, it is obvious that other factors play a role in the dispersal, recruitment, establishment, and subsequent recovery of the population. Such factors could include small-scale variation in the understory and soil moisture, and plant-plant interactions like competition and facilitation. Since fire is vital to Florida's ecosystems, it is important to continue to understand the dynamic role fire plays in the ecology of important species such as the slash pine.

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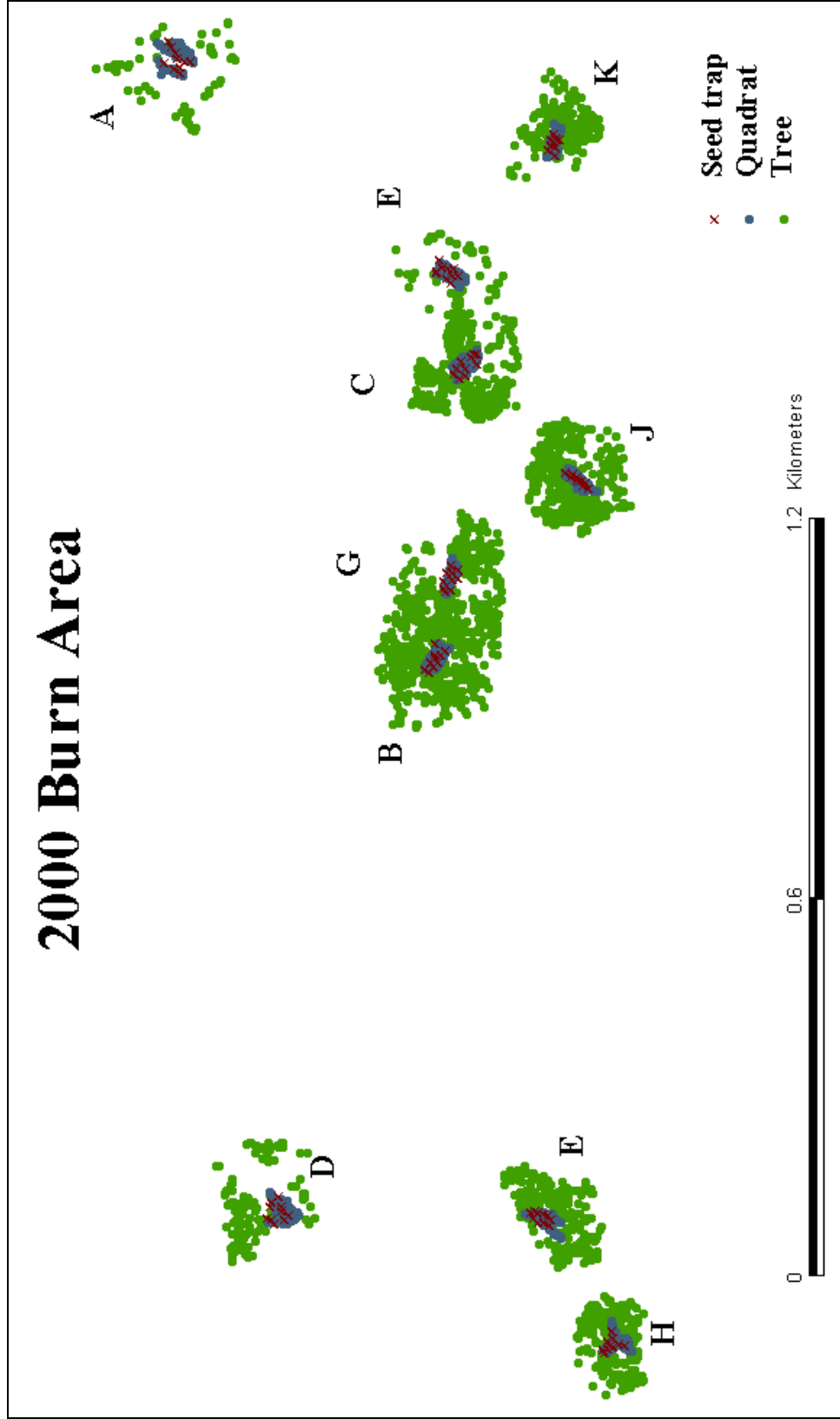
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Appendices

Appendix A: Map of research area in the T. Mabry Carlton Reserve, Sarasota, Florida.



Appendix B: Table of spatial patterns of adults for each stand. Ripley's K-function was employed to determine evidence of spatial pattern. The function is defined as:

$$K(d) = \lambda^{-1} E[\text{number of points} \leq \text{distance } d \text{ of an arbitrary point}],$$

where λ is the mean number of points per unit area (intensity) and $E[\]$ is the expectation. In some cases, bins showed evidence for a spatial pattern at most distances, but the pattern shifted at nearer distances (*) or farther distances (**). Some stands did not have enough individuals in a given bin to determine any evidence for spatial pattern (***). C=clustered, R=random, Re=regular.

Stand	Bin schemes for DBH									
	Total population	5 Bins			9 Bins			15 Bins		
	Spatial pattern	DBH range	Count	Spatial pattern	DBH range	Count	Spatial pattern	DBH range	Count	Spatial pattern
A	slight C	7.5-13.9	0	***	7.5-11.1	0	***	7.5-9.6	0	***
					11.2-14.6	0	***	9.7-11.8	0	***
								11.9-13.9	0	***
		14.0-20.3	7	***/Re	14.7-18.2	2	***	14.0-16.0	1	***
								16.1-18.2	1	***
					18.3-21.7	10	Re	18.3-20.3	5	***
		20.4-26.7	18	R*/Re	21.8-25.3	7	Re***	20.4-22.4	5	***
								22.5-24.6	6	***
					25.4-28.8	13	R*/Re	24.7-26.7	7	***
		26.8-33.1	17	C*/R				26.8-28.8	7	***
					28.9-32.4	9	R*/Re	28.9-31.0	5	***
				32.5-35.9	5	Re***	31.1-33.1	5	***	
	33.2-	14	R/ Re**				33.2-35.2	3	***	
				36.0-	10	R*/Re	35.3-37.4	4	***	
							37.5-	7	***	
B	C	7.5-13.9	160	C	7.5-11.1	40	R	7.5-9.6	11	Re
					11.2-14.6	152	C	9.7-11.8	53	C
								11.9-13.9	96	C
		14.0-20.3	254	C	14.7-18.2	156	C	14.0-16.0	109	C
								16.1-18.2	79	C
					18.3-21.7	94	C	18.3-20.3	66	C
		20.4-26.7	87	C	21.8-25.3	49	R	20.4-22.4	40	C
								22.5-24.6	29	R
					25.4-28.8	23	R	24.7-26.7	18	Re
		26.8-33.1	31	R				26.8-28.8	13	Re
					28.9-32.4	17	R	28.9-31.0	10	Re
				32.5-35.9	10	Re	31.1-33.1	8	Re***	
	33.2-	17	R				33.2-35.2	8	Re***	
				36.0-	8	Re	35.3-37.4	3	***	
							37.5-	6	***	
C	C	7.5-13.9	172	C	7.5-11.1	103	C	7.5-9.6	60	C*/R
					11.2-14.6	85	C*/R	9.7-11.8	60	C*/Re
								11.9-13.9	52	C*/R
		14.0-20.3	101	C	14.7-18.2	67	C*/R	14.0-16.0	43	R
								16.1-18.2	30	R
					18.3-21.7	39	C*/R	18.3-20.3	28	R
		20.4-26.7	37	R	21.8-25.3	18	R	20.4-22.4	13	C*/Re**
								22.5-24.6	14	Re
					25.4-28.8	17	R	24.7-26.7	10	Re
		26.8-33.1	33	C*/Re				26.8-28.8	9	Re
					28.9-32.4	20	R	28.9-31.0	14	Re
				32.5-35.9	15	Re	31.1-33.1	10	Re	
	33.2-	33	R				33.2-35.2	7	Re***	
				36.0-	22	R*/Re	35.3-37.4	9	Re***	
							37.5-	17	R	

Appendix B (Continued): C=clustered, R=random, Re=regular, nearer distances (*), farther distances (**), not enough to determine spatial pattern (***)

Stand	Bin schemes for DBH									
	Total population	5 Bins			9 Bins			15 Bins		
	Spatial pattern	DBH range	Count	Spatial pattern	DBH range	Count	Spatial pattern	DBH range	Count	Spatial pattern
D	C	7.5-13.9	35	C*/Re	7.5-11.1	13	C*/Re	7.5-9.6	6	***
					11.2-14.6	25	C/Re**	9.7-11.8	11	C***/Re
								11.9-13.9	18	C
		14.0-20.3	47	C*/R	14.7-18.2	23	C/Re**	14.0-16.0	12	C***/Re
								16.1-18.2	14	C***/Re
					18.3-21.7	34	R	18.3-20.3	21	R
		20.4-26.7	32	C*/R	21.8-25.3	17	R	20.4-22.4	17	R
								22.5-24.6	9	Re
					25.4-28.8	6	Re***	24.7-26.7	6	***
		26.8-33.1	6	Re***				26.8-28.8	4	***
					28.9-32.4	2	***	28.9-31.0	1	***
					32.5-35.9	5	***	31.1-33.1	1	***
		33.2-	7	Re***				33.2-35.2	4	***
				36.0-	2	***	35.3-37.4	1	***	
							37.5-	2	***	
E	C	7.5-13.9	23	C/Re**	7.5-11.1	4	***	7.5-9.6	0	***
					11.2-14.6	25	C	9.7-11.8	7	***
								11.9-13.9	16	C
		14.0-20.3	116	C/Re**	14.7-18.2	61	C	14.0-16.0	28	C***/Re
								16.1-18.2	39	R
					18.3-21.7	81	C	18.3-20.3	49	C
		20.4-26.7	90	C/Re**	21.8-25.3	46	C	20.4-22.4	43	C
								22.5-24.6	32	C
					25.4-28.8	25	slight C	24.7-26.7	15	R
		26.8-33.1	28	C/Re**				26.8-28.8	13	C***/Re
					28.9-32.4	13	C	28.9-31.0	13	C
					32.5-35.9	4	***	31.1-33.1	2	***
		33.2-	2	***				33.2-35.2	1	***
				36.0-	0	***	35.3-37.4	1	***	
							37.5-	0	***	
F	C***/R	7.5-13.9	13	C*/Re	7.5-11.1	7	***	7.5-9.6	3	***
					11.2-14.6	8	Re***	9.7-11.8	4	***
								11.9-13.9	6	***
		14.0-20.3	9	Re	14.7-18.2	3	***	14.0-16.0	4	***
								16.1-18.2	1	***
					18.3-21.7	6	***	18.3-20.3	4	***
		20.4-26.7	16	R***/Re	21.8-25.3	10	Re***	20.4-22.4	2	***
								22.5-24.6	8	***
					25.4-28.8	7	Re***	24.7-26.7	6	***
		26.8-33.1	8	Re***				26.8-28.8	3	***
					28.9-32.4	3	***	28.9-31.0	2	***
					32.5-35.9	6	***	31.1-33.1	3	***
		33.2-	9	Re***				33.2-35.2	2	***
				36.0-	5	***	35.3-37.4	5	***	
							37.5-	2	***	

Appendix B (Continued): C=clustered, R=random, Re=regular, nearer distances (*), farther distances (**), not enough to determine spatial pattern (***)

Stand	Bin schemes for DBH									
	Total population	5 Bins			9 Bins			15 Bins		
	Spatial pattern	DBH range	Count	Spatial pattern	DBH range	Count	Spatial pattern	DBH range	Count	Spatial pattern
G	C	7.5-13.9	95	C	7.5-11.1	30	C***/Re	7.5-9.6	11	C
					11.2-14.6	85	R	9.7-11.8	33	C
								11.9-13.9	51	C
		14.0-20.3	170	C	14.7-18.2	100	C	14.0-16.0	60	C
								16.1-18.2	60	C
					18.3-21.7	71	C	18.3-20.3	50	C
		20.4-26.7	81	slight C	21.8-25.3	48	R	20.4-22.4	35	slight C
								22.5-24.6	26	R
					25.4-28.8	29	R	24.7-26.7	20	R
		26.8-33.1	31	R				26.8-28.8	17	Re
					28.9-32.4	10	Re	28.9-31.0	6	Re
					32.5-35.9	14	Re	31.1-33.1	8	Re
	33.2-	23	Re				33.2-35.2	9	Re/R	
				36.0-	13	R	35.3-37.4	3	***	
							37.5-	11	Re	
H	C	7.5-13.9	29	slight C	7.5-11.1	6	Re***	7.5-9.6	3	***
					11.2-14.6	30	C	9.7-11.8	5	***
								11.9-13.9	21	R
		14.0-20.3	93	C	14.7-18.2	45	slight C	14.0-16.0	17	R***/C
								16.1-18.2	35	R
					18.3-21.7	63	C	18.3-20.3	41	R/C**
		20.4-26.7	87	C	21.8-25.3	50	R	20.4-22.4	29	slight C
								22.5-24.6	34	R
					25.4-28.8	28	R***/Re	24.7-26.7	24	R
		26.8-33.1	32	R				26.8-28.8	13	slight Re
					28.9-32.4	18	C/Re**	28.9-31.0	14	R/ Re**
					32.5-35.9	10	C***/R	31.1-33.1	5	***
	33.2-	10	***				33.2-35.2	7	***	
				36.0-	1	***	35.3-37.4	2	***	
							37.5-	1	***	
J	strong C	7.5-13.9	185	C	7.5-11.1	104	C	7.5-9.6	62	C
					11.2-14.6	100	C	9.7-11.8	69	C
								11.9-13.9	54	C
		14.0-20.3	118	C	14.7-18.2	70	C	14.0-16.0	52	C
								16.1-18.2	37	R
					18.3-21.7	51	R	18.3-20.3	29	R/Re**
		20.4-26.7	76	C	21.8-25.3	38	C	20.4-22.4	28	R
								22.5-24.6	29	R
					25.4-28.8	32	R	24.7-26.7	19	Re
		26.8-33.1	46	C				26.8-28.8	16	Re
					28.9-32.4	25	Re	28.9-31.0	12	Re
					32.5-35.9	25	Re	31.1-33.1	18	R
	33.2-	43	R/Re**				33.2-35.2	15	Re	
				36.0-	23	Re	35.3-37.4	11	Re	
							37.5-	17	Re	

Appendix B (Continued): C=clustered, R=random, Re=regular, nearer distances (*), farther distances (**), not enough to determine spatial pattern (***)

Stand	Bin schemes for DBH									
	Total population	5 Bins			9 Bins			15 Bins		
	Spatial pattern	DBH range	Count	Spatial pattern	DBH range	Count	Spatial pattern	DBH range	Count	Spatial pattern
K	C	7.5-13.9	20	C	7.5-11.1	6	Re***	7.5-9.6	4	***
					11.2-14.6	21	R	9.7-11.8	3	***
								11.9-13.9	13	R/Re**
		14.0-20.3	68	C	14.7-18.2	35	C	14.0-16.0	22	C
								16.1-18.2	20	C
					18.3-21.7	51	C	18.3-20.3	26	R
		20.4-26.7	93	C	21.8-25.3	48	C	20.4-22.4	32	C
								22.5-24.6	35	C
					25.4-28.8	40	C	24.7-26.7	26	C/Re**
		26.8-33.1	38	slight C				26.8-28.8	20	R
					28.9-32.4	16	R/Re**	28.9-31.0	13	R
					32.5-35.9	7	Re***	31.1-33.1	5	***
		33.2-	11	R				33.2-35.2	5	***
				36.0-	6	Re***	35.3-37.4	3	***	

Appendix C: Table of parameters estimates and AIC values for dispersal curves from seedling data. The model type is listed in the Stand column: Exp=exponential, Gau=Gaussian, and 2dt= Student's 2Dt.

Stand	alpha	Confidence Interval		beta	Confidence Interval		theta	Confidence Interval		b	Confidence Interval		u	Confidence Interval		Log Likelihood	AIC
		0.025	0.975		0.025	0.975		0.025	0.975		0.025	0.975		0.025	0.975		
A																	
Exp	7.369	4.228	14.961	0.949	1.24	0.421	1.684									59.53	125.06
Gau	22.979	10.357	42.373	0.879	1.228	0.728	2.148									61.934	129.867
2dt	0.9									0.984	0.414	1.203	82.21	50.168	328.86	63.669	131.337
B																	
Exp	11.574	3.472	46.298	0.012	0.027	0.384	1.537									23.814	53.628
Gau	20.33	6.099	67.148	0.012	0.022	0.404	1.617									23.68	53.361
2dt	31.213									0.013	0.004	0.025	500	150	2000	24.295	52.59
C																	
Exp	500			36.916		1.129										154.792	315.583
Gau	80	24	225.15	0.756	3.026	1.093	2.07									155.397	316.794
2dt	60.908									0.848			5000			184.467	372.933
E																	
Exp	500			1.594		100										21.16	48.321
Gau	11.221	4.753	44.884	0.037	0.062	100	400									21.655	49.311
2dt	96.625									0.036			5000			21.291	46.583
F																	
Exp	12.853	5.162	51.41	0.393	1.057	0.455	1.451									70.315	146.63
Gau	23.588	9.61	94.353	0.391	0.772	0.453	1.422									70.374	146.747
2dt	23.407									0.413	0.238	0.617	500.1	150.05	2000	78.036	160.071

Appendix C (Continued)

Stand	alpha	Confidence Interval		beta	Confidence Interval		theta	Confidence Interval		b	Confidence Interval		u	Confidence Interval		Log Liklihood	AIC
		0.025	0.975		0.025	0.975		0.025	0.975		0.025	0.975		0.025	0.975		
G																	
Exp	39.828	20.925	86.965	0.412	0.265	0.83	0.579	1.329								106.588	219.176
Gau	63.536	52.941	84.296	0.369	0.214	0.445	0.692	1.344								114.786	235.572
2dt	73.136								0.435				5000			127.636	259.271
H																	
Exp	500			13.75			0.638									89.644	185.288
Gau	8.766	4.553	35.064	0.052	0.03	0.102	0.642	2.566								89.681	185.362
2dt	10.993								0.057	0.033	0.089	67.2	20.175	269		103.42	210.84
J																	
Exp	3.598	2.548	14.393	0.079	0.025	0.148	0.221	0.884								49.393	104.786
Gau	8.089	5.099	16.998	0.079	0.026	0.142	0.243	0.971								48.578	103.157
2dt	9.461								0.074	0.026	0.116	51.36	32.472	205.41		64.968	133.937
K																	
Exp	500			43.206			0.566									152.096	310.192
Gau	80	149.35	225.2	0.728	2.913	2.913	0.532	0.898								153.446	312.891
2dt	64.469								0.703			5000				225.239	454.478

Appendix D: Dispersal curves for the seedling shadow
Figure 7--Stand A, Exponential model

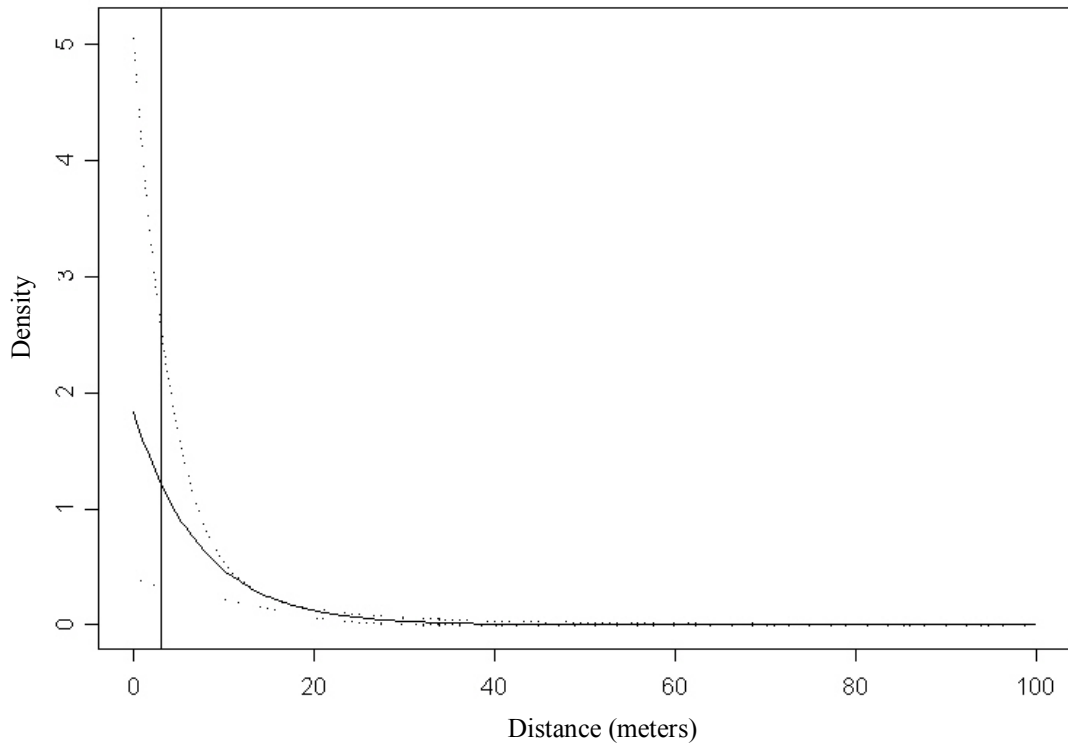


Figure 8--Stand A, 2Dt model

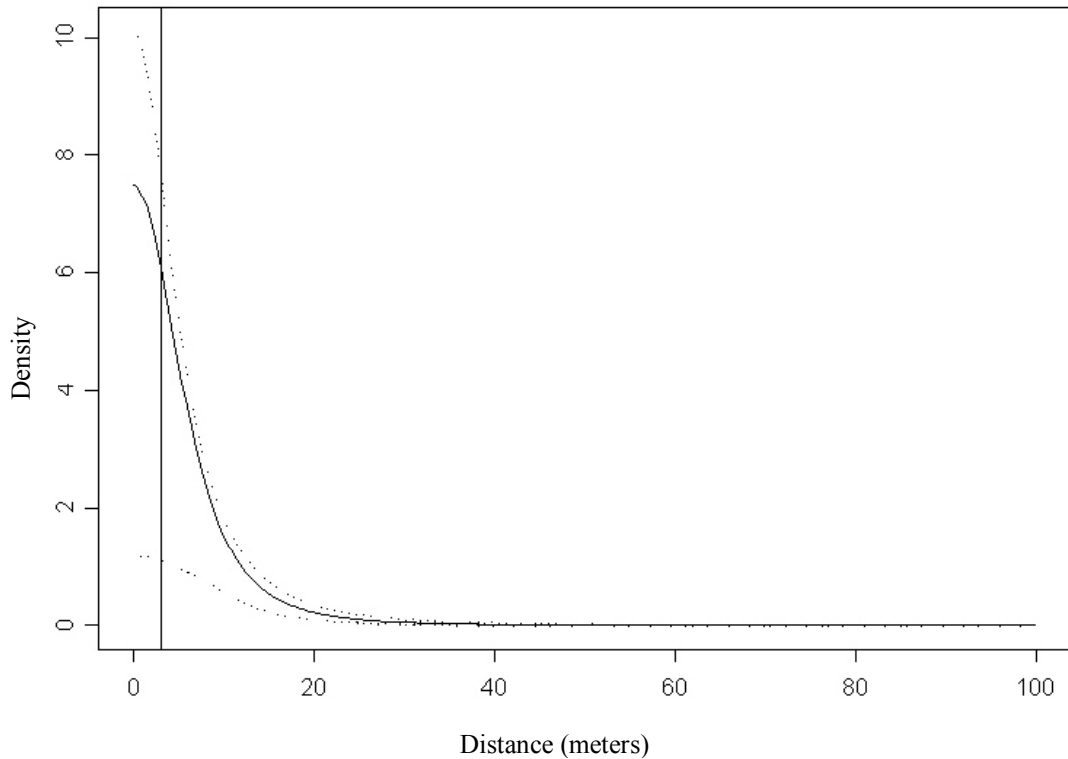


Figure 9--Stand B, Exponential model

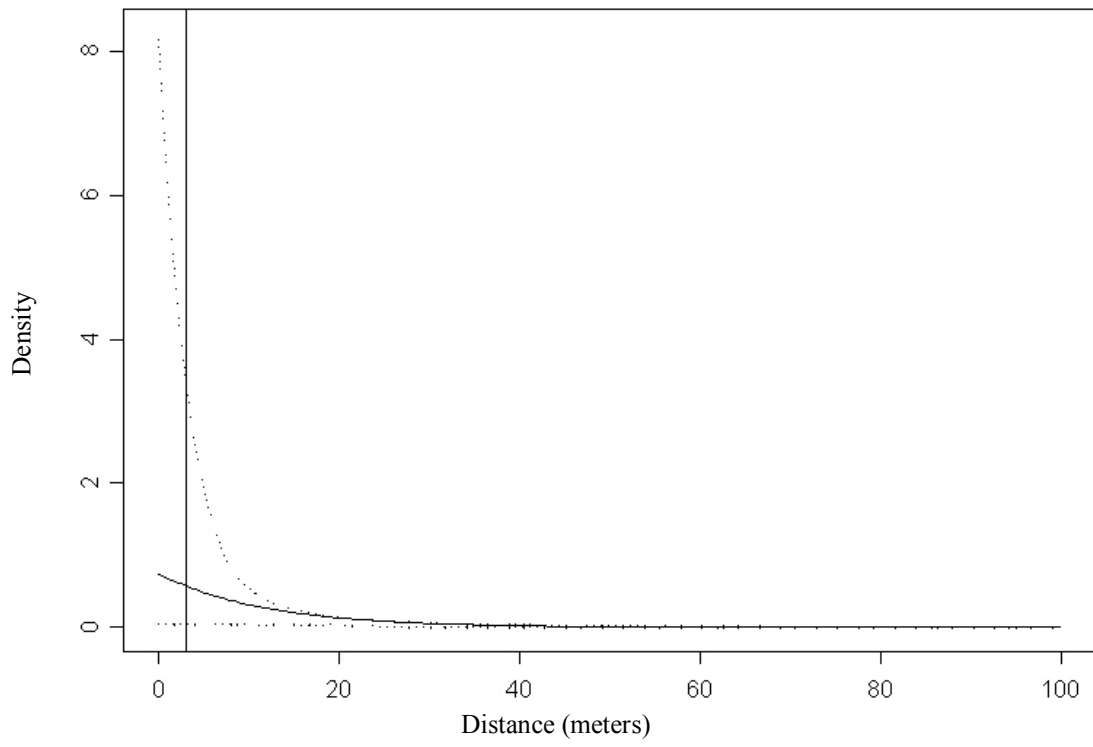


Figure 10--Stand B, Gaussian model

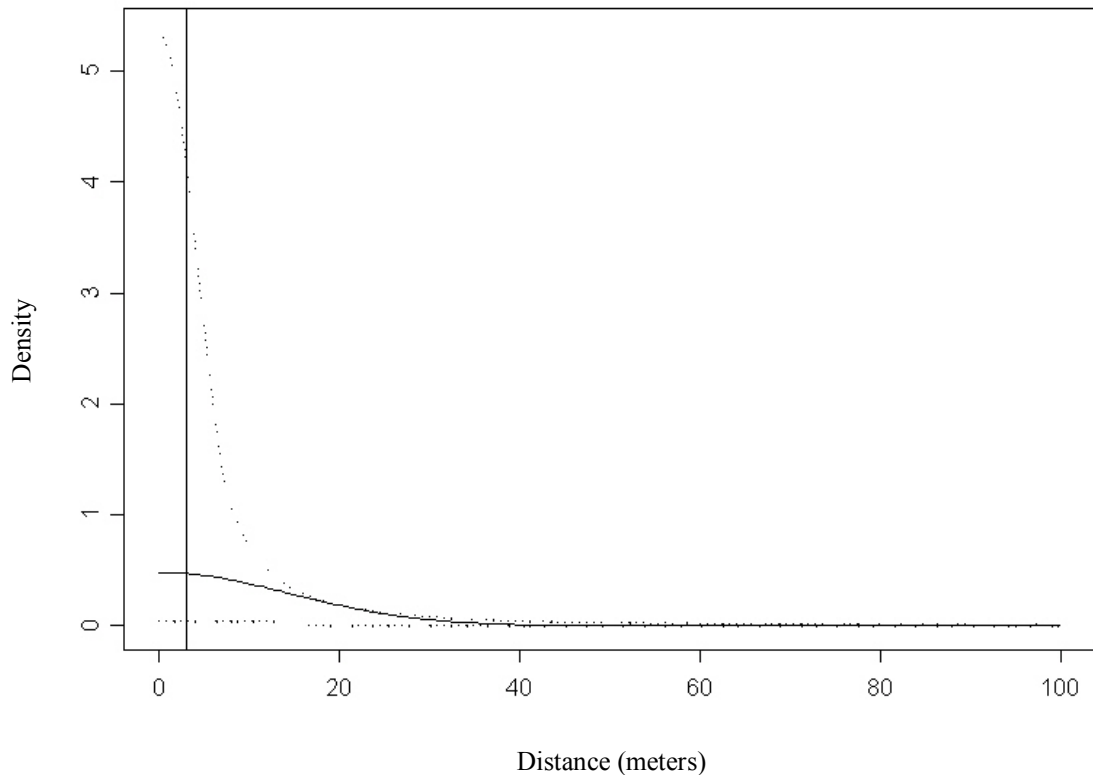


Figure 11--Stand B, 2Dt model

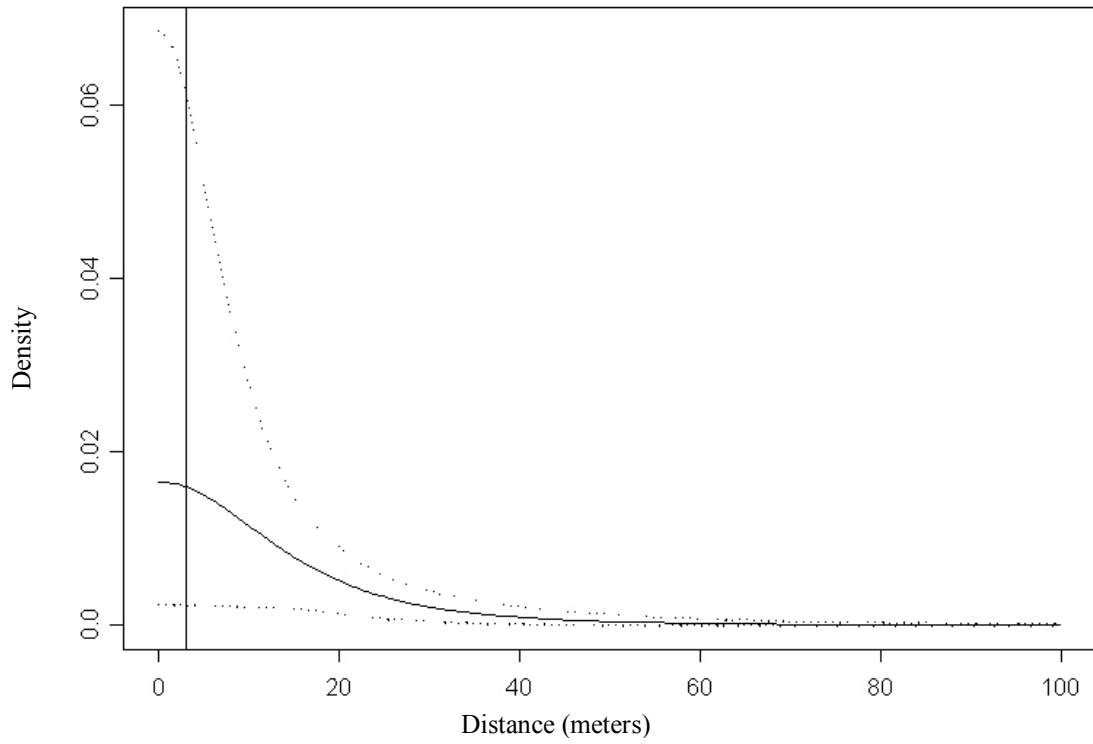


Figure 12--Stand C, Gaussian model

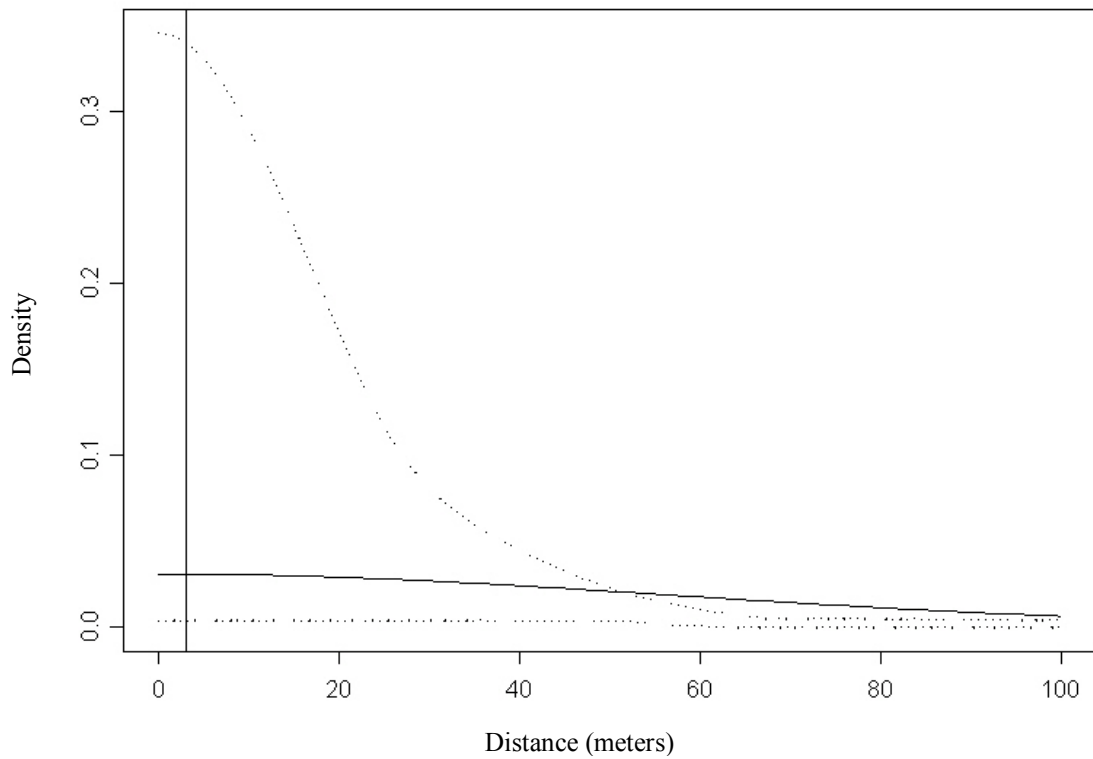


Figure 13--Stand E, Gaussian model

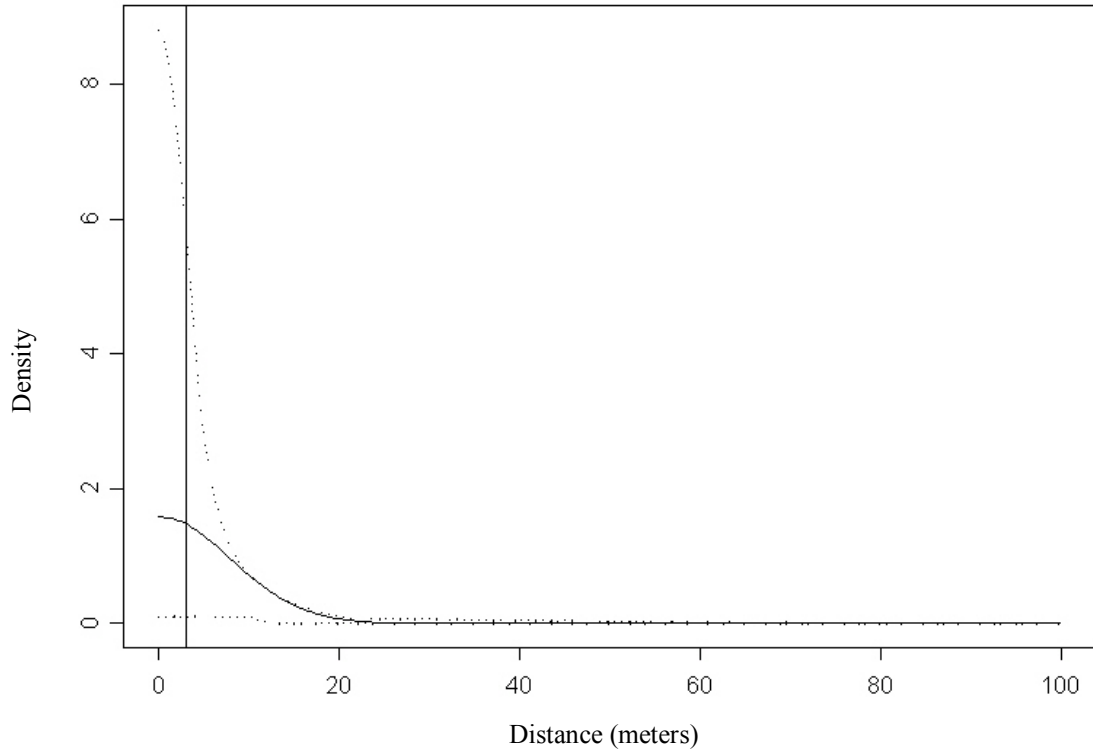


Figure 14--Stand F, Exponential model

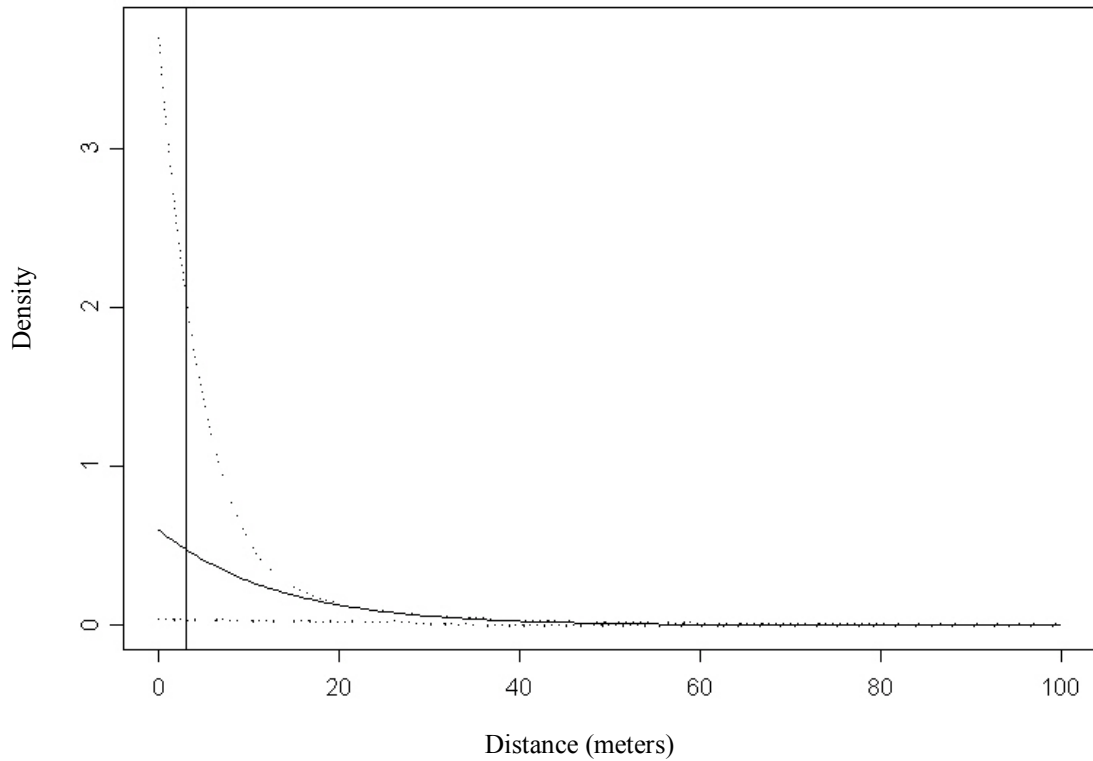


Figure 15--Stand F, 2Dt model

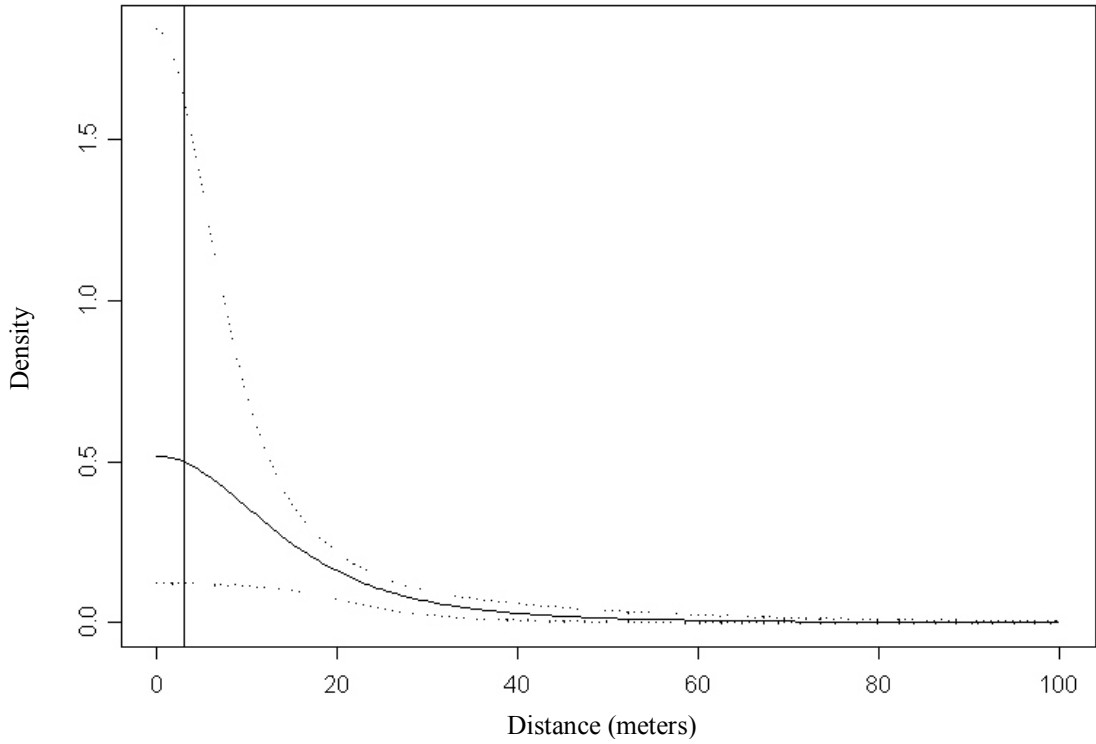


Figure 16--Stand G, Exponential model

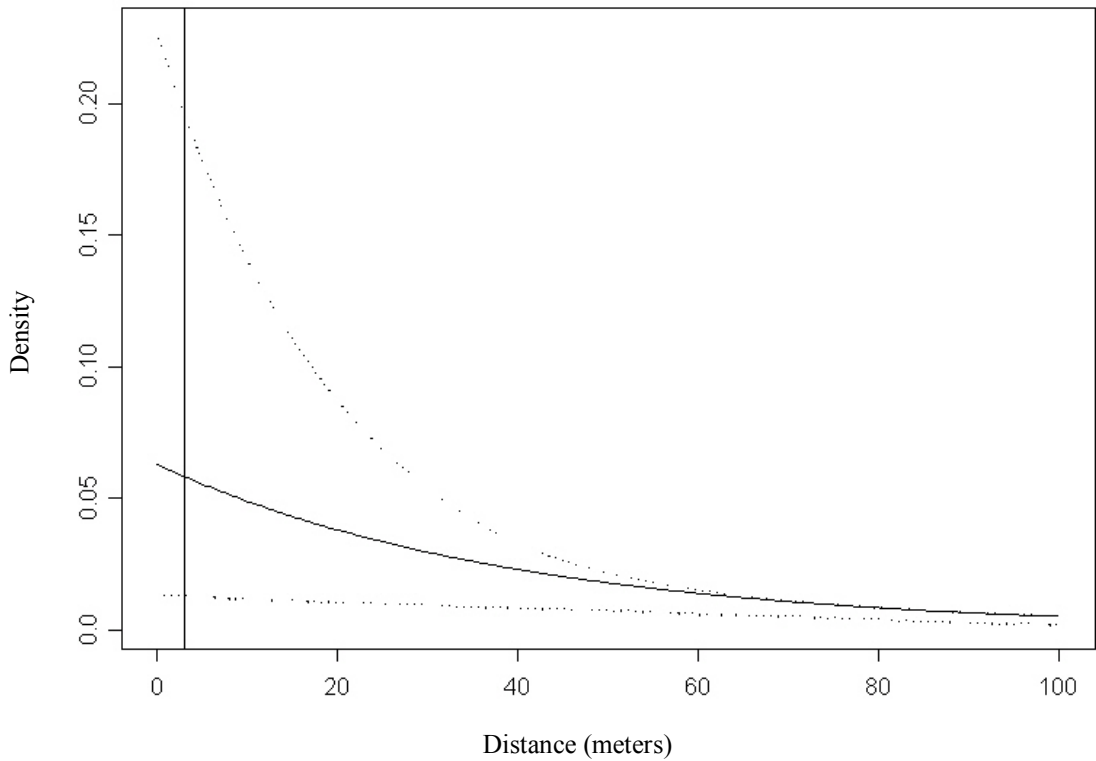


Figure 47--Stand G, Gaussian model

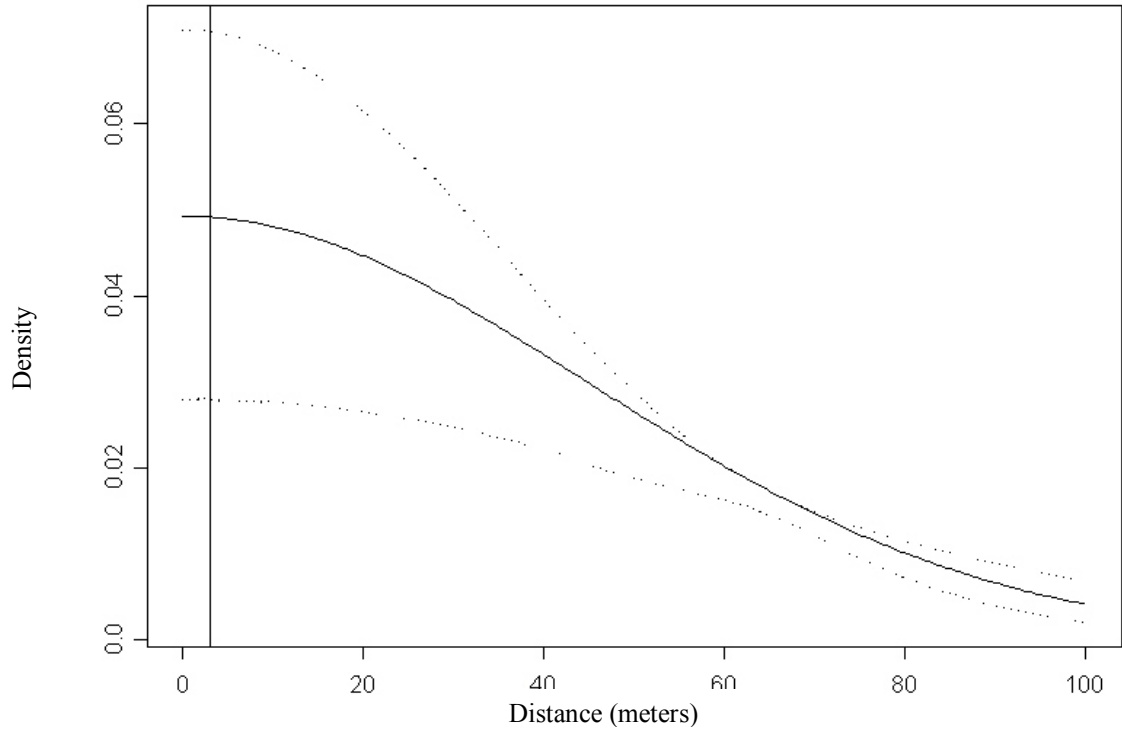


Figure 58--Stand H, Gaussian model

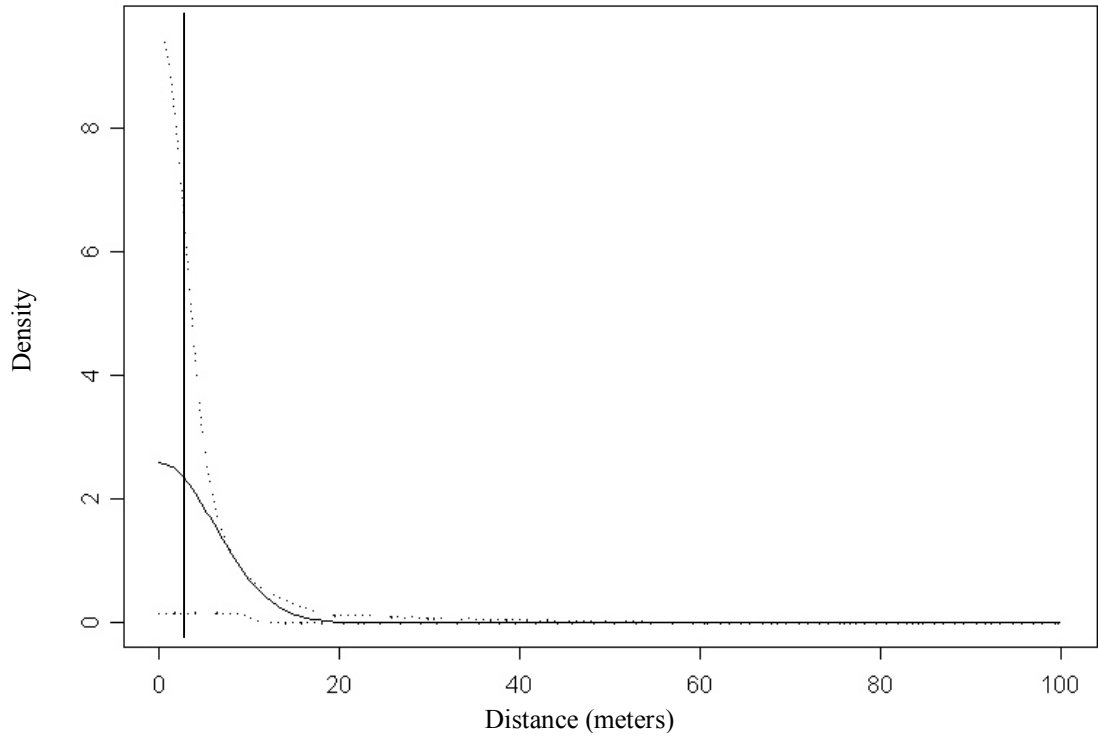


Figure 19--Stand H, 2Dt model

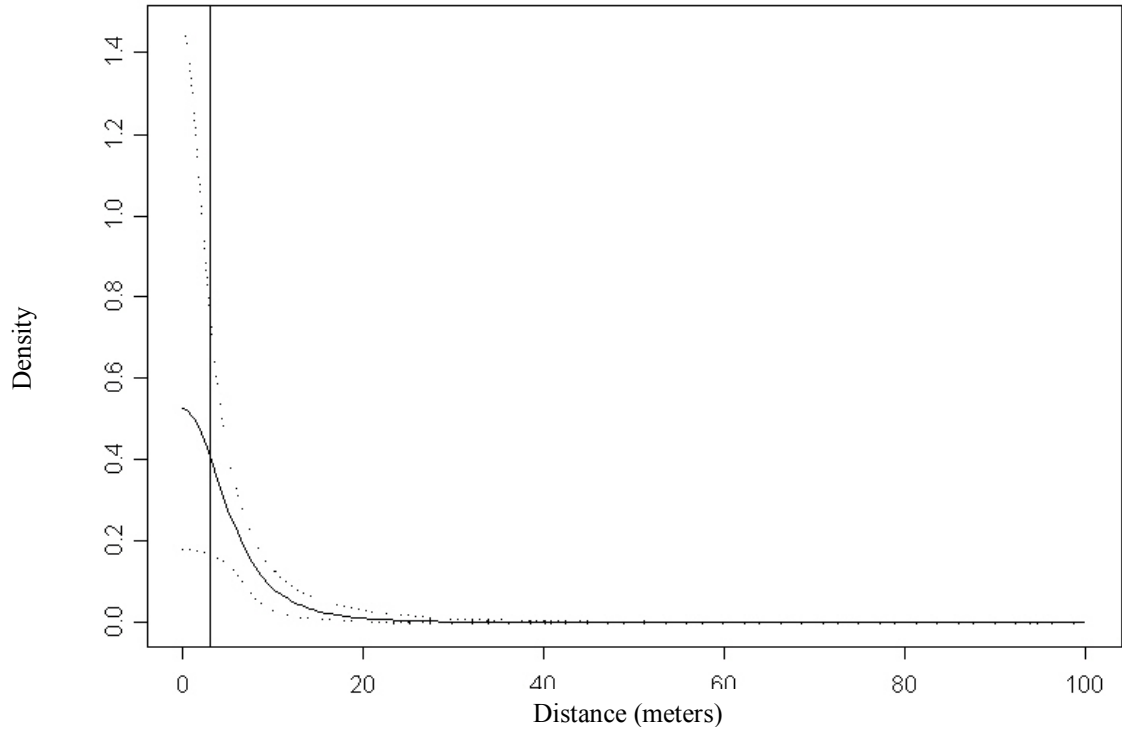


Figure 20--Stand J, Exponential model

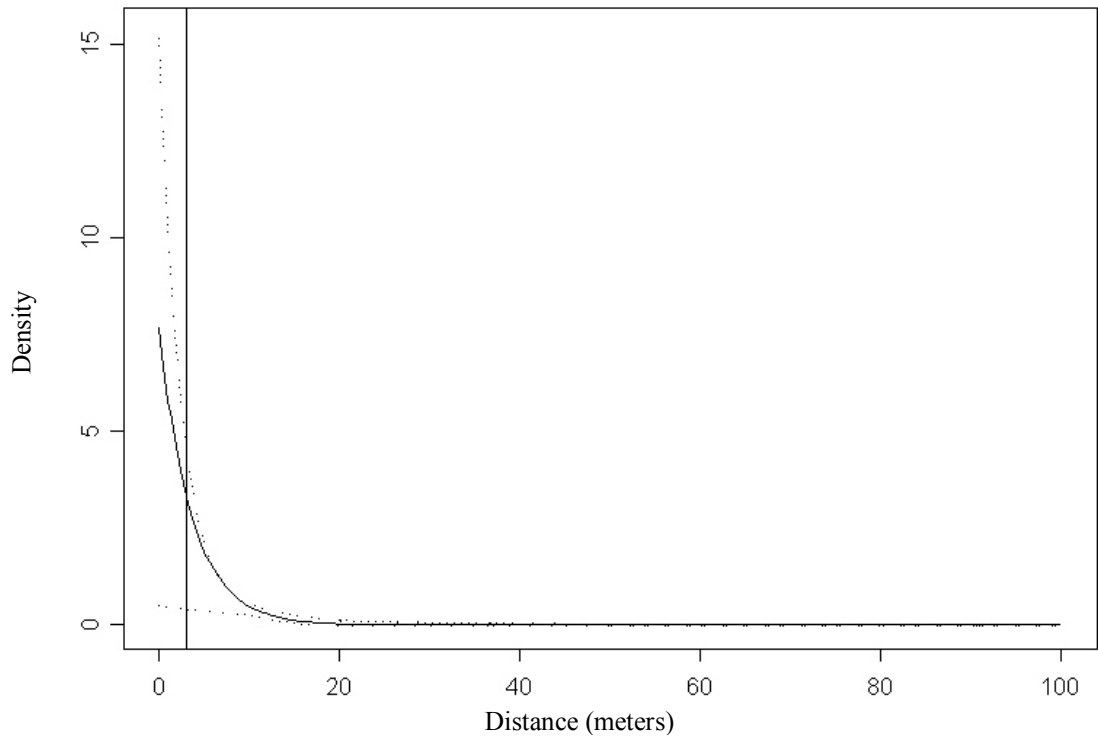


Figure 21--Stand J, Gaussian model

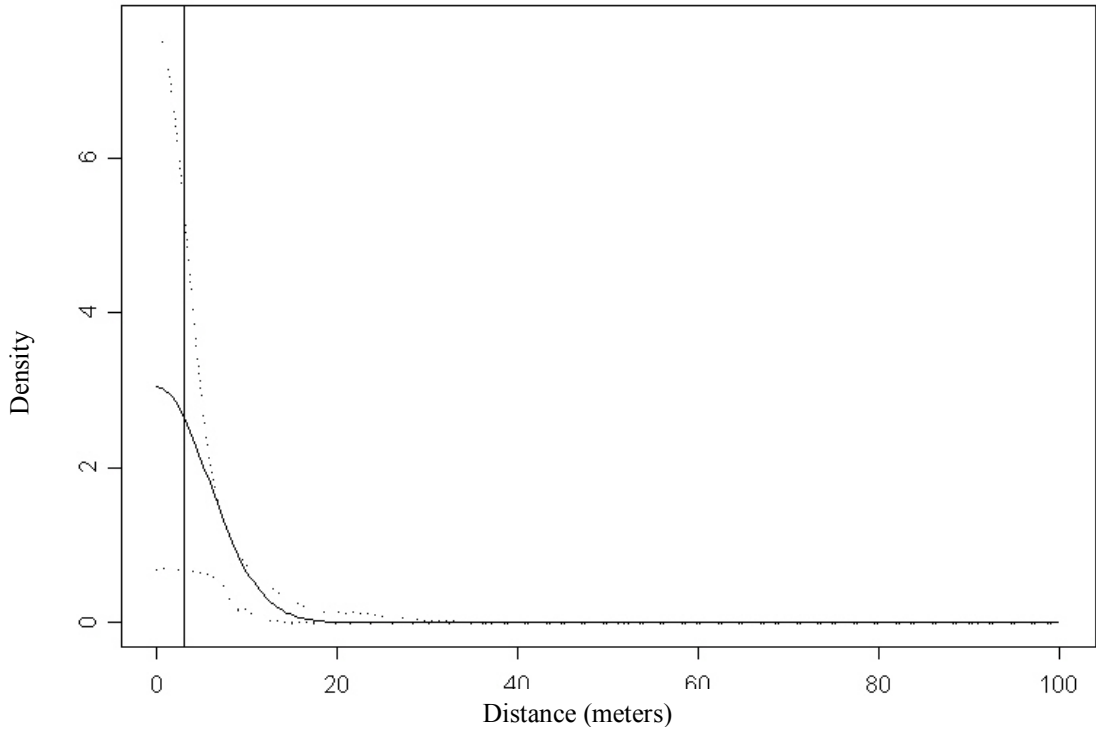


Figure 22--Stand J, 2Dt model

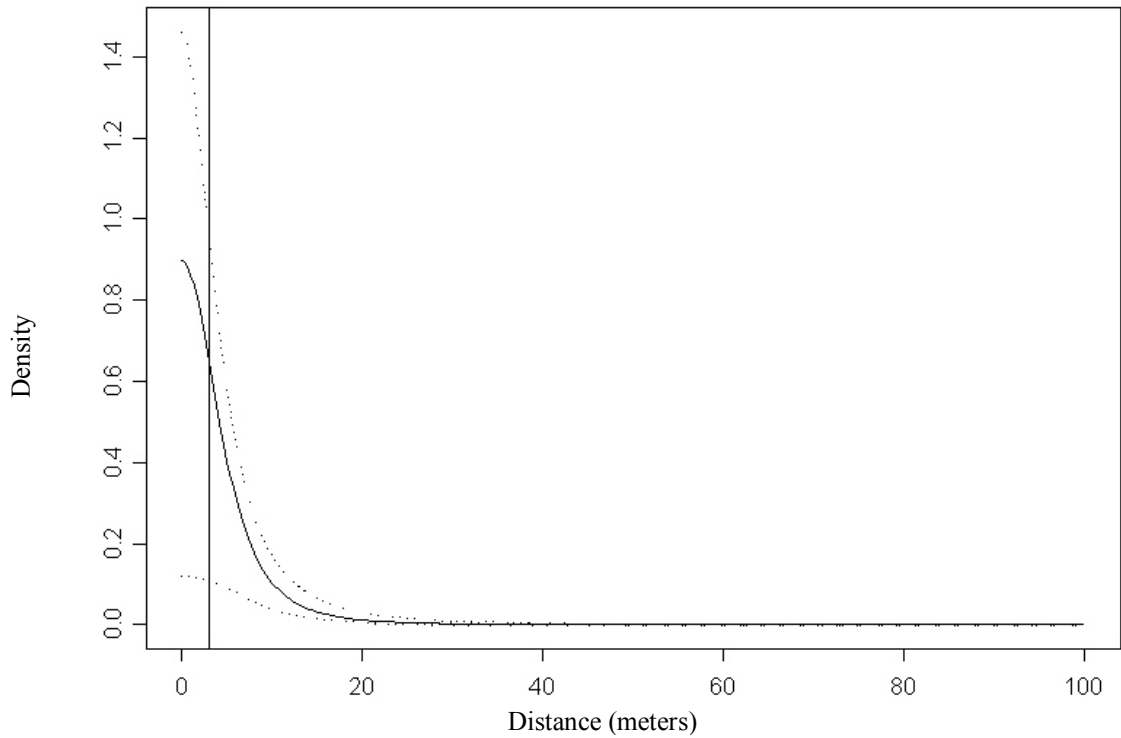


Figure 23--Stand K, Gaussian model

