

SPATIAL ANALYSES AND GROWTH OF TREES IN SELECTED
BOTTOMLAND HARDWOOD STANDS

A Dissertation

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ABSTRACT

Sustainable management and conservation of the extensive bottomland hardwood forest resource in the southeastern U.S. requires a good understanding of basic structural and competitive relationships within these forests. To gain an insight into these relationships, plot information from stands in Arkansas, Louisiana, and Mississippi were analyzed. The effects of individual tree attributes, distance-dependant, and distance-independent competition measures on 5-yr radial growth of red oak crop trees were examined. Selected species included cherrybark oak (*Quercus pagoda* Raf.), water oak (*Q. nigra* L.), and Nuttall oak (*Q. nuttallii* Palmer). Spatial continuity of tree variables was explored through geostatistical analysis. Finally, spatial distribution patterns of all species, the intraspecific pattern of cherrybark oak, water oak, and sweetgum (*Liquidambar styraciflua* L.), and the interspecific pattern of their pairs was examined with point pattern analysis.

In the analysis of 5-yr radial growth, the crown class score (from Meadows et al. 2001) accounted for a large portion of tree diameter growth. However, average plot-level characteristics failed to account for a significant proportion of the variability in tree growth. The basal area of trees taller than the crop trees and located within 2.5 mean crown radii had the highest negative correlation with crop tree 5-yr radial growth. Red oaks were likely exerting the greatest competition. Crop tree radial growth was also positively associated with the basal area of other red oaks taller than the crop tree and located between 3 and 4 mean crown radii from the crop tree (the indirect neighbors). Geostatistical analysis demonstrated that spatial continuity of unsuppressed tree attributes extended to a distance equal to 4 times the mean crown radius, suggesting that when resources are nonlimiting, multiple trees may be able to coexist and grow well in close proximity. Spatial point pattern analysis indicated that when species were

combined, they were frequently aggregated and sometimes overdispersed. Plots with larger trees were more likely to exhibit overdispersion suggesting a shift to this pattern as trees grow.

Interspecific and intraspecific pattern analyses suggested that strong interspecific competition resulted in species segregation, while weaker intraspecific competition led to aggregations of conspecifics.

CHAPTER 1

INTRODUCTION

The bottomland forest ecosystems of the southern United States, excluding the state of Kentucky, occupy almost 12 million hectares (Conner and Hartsell 2002). Southern bottomland forests represent 16% of all forest types in the region. These forests commonly occupy productive sites on major and minor stream bottoms (Hodges 1995). Bottomland forests are habitat for a large number of species, some of which are rare, and provide multiple benefits to their mostly non-industrial private owners and their communities (Smith and Linnartz 1980). Often located in areas that may experience flooding, bottomland forests provide environmental benefits through water quality enhancement, slowing down flood waters, and increasing sedimentation. Additional benefits from bottomland hardwood forests include reduction in soil erosion near stream channels and filtration of agricultural fields and roads runoff (Fulton and West 2002, West 2002).

Southern bottomland forests are often characterized by a complex vertical structure combined with a diverse species composition (Hodges 1995). A single tract of bottomland hardwood forest often contains over 50 tree species (Putnam et al. 1960), although those that attain commercial size are substantially fewer. Their complexity and the presence of intricate interspecific and intraspecific relationships complicate their management and make research both necessary and challenging. Despite their substantial economic, environmental, and aesthetic values, there are still many questions regarding basic processes and characteristics of bottomland forests that remain unexplored. The works of Putnam et al. (1960), Meadows (1994), Hodges (1997), and Meadows and Stanturf (1997) provide a useful synthesis of related research and characterize the geomorphology, origin, succession, inventory, silviculture, and management of

bottomland forests. Available publications address a plethora of additional research issues, but there are still interesting key research and management questions that have not been addressed in sufficient detail or at all. Some of them concern the effect of local competition on individual tree radial growth, spatial continuity (dependence) of some stand variables, and tree spatial distribution patterns and spatial interaction effects.

Research related to individual tree growth is crucial in light of the often employed silvicultural practice of crop tree management, by which individual high-quality trees from predetermined species are selected fairly early in the life of the stand with the intention to be kept throughout the rotation. Such crop trees are also selected on the basis of the value of the species for the landowner's objectives. An understanding of the influence of neighboring trees on the growth of the crop tree is critical. Providing the most favorable growing conditions through silvicultural operations to these crop trees during the rotation requires prior knowledge of the interspecific and intraspecific competition effects that may exist. For instance, studies with northern red oak (*Quercus rubra* L) in natural stands indicate that red oak starts to dominate over other species by the age of 40 yr, while after that the only serious competitors are other red oak species within the stand (Oliver 1978a, 1978b, Hibbs 1981, 1983). Hibbs and Bentley (1984), suggest that the red oaks, in the studied conditions, do not need to be as dense as other species at their early developmental stages, that oak release from competition is generally not needed, and that thinning should only be used when the oaks start to compete with other oaks. Kittredge (1988) confirms the notion of the importance of competition between trees of the same subgenus with the finding that the basal area increment of red oaks is more negatively correlated with the proportion of other red oaks in the same strata, rather than with oaks in the lower strata or with other species. An example of the implications of interspecific competition in bottomland settings

is presented by Clatterbuck and Hodges (1988) who found that cherrybark oak (*Quercus pagoda* Raf.) and sweetgum (*Liquidambar styraciflua* L.) stands exhibited “restricted” or “unrestricted” development patterns based on the spacing. The more dense stands (spacing of less than 5.5 m) resulted in the oaks being outgrown by the sweetgum during the first 20 to 25 years, which led to their greater merchantable height and smaller diameters compared to the oaks in the less dense stands. Such examples from the literature illustrate but a few of the many possible interactions among the dozens of tree species found to coexist in the bottomland forests and the significance of competition on stand development and management decision making.

Research related to competition effects on tree growth is based on two broad types of models (Munro 1974): (1) distance-independent models where the predictor variables represent mostly stand-level or plot-level characteristics, including density and basal area of all trees, or the basal area of only the trees with height or diameter above a certain threshold (Martin and Ek 1984, Daniels et al. 1986, Wykoff 1990, Wimberly and Bare 1996) (some authors include selected individual tree characteristics in this category) and (2) distance-dependent models developed to better account for the variation found in stand conditions with heterogeneous species composition, density, and spatial structure. These distance-dependent models range in their degree of complexity from some simpler ones that use intertree distances or competitor size (Daniels 1976, Martin and Ek 1984, Biging and Dobbertin 1992) to more elaborate models incorporating estimates of available growing space for the subject tree and influence zone overlaps (Spurr 1962, Opie 1968, Bella 1971, Hegyi 1974, Lin 1974). The distance-independent and distance-dependent models in the literature vary in their performance in accounting for tree growth with neither type having a clear advantage over the other.

To identify and successfully take advantage of basic underlying processes that could be responsible for the formation of observed or desired stand structures, some description and understanding of basic spatial features of tree distribution in bottomland forests is needed. A fairly recently implemented aid in the study of forest ecosystems is the set of spatial statistical tools called geostatistics (Isaaks and Srivastava 1989). It is a branch of spatial statistics that explores the spatial continuity (dependence) of a variable. It has been widely used in earth sciences and has become increasingly used in forestry and ecology. Among the capabilities of geostatistics is its power to explore how a variable varies over space and to determine the extent to which samples at different locations are spatially continuous. The application of geostatistics in forestry research has so far been limited, but expanding. A number of geostatistical analytical methods have been used in studies that examine tree-ring data (Meko et al. 1993), model stem size and growth (Biondi et al. 1994), analyze remote sensing data, (Treitz 2001), scale leaf area index to landscape scales (Burrows et al. 2002), examine spatial variation of throughfall (Loescher et al. 2002), and compare stand structure and spatial heterogeneity in stands subjected to different silvicultural treatments (Grushecky and Fajvan 1999).

Another branch of spatial statistics, which deals with the arrangement of the locations of discrete objects and examines various properties of their distribution pattern, is the spatial point pattern analysis (Diggle 1983). Its methods have a long history of use in the biological sciences. Early observations in the tropics (Wallace 1853, 1878) indicated how difficult it is to find two individuals of the same tree species in a tropical forest. Botanists Clark and Evans (1954) were among the first scientists to develop an effective measure of spatial distribution of plants with their nearest neighbor index. Spatial point pattern analysis has developed continuously through present time providing ecologists with valuable analytical tools. Most spatial distribution pattern

analysis applied to tree species has been performed in the tropics, as the forests there impressed researchers in the biological, ecological, and forestry fields with their diversity of species (Black et al. 1950, Janzen 1970, Connell 1971, Hubbell 1979). With the development of better techniques and methods for determining the spatial patterns of trees, the initial observations that conspecifics appear to be rather scattered and dispersed gave way to the acknowledgment that most species actually exhibit aggregation, which is also referred to as clumping (Hubbell 1979, Condit et al. 2000). Some relatively recent developments of this branch of spatial statistics (Lotwick and Silverman 1982) gave rise to a statistic that made it possible to ascertain bivariate spatial point patterns, i.e., how trees from two species interact spatially. Despite the enormous amount of work on spatial pattern analysis in the tropics and the work done in other regions, including some temperate forests (Rebertus et al. 1989, Aldrich et al. 2003, Call and Nilsen 2003), a review of the literature did not reveal work that explores the spatial patterns in bottomland hardwood forests of the eastern United States.

This study acknowledges the lack of research and knowledge of the influence of neighboring trees on tree radial growth and the effect of the neighboring trees distance, relative dimensions, and species on the growth of potential crop trees in bottomland hardwood stands. Moreover, it is believed that exploring the spatial patterns and the continuity of tree attributes in bottomland hardwood forests, will allow for a better insight and understanding of their structure and dynamics. These analyses should provide a better understanding of the interspecific and intraspecific interaction within these forests and provide a better understanding, and consequently lead to better thinning practices and management of the bottomland hardwood resource.

The specific objectives of the research presented in Chapter 2 are to determine the relationship between diameter growth, basal area growth of selected subject trees (crop trees) from the red oak subgenus (mostly cherrybark oak), and several plot level factors and factors related to their neighboring trees. The independent variables include distance-independent plot level variables, as well as a number of variables that take into account the distance to the subject tree. They include the basal area of trees from particular species and the basal area of trees of certain heights relative to the height of the subject tree. In each case the relationship of these groups of neighboring tree basal areas is studied at consecutive distances away within expanding circles and annuli around the subject tree.

In Chapter 3 this study examines the spatial continuity of tree basal area and crown projection area to determine the degree of “similarity” of tree parameters at consecutive distances away from each tree. Geostatistical analysis was used to reveal these relationships.

In Chapter 4 point pattern analysis was employed to explore the relative patterns of spatial distribution of (1) all species on individual plots, (2) three specific species – cherrybark oak, water oak, and sweetgum, and (3) the bivariate distribution patterns, i.e., presence of spatial segregation and aggregation between pairs of these three species. Conclusion from the previous three chapters and practical implications are presented in Chapter 5.

CHAPTER 2

FIVE-YEAR RADIAL GROWTH OF RED OAKS IN MIXED BOTTOMLAND HARDWOOD STANDS

2.1. Introduction

Tree competition has been a subject of substantial scientific interest in much of forestry research. Researchers often employ a variety of independent variables representing competitive effects to explain diameter, basal area, and other growth traits of individual trees. Some of these variables characterize the vigor and competitiveness of the chosen subject tree through its absolute or relative dimensions, while other variables account for the amount of competition exerted on the subject tree by surrounding trees. The variables reflecting potential tree competitiveness are primarily individual tree characteristics, some of which are relative to the tree's neighbors. Some of these variables include diameter, basal area, height, crown class, projected crown area, and portion of the crown exposed to direct sunlight. Measures of competition from the rest of the trees in the stand are classified by Munro (1974) and many subsequent publications (Dale et al. 1985, Daniels et al. 1986, Tome and Burkhart 1989, Biging and Dobbertin 1992, 1995) into two broad categories: distance-independent and distance-dependent competition measures (or indices). The distance-independent variables represent mostly stand-level or plot-level characteristics, including total basal area, density, and basal area of the trees with height or diameter above a certain threshold (Belcher et al. 1982, Martin and Ek 1984, Daniels et al. 1986, Wykoff 1990, Biging and Dobbertin 1995, Wimberly and Bare 1996). Accounting for the overall competition through use of distance-independent variables appears to be a good choice in many situations, particularly in monospecific plantations, where the trees are uniformly distributed and similar in size, growth, and age. Variables associated with attributes of

the individual trees, whose growth is modeled, are sometimes included in the distance-independent category.

To increase model relevance and improve the performance of growth models in stands that are heterogeneous in species composition or structure, models with higher spatial resolution are used. In these models local competition effects are accounted for by the proximity to competitors and their relative size with respect to a subject tree. A variety of distance-dependent measures developed by various authors range in complexity from some simpler ones based on the intertree distance and size (Aaltonen 1926, Daniels 1976, Martin and Ek 1984, Holmes and Reed 1991, Biging and Dobbertin 1992) to some more complex ones incorporating elements such as estimates of available growing space for the subject tree, point density indices, and influence zone overlaps between a subject tree and its competitors (Spurr 1962, Opie 1968, Hamilton 1969, Bella 1971, Hegyi 1974, Lin 1974, Miina and Pukkala 2002). The influence zone is usually defined as an area where the tree obtains or competes for resources (Opie 1968). Some studies have indicated, however, that the inclusion of intertree distance in the measure of competition does not necessarily improve model ability to account for the variation in tree growth (Lorimer 1983, Ganzlin and Lorimer 1983, Martin and Ek 1984, Biging and Dobbertin 1992). Nevertheless, in mixed species, multi-strata stands, distance-dependent measures of competition might provide a more accurate estimate of a heterogeneous neighborhood influence on individual trees.

One of the many difficulties associated with distance-dependent competition measures is identification of potential competitors. Such identification relates not only to proximity to the subject trees and their relative dimensions, but also to their species. Kittredge (1988) found that in mixed hardwood stands in New England, the basal area of only red oaks (subgenus

Erythrobalanus) in the overstory located within 10 m of northern red oak (*Quercus rubra* L.) subject trees is negatively correlated with the basal area growth of these subject trees. Taking into account other overstory species actually decreases the observed correlation suggesting that only the trees from the red oak group are exerting competitive stress on the crop trees or subject trees. Additionally, understory trees were found not to have negative effect on the basal area growth of overstory oak subject trees, suggesting that moisture and nutrients may not be a limiting factor on these sites and that competition in the root system zone is minimal when soil conditions are less limiting. An interesting question is whether trees located even farther away would have an indirect impact on subject tree growth.

Many of the published studies investigating competition among trees have been restricted to plantations, or to even-aged, monospecific stands with homogeneous structure (little variation in tree attributes). This may be why the knowledge of tree locations may be of little or no value in some models. Studies that are exceptions and have explored more heterogeneous stand conditions include studies with northern hardwoods (Lorimer 1983, Holmes and Reed 1991, Cole and Lorimer 1994), mixed conifer species (Biging and Dobbertin 1992), and upland hardwoods (O'Neal et al. 1994). The review of the literature did not, however, reveal similar studies in naturally regenerated southern bottomland hardwood forests. Consideration of spatial relationships and species may be important in modeling growth of individual trees in such forests, because they are fairly complex in structure and represent highly heterogeneous mixtures of species (Smith and Linnartz 1980). Putnam (1960) notes that a single tract of land can have as many as 50 different tree species, although not all of them are considered commercially important.

The current study attempts to fill a gap in our knowledge related to the competitive interactions influencing radial growth of selected crop trees from subgenus *Erythrobalanus* (hereafter referred to as red oaks) in bottomland hardwood stands. The study examines the ability of subject tree vigor and attributes, and neighborhood tree characteristics to account for the observed 5-yr crop tree growth in diameter and basal area. A period of 5 yr is typical for such studies. It is considered of appropriate length because it is long enough to demonstrate characteristic growth patterns without some possible annual interference, but is short enough to avoid violating the assumption for unchanged canopy position of plot trees (Kittredge 1988).

Several previous studies established that species from the red oak subgenus exert more intense competition on northern red oak (*Quercus rubra* L.) crop trees in New England than do other associated species (Oliver 1978b, Hibbs and Bentley 1984, Kittredge 1988). It is therefore suggested that in mixed-species stands early thinning to release the oaks is unnecessary unless they are entirely overtopped. It is indicated that initial oak density does not need to be much higher than the desired density of an oak dominated stand at the end of a rotation. Oliver (1978b), however, suggests maintaining about a third greater density, which he terms “insurance factor”. The current study examines if the findings for northern red oak in New England are also applicable to the studied southern species of red oaks, i.e., that red oaks appear to be the major competitors of other oak crop trees in the same strata. Such relationship would have the management benefit of possibly reducing thinning efforts aimed at releasing oak trees in some mixed southern bottomland stands.

Rather than add to the existing wide array of competition indices or testing their performance, this study tried to uncover underlying competitive or mutualist interactions and associations, especially with consideration to spatial properties. This entailed the collection of

data on tree spatial locations on a local coordinate system, many of their attributes, and harvesting of selected individual red oak trees to examine the radial growth over the previous 5-yr period.

2.2. Materials and Methods

2.2.1. Study Areas

The study was conducted in relatively undisturbed naturally regenerated stands in major and minor stream bottomlands in the southern United States. The oak component criteria for stand selection included the presence of cherrybark oak (*Quercus pagoda* Raf.), the species of main interest, and a visually estimated red oak component of at least 10% by basal area. The stands were selected to be naturally regenerated, with mixed-species composition, even-aged, and established over 40 yr ago. Initial reconnaissance was used in each stand to select crop trees within areas that met the search criteria. Potential plots were selected with a crop tree serving as the plot center. Geographic positioning system (GPS) coordinates were recorded for the plot center of each potential plot. Three plots were then randomly selected from among the 12 or more potential plots.

A total of 4 bottomland hardwood stands from a three-state area were selected for the study (Table 2.1). The site in central Louisiana, located in St. Landry Parish, is on a major stream bottom of the Mississippi River that is no longer hydrologically attached to the river. The remaining three sites are on minor stream bottoms: one located in Jackson Parish (Cypress Creek) in northern Louisiana, one in Drew County (Hungerrun Creek) in southeastern Arkansas, and one in Oktibbeha County (Noxubee River) in northeastern Mississippi. The stands were naturally regenerated, growing on either clay loam or silt loam soils, with little or no harvesting since establishment (Table 2.1).

Table 2.1. General study site characteristics.

State	Parish or County	Stream type ^b	River or stream name	Plot number	Age ^a (yr)	Time since most recent thinning (yr)	Soils
Central Louisiana	St. Landry Parish	Major	Mississippi River	1	83	25	Clay loam (fine montmorillonitic, thermic Vertic Epiaqualfs)
				2	75		
				3	75		
Northern Louisiana	Jackson Parish	Minor	Cypress Creek	1	71	12	Silt loam (fine-silty, siliceous, thermic Typic Glossaqualfs)
				2	61		
				3	72		
Arkansas	Drew County	Minor	Hungerrun Creek	1	76	Not cut	Silt loam (fine-silty, siliceous, thermic Fluventic Dystrochrepts)
				2	67		
				3	75		
Mississippi	Oktibbeha County	Minor	Noxubee River	1	46	Not cut	Clay loam (fine, montmorillonitic, thermic Vertic Halpudalfs)
				2	61		
				3	74		

^aAge on the plots estimated from annual ring count of basal tree sections of one to three overstory red oak trees, i.e., from genus *Quercus* and subgenus *Erythrobalanus*

^bStream type classified as major and minor. Major stream bottoms are defined as large streams with deep and minerally diverse alluvium brought from very large distances, while minor stream bottoms are floodplains and terraces with small streams and somewhat shallower alluvium with local origin (Hodges and Switzer 1979, Hodges 1997)

The stands were assumed to have a relatively even-aged overstory. Many mixed hardwood stands establish after major disturbances and most trees occupy the site within a relatively short period of time (Oliver 1978a, 1980). Further canopy stratification is usually a result of species-specific height growth pattern and biological limitation, rather than substantial age differences.

Three plots were established in each of the 4 stands for a total of 12 plots. One to 3 overstory red oaks subject trees on each plot were harvested for a total of 32 trees. Their average age was considered an indicator of stand age. Tree ages were determined by counting the rings of the cross-section obtained from the tree base. Stand ages for the central Louisiana, northern Louisiana, Arkansas, and Mississippi stands were determined to be 78, 68, 73, and 60 yr, respectively. The 32 subject trees were from three species represented by 22 cherrybark oaks, 9 water oaks (*Q. nigra* L.), and 1 Nuttall oak (*Q. nuttallii* Palmer). Their dbh ranged from 28.8 cm to 66.3 cm. For the purposes of this study, species differences among the three oaks (Burns and Honkala 1990) were not taken into consideration and all were combined for the analysis because they do occur naturally in the same stands and are from the same subgenus. The value of ΔD was calculated as the average 5-yr radial growth measured in 8 directions for a cross section, multiplied by two. Eight radii were used for calculating the basal area growth as well. The more radii measured, the higher the precision in determining the basal area. This is especially true for cross sections whose shape significantly deviates from perfect circle.

2.2.2. Data Collected

All potential plots had a dominant or codominant cherrybark oak subject tree at the center of the plot. Cases where at least one adjacent tree in the same strata was a red oak were preferred for the pool of potential plots. Square plots enclosing 0.64 ha were used for this study. All plot

trees with diameter at breast height (dbh, 1.37 m above ground) greater than 10.0 cm (pulpwood size) were flagged and numbered. The dbh, species, coordinates on the plot, and crown class were recorded. The crown classification used was developed by Kraft (1884) (as cited by Assmann 1970), and later modified to its present form by Smith et al. (1997). Total tree height and crown radius in the four cardinal directions were collected for all dominant, codominant, and intermediate trees. Two overstory trees that were immediate neighbors of the central tree, as defined by “touching” crowns or proximity, were selected and later harvested with the central tree and used for growth measurements. For the central tree and the 2 selected neighbor trees, the radius of the vertical crown projection was measured in eight directions and a numeric crown class score was determined as described by Meadows et al. (2001). This crown classification scoring system assigns numeric values to the tree crown according to the following four criteria: (1) direct sunlight from above - values from 0 to 10; (2) direct sunlight from the sides - values from 0 to 10; only the upper half of the crown is used; (3) crown balance - values from 1 to 4 are assigned according to the number of quadrants occupied by 20% or more of the total crown volume; (4) relative crown size - values from 1 to 4 are assigned for appropriate crown size and density as related to a tree of that diameter and species; one point is assigned if crown size and density are considered to be severely limiting to growth, two points if limiting to growth, three points if somewhat limiting to growth, and four points if not limiting to growth. The point values for the criteria are then summed, and crown class is assigned in accordance with these categories: 24-28 points: dominant; 17-23 points: codominant; 10-16 points: intermediate; and 2-9 points: suppressed.

The dbh was measured with a diameter tape, while the tree locations were determined using a laser hypsometer-rangefinder for the distances and a digital angle encoder for the

horizontal angles. During the mapping procedures the horizontal distance and the angle from North were measured from locations within the plot to each tree. These measured distances and angles were later transformed to Cartesian coordinates (to the nearest 0.01 m). The laser hypsometer-rangefinder was also used for measuring tree height. The edges of the vertical crown projections were determined with a densitometer (GRS, Arkata, CA, USA), unless severe crown overlapping existed, to ensure vertical viewing. The distance from the center of the bole to the projected crown edge was measured with the laser hypsometer-rangefinder or a measuring tape. Diameters were measured to the nearest mm, horizontal angles to the nearest 0.01° , and distances and heights to the nearest cm.

Cross sections about 4 cm thick were obtained from the base, breast height, and every meter to the top of each harvested tree. The cardinal directions were marked on the bark at 1.37 m height prior to felling and on the cross section at that height after felling. The cross sections were placed in plastic bags as soon as they were obtained. The samples were stored at a temperature of 5°C for about 2-4 weeks before measurements. The annual radial growth for the previous 5 full years was measured from the sections obtained from breast height. The samples were planed and sanded and the radius was measured with a tape along a line from the pith in the four cardinal directions and in four additional radii at 45 degrees from the cardinal directions. The annual growth was measured through a video image of the cross section (single axis rapid advance UniSlide measuring stage with ACU-RITE encoder, Acu-Rite Co Inc, Jamestown, NY, USA, and Metronics Qwickcheck DRO with resolution 0.002 mm, Metronics Inc, Bedford, NH, USA).

Trees were harvested from April through June of 2002 on the sites in central Louisiana, northern Louisiana, and Arkansas. Trees in Mississippi were harvested in March of 2003.

Therefore, the 5-yr radial growth measured for these trees occurred in growing seasons 1997 through 2001 on all but the Mississippi site, where the growth was examined from 1998 through 2002.

Since no prior measurements were available, an assumption was made that the data collected for the plot trees, except for the harvested trees initial diameter, represents the initial condition in the stand, i.e., 5 yr ago. It is indeed likely that tree relative dimensions and canopy status probably change little over a 5-yr period. Other studies that have made similar assumptions are also available in the literature (e.g., Holsoe 1948, Hatch et al. 1975, Kittredge 1988).

2.2.3. Analysis

Regression models were developed for the 5-yr diameter growth (ΔD) of the harvested red oak trees. Regression models were also developed for their 5-yr basal area growth (ΔBA). Subject tree ΔBA was selected as dependent variable as it more accurately represents tree growth in volume compared to ΔD , which was used so comparisons with published studies can be readily available. Some differences in the results of the two dependent variables are to be expected, as the same diameter growth in two trees with different initial diameters will result in greater basal area growth in the tree with larger initial diameter.

Three classes of independent variables were used in the regression models for both ΔD and ΔBA . These classes were: individual tree variables (of the subject trees), distance-independent (or plot level) variables, and distance-dependent variables.

Individual Tree Variables. The individual tree variables were initial tree dbh (the diameter of the tree 5 yr prior to cutting); initial basal area (the basal area of the tree 5 yr prior to cutting); crown class score (from Meadows et al. 2001); sum of the score for direct sunlight from

above and from the sides (from Meadows et al. 2001); crown diameter; crown projection area (crown projection area was calculated as the sum of the areas of eight 1/8th circle areas with their respective radii from the crown projection); and tree height.

Distance-independent Variables. The distance-independent (or plot level) variables were the basal areas for each of the following 4 subclasses: all trees with dbh>10.0 cm; all unsuppressed trees; all red oak trees; and all unsuppressed red oak trees.

Distance-dependent Variables. The third class of independent variables, the distance-dependent variables, included 3 subclasses. Subclass 1 was $BA_{j,k,m}$ - total basal area (BA) of the trees that satisfy conditions j , k , and m . In these subclasses j indicates which trees are included in the calculation of neighborhood basal area according to their height relative to the subject tree, with each height category being above certain percent of the height of the subject tree. The relative height categories for j include “all hts”, i.e., trees of all heights were included in the calculation of neighborhood basal area; and heights of 80 and 100%, indicating that the neighbor tree height had to be equal or larger than that percent of subject tree height for the neighbors to be included in the calculation of basal area. The k represents species and has values “all species” or “red oak species”, i.e., species from the red oak subgenus. Finally, m indicates the radii of circles about the subject tree from 2.0 m to 21.5 m in 1.5 m increments. If the center of the tree bole of a certain tree was within the examined distance and it satisfied conditions for species and minimal height, its basal area was included. Therefore, a designation $BA_{100\%, \text{ red oaks}, 15.0\text{m}}$ for example, indicates the basal area (BA) of the trees that are equal in height or taller than the subject tree (100%), are red oaks (red oaks), and are within a distance of 15.0 m from the subject tree (15.0m).

Subclass 2 was $BA_{j,k,p}$ - total basal area (BA) of the trees that satisfy conditions j , k , p , where p represents an annulus (the space between two concentric circles) between X and $(X + \Delta X)$ meters from the subject tree, where the radius X ranges from 2.0 m to 21.5 m in 1.5 m increments, and ΔX ranges from 1.5 m to 19.5 m in 1.5 m increments, where A is an integer from 1 to 13, and $(X + \Delta X)$ does not exceed 21.5 m (Figure 2.1). For illustration only three radii X are shown as an example on figure 2.1, which yields 3 possible circles and 3 annuli. In the calculations for the study there were 14 circles and 91 annuli. Thus, a designation $BA_{100\%, \text{red oaks}, 3.5-15.0\text{m}}$ for example, indicates the basal area (BA) of the trees that are equal in height or taller than the subject tree (100%), are red oaks (red oaks), and are between 3.5 and 15.0 m from the subject tree (3.5-15.0m).

Subclass 3 consisted of competition indices calculated for the independent variables from subclasses 1 and 2. Their form was similar to competition index 1 in Cole and Lorimer (1994) and had a form of the following expression:

$$C = \frac{\sum BA}{BA_i} \quad (1)$$

where C is the dimensionless competition index, or competition index, based on relative basal area, BA_i is the basal area of the subject tree, and $\sum BA$ is the sum of the basal areas of the trees in the circles and annuli as described in subclass 1 and 2 respectively. Intertree distance is considered the distance from the center of the base of one tree to the center of the base of another and not the distance between adjacent crown edges.

The score for direct sunlight from above and from the sides (derived by using two of the four criteria of crown class score of Meadows et al. (2001) by summing up the score for direct sunlight from above with the score for direct sunlight from the sides) was examined to determine

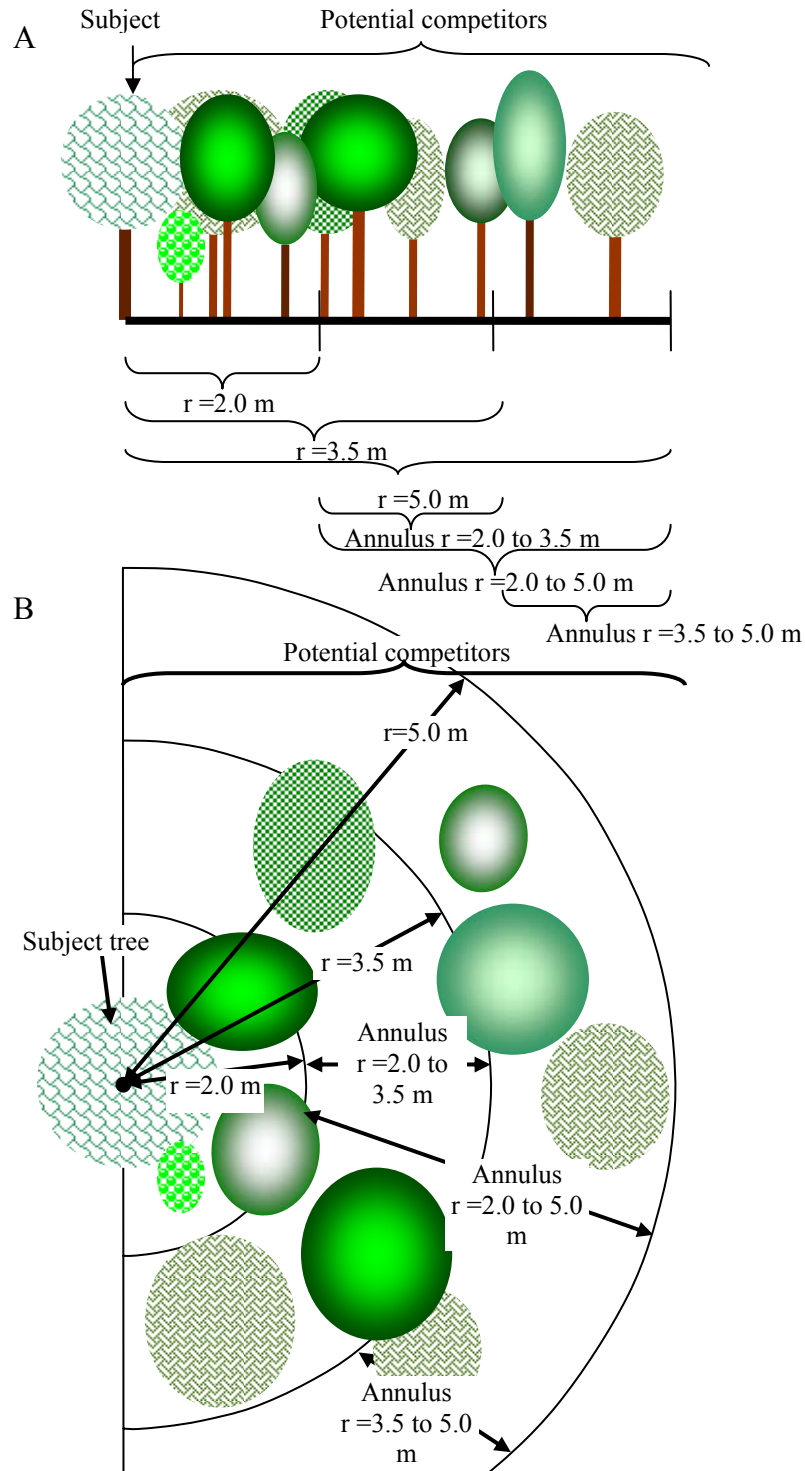


Figure 2.1. Semicircle side view (A) and top view (B) representation of the method for determining the basal area (BA) of potential competing trees within concentric circles, with radius r and annuli (concentric bands) centered on the harvested subject tree. The basal area was summed for each circle and annulus starting from the subject tree up to a distance of 21.5 m. Only three intervals are illustrated for simplification. The actual number of intervals was 14, resulting in 14 circles and 91 annuli.

if accounting for only the amount of direct sunlight received by the crown was sufficient to explain the variation in radial growth. If excluding the remaining two criteria, crown balance and relative crown size, does not result in decrease in the variance in ΔD and ΔBA accounted for, then using only these criteria instead of all 4 would be justified and this would potentially save field time.

The performance of each group of predictor variables was examined in relation to their ability to account for the variability in ΔD and ΔBA of the harvested trees. In the simple linear regression models a predictor variable was considered significant if the slope had a p-value of less than 0.05, while in the multiple linear regression models a variable had to have a p-value of over 0.15 to be entered. Multiple regression models were tested where the dependent variables were ΔD or ΔBA and predictor variables for each were (1) the individual tree variables, (2) the distance-independent variables, (3) the distance-dependent variables, and (4) variables from all three groups.

The variable selection procedure used in the multiple regression models was stepwise regression (SAS v.9). The best model was considered the model where all variables were significant, the model appeared adequate for the data (determined by examining the residuals) and had highest adjusted coefficient of multiple determination and lowest corrected sum of squares. The coefficient of multiple determination always increases with the addition of more independent variables to the model, whether or not they are good predictors. The adjusted coefficient of multiple determination, however, can actually decrease when a new variable is introduced in the model. For a variable to stay in the model it had to contribute significantly (according to its p-value) to accounting for the variability in the dependent variable in combination with other selected variables. Some of the predictor variables were derived from

others and were consequently either highly or perfectly correlated. For example the initial basal area was derived from the initial diameter; crown diameter was used for calculating crown projection; and the direct sunlight from above was derived from the crown class score.

Therefore, none of these variable pairs were allowed in the same model together.

Multicollinearity was evaluated by employing the variance inflation factor (VIF). As few predictor variables as reasonable were kept in the models, because a regression model with numerous variables are difficult to maintain and an overfitted model will often result in variances of the estimated parameters that are larger than those of simpler models (Neter et al. 1996).

Additionally, models with limited number of variables are easier to work with and understand (Neter et al. 1996). Some variable transformations, namely log-normal transformations, utilized in some of the literature in this area of research (e.g., Cole and Lorimer 1994) were also considered and used as recommended in the statistical literature (Neter et al. 1996).

For observations that appeared as outliers, the Bonferroni simultaneous test procedure was performed with significance level of $\alpha = 0.10$. The critical value was $t(1 - \alpha / 2n; n-p-1)$, where n is the total number of observations and p is the number of model parameters. In cases where the calculated value was larger than the value of the studentized deleted residual, the observations were not considered outliers and were therefore kept.

2.3. Results

The number of trees with diameters larger than 10.0 cm ranged from 309 to 614 trees per hectare, with a mean of 476 ± 109 (Table 2.2). Red oaks accounted for 5% to 43% of the total number of trees per plot and 13% to 73% of the basal area. On the average, red oaks represented $22 \pm 12\%$ of the trees and $42 \pm 20\%$ of the basal area, indicating that red oaks were among the trees with largest diameters. Stocking was calculated using the guide for southern bottomland

Table 2.2. Summary of stand and plot characteristics at the four study locations

Location	Years for which growth was modeled	Plot number	Number of trees per plot	Density (trees/ha)	Proportion in red oak trees ^a (%)	BA ^b (m ² /ha)	Proportion of BA in red oaks (%)	Stocking ^c (%)
Central Louisiana	1997-2001	1	198	309	32	28.59	66	104
		2	242	378	27	32.39	46	119
		3	222	347	29	32.81	60	119
		Mean	221	345	29	31.26	57	114
Northern Louisiana	1997-2001	1	332	519	13	33.44	35	127
		2	370	578	21	31.03	47	120
		3	380	594	9	31.59	23	122
		Mean	361	564	14	32.02	35	123
Arkansas	1997-2001	1	278	434	33	32.02	55	119
		2	259	405	27	24.75	46	94
		3	252	394	43	29.06	73	108
		Mean	263	411	35	28.61	59	107
Mississippi	1998-2002	1	393	614	13	29.72	21	116
		2	381	595	5	36.50	13	139
		3	348	545	6	32.41	19	124
		Mean	374	585	8	32.88	17	126

^aRed oaks refers to species from genus *Quercus* and subgenus *Erythrobalanus*

^bBA = basal area or cross-sectional area of all tree stems

^cStocking calculated by the formula in Goelz (1995) and modified here for metric units:

$$S = 0.033927 \text{ TPH} + 0.060254 (\text{TPH})(\text{QMD}) + 0.023725 (\text{TPH})(\text{QMD})^2$$

where S=stocking (%), TPH= Trees Per Hectare, QMD= Quadratic Mean Diameter (cm)

hardwoods from Goelz (1995). Only one of the twelve plots had stocking under 100% (Table 2.2). Plot stocking ranged from 94% to 139% and averaged $118 \pm 12\%$. Thirty-two of the harvested trees were red oaks and according to the crown class system of Meadows et al. (2001) 20 of the red oaks were classified as dominants, 10 as codominants, and 2 as intermediates. The limited number of intermediate trees and the absence of suppressed trees in the dataset is a result of the study's focus on the growth of crop trees. Crop trees are usually chosen from the upper crown classes.

2.3.1. Individual Tree Variables

2.3.1.1. Simple Linear Regression Models

The potential relationships between ΔD and the individual tree variables were evaluated with simple linear regression analysis. The relationships inferred from scatterplots and plots of residuals suggested that the use of linear regression models were justified. The independent variables with significant slopes with ΔD (Table 2.3) show that the crown class score (Meadows et al. 2001) alone explained 41% of the variability in ΔD . The amount of direct sunlight from above and from the sides, a variable derived from the crown class system of Meadows et al. (2001), accounted for 36% of the variability in ΔD of the harvested trees. Tree height was also a significant variable, but its coefficient of determination of 0.14 was much lower than the coefficient of determination of the crown class score.

All of the considered individual tree predictor variables were highly significant in the regression models with the second dependent variable, ΔBA (Table 2.3). Initial tree diameter and initial basal area accounted for nearly half of the variability in ΔBA . The crown-based tree attributes, crown diameter and crown projection, had coefficients of determination of 0.43 and 0.42, respectively, while the crown class score explained 30% of ΔBA variation. The amount of

Table 2.3. General statistics from simple linear regression models

Independent variables	ΔD				ΔBA			
	Intercept	Slope	r^2	P-value	Intercept	Slope	r^2	P-value
Initial tree diameter	16.94520	0.21052	0.06	0.188	-62.42458	5.22039	0.50	<0.001
Initial tree basal area	22.83222	0.00243	0.04	0.298	65.61440	0.07181	0.45	<0.001
Crown class score ^a (Meadows et al. 2001)	-9.55467	1.56442	0.41	<0.001	-78.24814	11.02387	0.30	0.001
Score for direct sunlight from above and from the sides ^b (Meadows et al. 2001)	-5.22612	1.92362	0.36	<0.001	-51.78357	13.79919	0.26	0.003
Crown diameter	18.80316	0.73097	0.05	0.204	-7.57523	17.30023	0.43	<0.001
Crown projection area	22.70582	0.03598	0.05	0.197	86.97524	0.83115	0.42	<0.001
Tree height	0.28742	0.80950	0.14	0.034	-204.90362	11.74045	0.43	<0.001

^{a,b}Calculation of the crown class score and the scores for direct sunlight from above and from the sides (Meadows et al. 2001) are explained in detail in Methods

direct sunlight from above and from the sides alone accounted for 26% of the variability in ΔBA for the harvested trees, which was only 4 percentage points less than when using all four components of the crown class score. The remaining individual tree variable, tree height, was found to be more significant in the models for ΔBA than in those for ΔD , with a correspondingly higher coefficient of determination of 0.43 compared to 0.14 in the ΔD prediction.

2.3.1.2. Multiple Linear Regression Models

It was not possible to obtain a multiple regression model for the dependent variable ΔD with the individual tree variables included in this study, because after the independent variable crown class score is entered into the model, none of the remaining variables were significant (at the 0.15 level). Crown class score accounted for 41% of the variability in ΔD . Implementation of log transformations on both the predictor and predicted variables, resulted in an increase in the coefficient of determination value to 0.54 (Table 2.4).

On the other hand, the selected model for ΔBA contained two independent variables, had an R^2 of 0.71, and both predictor variables were highly significant (Table 2.4). The selected variables were the initial diameter and the crown class score. The values of the standardized estimates of the two regression coefficients revealed that the relative importance of the two variables was approximately equal in the fitted model.

2.3.2. Distance-independent Variables

The use of distance-independent, or plot-level variables, was not as successful as the use of individual tree variables in explaining the variation in the dependent variables ΔD and ΔBA . The scatterplots of the two dependent variables versus each of the distance-independent plot variables revealed no particular patterns. In the simple linear regression models for ΔD and ΔBA , there was no predictor variable that was significant. Similarly, the multiple regression models,

Table 2.4. Selected regression models for the dependent variables 5-yr diameter growth at breast height (dbh, 1.37 m above ground) growth (ΔD) and 5-yr basal area growth (ΔBA). The models were obtained after selection from among all individual tree variables: diameter and basal area of the harvested tree 5-yr prior to cutting, crown class score (from Meadows et al. 2001), score for direct sunlight from above and from the sides (from Meadows et al. 2001), crown diameter, crown projection area, and tree height. Variables were included in the model if they were significant at the 0.15 level

Dependent variable	Independent variable	Parameter estimate	Standardized parameter estimate	P-value	R ²
ln ^a (ΔD)	Intercept	-1.97401	0	0.030	0.54
	ln(crscore ^b)	1.66127	0.73216	<0.001	
ln(ΔBA)	Intercept	-4.27738	0	<0.001	0.71
	ln(INIDBH ^c)	1.20341	0.54796	<0.001	
	ln(CRSCORE)	1.52946	0.53906	<0.001	

^aln is the natural logarithm

^bCRSCORE is the crown class score (Meadows et al. 2001)

^cINIDBH is the initial diameter (5 full growing seasons prior to cutting)

consisting of combinations of the distance dependent variables, failed to account for any significant amount of the variability of either one of the dependent variables.

2.3.3. Distance-dependent Variables

For the distance-dependent variables, variation in ΔD and ΔBA was related to the basal area of the trees with height greater than or equal to 80% of the height of the harvested subject trees ($BA_{80\%, \text{ all species}}$) and located within consecutive concentric circles and annuli around the subject tree. Trees with such heights are probably tall enough to influence the crowns of the subject trees and their basal area may provide an indication of competition on the subject trees. For the dependent variable ΔD , there were two annuli in which $BA_{80\%, \text{ all species}}$ was a significant predictor at $\alpha = 0.05$. These were the 2.0 to 8.0 m annulus (i.e., $BA_{80\%, \text{ all species}, 2.0-8.0\text{m}}$ – the basal area of the trees of all species whose height is equal to or greater than 80% of the height of the subject tree and are located in the 6-m-wide annulus that is between 2.0 and 8.0 m away from the subject tree) and the 3.5 to 8.0 m annulus (Table 2.5). The basal area in these two annuli accounted for 16% of the variability in ΔD . For the response variable ΔBA there were no circles or annuli where $BA_{80\%, \text{ all species}}$ was significant.

The independent variable $BA_{80\%, \text{ red oak species}}$ consisted of the basal area of red oaks located in concentric circles and annuli around the subject tree. There were six annuli where $BA_{80\%, \text{ red oak species}}$ was significant at $\alpha = 0.05$ (Table 2.5). Using the $BA_{80\%, \text{ red oak species}}$ instead of $BA_{80\%, \text{ all species}}$ resulted in a 4 percentage points increase in variability explained for the 2.0 to 8.0 m annulus but a 2 percentage points decrease for the 3.5 to 8.0 m annulus. The annulus for which the r^2 was highest was again 2.0 to 8.0 m. Other annuli where $BA_{80\%, \text{ red oak species}}$ was also significant were 2.0 to 11.0 m, 2.0 to 12.5 m, 2.0 to 14.0, and 2.0 to 15.5 m, and the variance accounted for ranged from 13 to 20%. There were no circles or annuli where tree basal area

Table 2.5. General statistics regarding the coefficients of determination (r^2) and P-values (p) for simple linear regressions with independent variables: (1) basal area of trees from all species whose height is equal to or greater than 80% of the height of the subject tree ($BA_{80\%, \text{ all species}}$); (2) basal area of trees from the red oak species (subgenus *Erythrobalanus*) whose height is equal to or greater than 80% of the height of the subject tree ($BA_{80\%, \text{ red oak species}}$); and (3) basal area of trees from all species regardless of their height ($BA_{\text{all hts, all species}}$). The basal areas are of trees located within concentric circles and annuli^a centered at the subject tree. The dependent variables are the 5-yr diameter growth (ΔD) and the 5-yr basal area growth (ΔBA). Only the circles and annuli where basal area was a significant predictor ($p \leq 0.05$) are shown. The slope of all regression models was negative

Annuli radii (R) (m)		$BA_{80\%, \text{ all species}}$				$BA_{80\%, \text{ red oak species}}$				$BA_{\text{all hts, all species}}$			
		ΔD		ΔBA		ΔD		ΔBA		ΔD		ΔBA	
Inner R	Outer R	r^2	p	r^2	p	R^2	p	r^2	p	R^2	p	r^2	p
5.0	6.5									0.20	0.01		
2.0	6.5									0.14	0.04		
2.0	8.0	0.16	0.02			0.20	0.01			0.17	0.02		
2.0	9.5												
2.0	11.0					0.15	0.03						
2.0	12.5					0.13	0.04						
2.0	14.0					0.15	0.03						
2.0	15.5					0.14	0.03						
3.5	6.5									0.16	0.02	0.15	0.03
3.5	8.0	0.16	0.02			0.14	0.03			0.19	0.01		
5.0	8.0									0.15	0.03		

^aAn annulus is the space between two concentric circles

explained a significant amount of the variability in the second dependent variable of ΔBA .

Unlike the previous two distance-dependent variables, $BA_{\text{all hts,all species}}$ (basal area of all trees, regardless of their height and species) included the suppressed trees. In this case the annulus accounting for the most variability (20%) in ΔD was from 5.0 to 6.5 m. The basal areas in several more annuli were significant predictor variables (Table 2.5), but all were fairly similar in their ability to account for the variability in ΔD (14 to 19%). For the dependent variable ΔBA , the only annulus where $BA_{\text{all hts,all species}}$ was significant was the 3.5 to 6.5 m annulus, accounting for of 15% of the variance.

Another predictor variable tested as a measure of competition was the basal area of trees that were taller than the subject tree and regardless of their species - $BA_{100\%,\text{all species}}$. The basal area of these trees in the 3.5 to 11.0 m annulus appeared to explain the greatest amount of variability (46%) in ΔD of the subject trees (Table 2.6). Other highly significant annuli with $r^2 > 0.40$ were 2.0 to 11.0 m ($r^2 = 0.45$), 2.0 to 8.0 m ($r^2 = 0.43$), and 3.5 to 8.0 m ($r^2 = 0.42$). For ΔBA , the annuli whose basal area accounted for the most variability in subject tree basal area growth were similar to those for diameter growth, but they all had lower coefficients of determination (Table 2.6). The $BA_{100\%,\text{all species}}$ of the trees at a distance between 2.0 and 11.0 m had the highest coefficient of determination (0.25) with ΔBA .

Using the basal area of only the red oak trees taller than the subject trees ($BA_{100\%,\text{red oak species}}$) did not contribute to a better model fit. As evident from Table 2.6, the exclusion of the non-oak species reduced the variance accounted for across nearly all annuli.

The competition index C (related to relative basal area) from equation (1) was calculated for each of the circles and annuli for the five distance-dependent predictor variables ($BA_{80\%,\text{all species}}$, $BA_{80\%,\text{red oak species}}$, $BA_{\text{all hts,all species}}$, $BA_{100\%,\text{all species}}$, $BA_{100\%,\text{red oak species}}$) and regressed

Table 2.6. Coefficients of determination (r^2) and P-values for simple linear regressions with independent variables: (1) basal area of trees from all species with height equal to or greater than the subject tree height ($BA_{100\%, \text{all species}}$), and (2) basal area of trees from the red oak species (subgenus *Erythrobalanus*) with height equal to or greater than the subject tree height ($BA_{100\%, \text{all species}}$). The basal areas are of trees located within concentric circles and annuli^a centered at the subject tree. Only circles and annuli where basal area was a significant predictor ($p \leq 0.05$) of the 5-yr diameter growth (ΔD) or 5-yr basal area growth (ΔBA) are shown. The slope of all regression models was negative

Annuli radii (R) (m)		$BA_{100\%, \text{all species}}$				$BA_{100\%, \text{red oak species}}$			
		ΔD		ΔBA		ΔD		ΔBA	
Inner R	Outer R	r^2	P	r^2	P	r^2	p	r^2	p
6.5	8.0	0.20	0.010			0.18	0.017		
9.5	11.0	0.20	0.010			0.20	0.013		
2.0	5.0	0.13	0.039	0.15	0.026				
2.0	6.5	0.23	0.005	0.18	0.015	0.14	0.036	0.14	0.034
2.0	8.0	0.43	<0.001	0.23	0.005	0.37	<0.001	0.21	0.009
2.0	9.5	0.34	<0.001	0.18	0.015	0.27	0.002	0.13	0.044
2.0	11.0	0.45	<0.001	0.25	0.004	0.41	<0.001	0.21	0.009
2.0	12.5	0.36	<0.001	0.19	0.012	0.31	<0.001	0.15	0.027
2.0	14.0	0.31	<0.001	0.22	0.006	0.30	0.001	0.16	0.023
2.0	15.5	0.24	0.004	0.17	0.017	0.26	0.003		
2.0	17.0	0.25	0.003	0.20	0.010	0.28	0.002	0.14	0.036
2.0	18.5	0.19	0.013	0.20	0.010	0.25	0.003	0.14	0.035
2.0	20.0	0.13	0.040	0.20	0.011	0.16	0.023		
2.0	21.5			0.20	0.011				
3.5	6.5	0.21	0.008	0.16	0.025				
3.5	8.0	0.42	<0.001	0.22	0.007	0.35	<0.001	0.18	0.015
3.5	9.5	0.33	<0.001	0.17	0.020	0.24	0.004		
3.5	11.0	0.46	<0.001	0.24	0.004	0.40	<0.001	0.19	0.013
3.5	12.5	0.36	<0.001	0.18	0.014	0.29	0.001	0.14	0.04
3.5	14.0	0.31	<0.001	0.22	0.007	0.29	0.002	0.15	0.038
3.5	15.5	0.24	0.005	0.17	0.019	0.25	0.003		
3.5	17.0	0.25	0.003	0.20	0.010	0.28	0.002	0.13	0.041
3.5	18.5	0.19	0.013	0.20	0.011	0.25	0.004	0.13	0.039
3.5	20.0	0.13	0.040	0.19	0.011	0.15	0.027		

(table 2.6 continued)

Annuli radii (R) (m)		BA _{100%} , all species				BA _{100%} , red oak species			
Inner R	Outer R	ΔD		ΔBA		ΔD		ΔBA	
		r ²	P	r ²	P	r ²	P	r ²	p
5.0	8.0	0.26	0.003			0.24	0.004		
5.0	9.5	0.21	0.009			0.15	0.027		
5.0	11.0	0.39	<0.001	0.18	0.016	0.35	<0.001	0.14	0.033
5.0	12.5	0.29	0.002	0.13	0.044	0.24	0.004		
5.0	14.0	0.24	0.004	0.16	0.024	0.23	0.005		
5.0	15.5	0.18	0.015			0.21	0.009		
5.0	17.0	0.20	0.010	0.15	0.029	0.23	0.006		
5.0	18.5	0.15	0.026	0.16	0.022	0.21	0.009		
5.0	20.0			0.16	0.022	0.13	0.045		
5.0	21.5			0.17	0.019				
6.5	9.5	0.15	0.030						
6.5	11.0	0.38	<0.001	0.18	0.017	0.32	<0.001		
6.5	12.5	0.28	0.002			0.21	0.008		
6.5	14.0	0.22	0.007	0.15	0.027	0.20	0.010		
6.5	15.5	0.16	0.025			0.17	0.017		
6.5	17.0	0.17	0.027	0.14	0.035	0.20	0.011		
6.5	18.5	0.14	0.037	0.16	0.024	0.18	0.014		
6.5	20.0			0.16	0.024				
6.5	21.5			0.17	0.020				
8.0	11.0	0.13	0.041						
9.5	12.5	0.13	0.042						

^aAn annulus is the space between two concentric circles

against the two dependent variables: ΔD and ΔBA . Simple linear regression models showed that dividing the summed basal area of the competitors by the basal area of the subject tree improved the amount of variance accounted for (Table 2.7). The largest coefficients of determination associated with the use of the competition indices were 0.53 for ΔD and 0.49 for ΔBA . Regardless of the independent variable used, the strongest relationships with ΔD and ΔBA were achieved with the basal area of the trees located within part of or the entire 2.0 to 11.0 m annulus (Table 2.7, Figure 2.2, Figure 2.3).

The increase in basal area of the neighbors in the annuli around the subject trees was associated with a decrease in ΔD and ΔBA (Figure 2.4). This was observed for most annuli, but there were exceptions. One such exception occurred with the 14.0 to 17.0 m annulus (Figures 2.5a and 2.5b). The scatterplots of ΔD and ΔBA were plotted against the basal area of the red oak trees that were taller than the subject tree. No meaningful relationship could be discerned from the scatterplots for this annulus. Closer inspection of the two plots showed that when there was no competition present ($BA_{100\%, \text{red oak species}, 14.0-17.0\text{m}} = 0$) within this annulus there was a substantial variability in the resulting growth (Figures 2.5a and 2.5b). The exclusion of the datapoints where $BA_{100\%, \text{red oak species}, 14.0-17.0\text{m}} = 0$ however, reveals a relationship for both dependent variables which was not observed for any other annulus. The relationship was such that the parameter estimates of the slopes were positive and the increase in the amount of competition in this annulus corresponded to an increase, rather than decrease, in growth in both diameter and basal area. After excluding the cases where there were no competitors in the 14.0 to 17.0 m annulus, the resulting simple linear regression model could account for as much as 30% of the variability in ΔD ($P=0.06$, $n=12$) and 41% of the variability in ΔBA ($P=0.02$, $n=12$). Unfortunately, excluding the observations with no competitors in the studied annulus reduced the

Table 2.7. Annuli^a radii with basal area (BA) most highly correlated with the 5-yr growth in diameter (ΔD) and basal area (ΔBA). The slope of all regression models was negative

Independent variable	ΔD		ΔBA	
	Annulus ^a (m)	r^2	Annulus (m)	r^2
BA _{80%} , all species	2.0 to 8.0	0.16		
	3.5 to 8.0	0.16		
C(BA _{80%} , all species)	2.0 to 8.0	0.21	2.0 to 11.0	0.49
	3.5 to 8.0	0.21	3.5 to 11.0	0.49
BA _{80%} , red oak species	2.0 to 8.0	0.20		
C(BA _{80%} , red oak species) ^b	2.0 to 11.0	0.32	2.0 to 11.0	0.42
BA _{all hts} , all species	5.0 to 6.5	0.20	3.5 to 6.5	0.15
C(BA _{all hts} , all species)	5.0 to 6.5	0.30	3.5 to 9.5	0.49
			3.5 to 11.0	0.49
BA _{100%} , all species	3.5 to 11.0	0.46	2.0 to 11	0.25
C(BA _{100%} , all species)	3.5 to 8.0	0.53	3.5 to 11.0	0.43
	3.5 to 11.0	0.53		
BA _{100%} , red oak species	2.0 to 11.0	0.41	2.0 to 8.0	0.21
			2.0 to 11.0	0.21
C(BA _{100%} , red oak species)	2.0 to 11	0.50	2.0 to 11.0	0.39

^aAn annulus is the space between two concentric circles

^bThe competition index (C) is calculated by the formula $C = BA_i^{-1} * (\sum BA_{j,k})$, where BA_i is the basal area of the subject tree, and $\sum BA_{j,k}$ is the sum of the basal areas of the trees that satisfy conditions j and k , where j indicates the minimum height of the trees relative to the height of the subject tree and has values of either “all hts”, 80%, or 100% of the height of the subject tree, and k represents the species and takes values “all species” or “red oak species”, i.e., species from the red oak subgenus (*Erythrobalanus*)

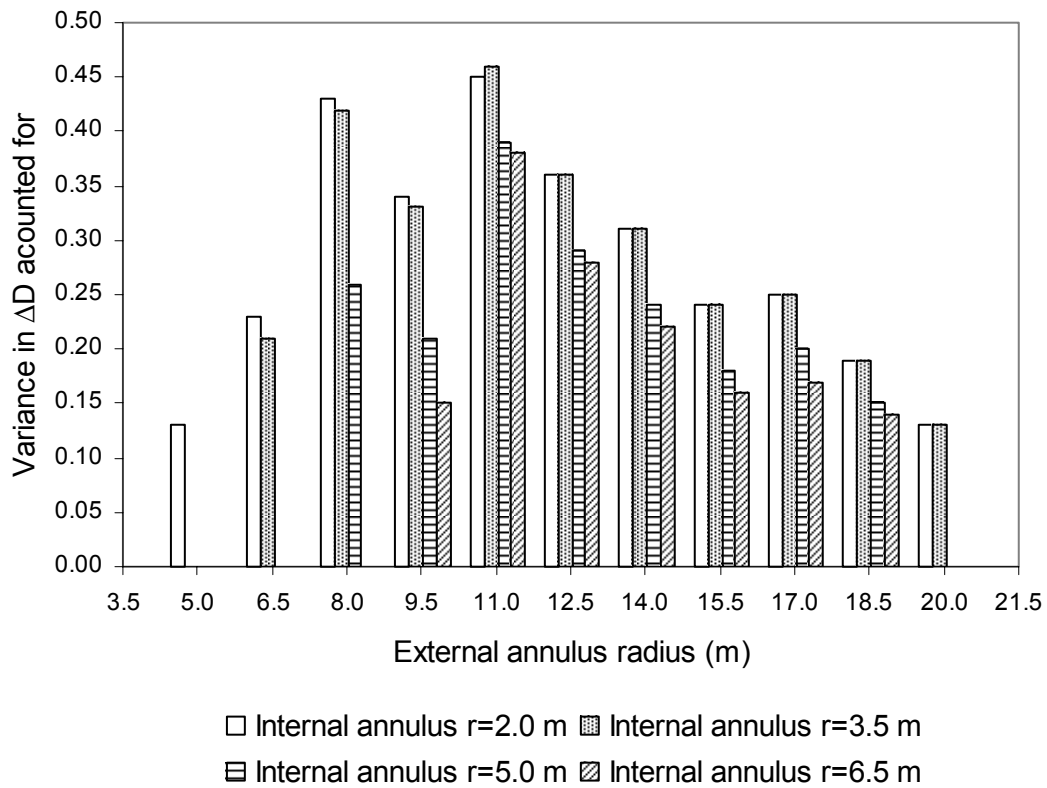


Figure. 2.2. Coefficients of determination for 5-yr diameter growth (ΔD) from simple linear regression models. The independent variables are the basal areas of all trees that are equal in height or taller than the subject tree and located within specific concentric annuli around the it.

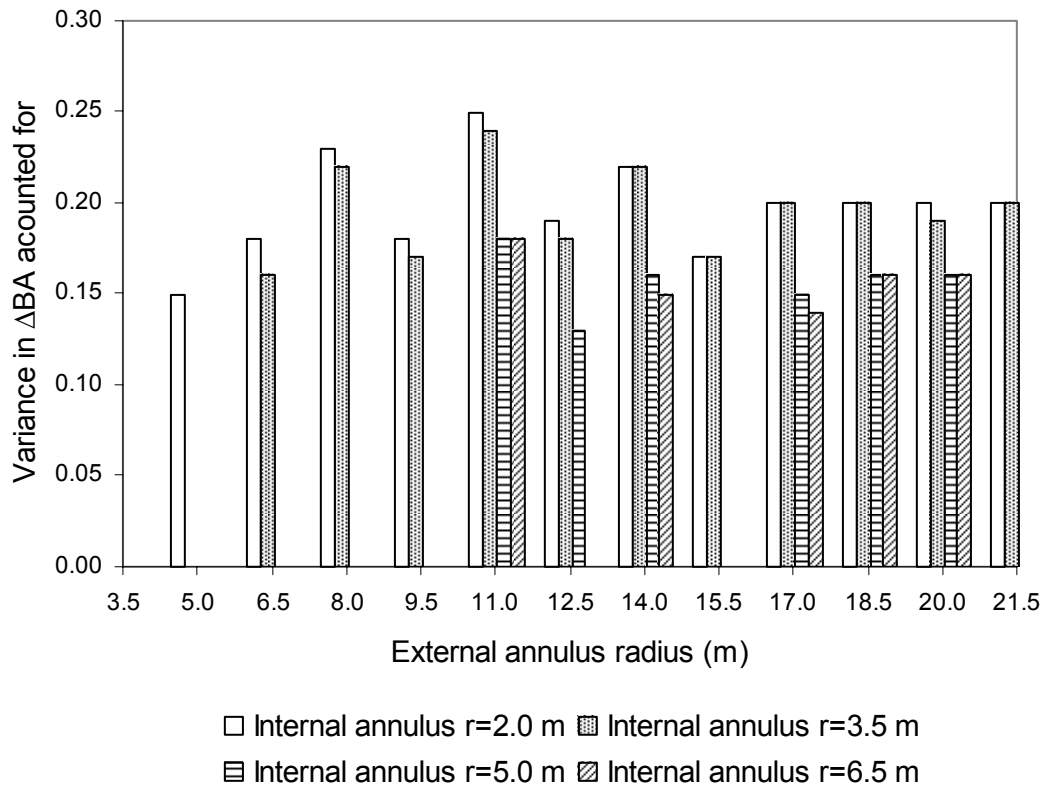


Figure. 2.3. Coefficients of determination for 5-yr basal area growth (ΔBA) from simple linear regression models. The independent variables are the basal areas of all trees that are equal in height or taller than the subject tree and located within specific concentric annuli around it.

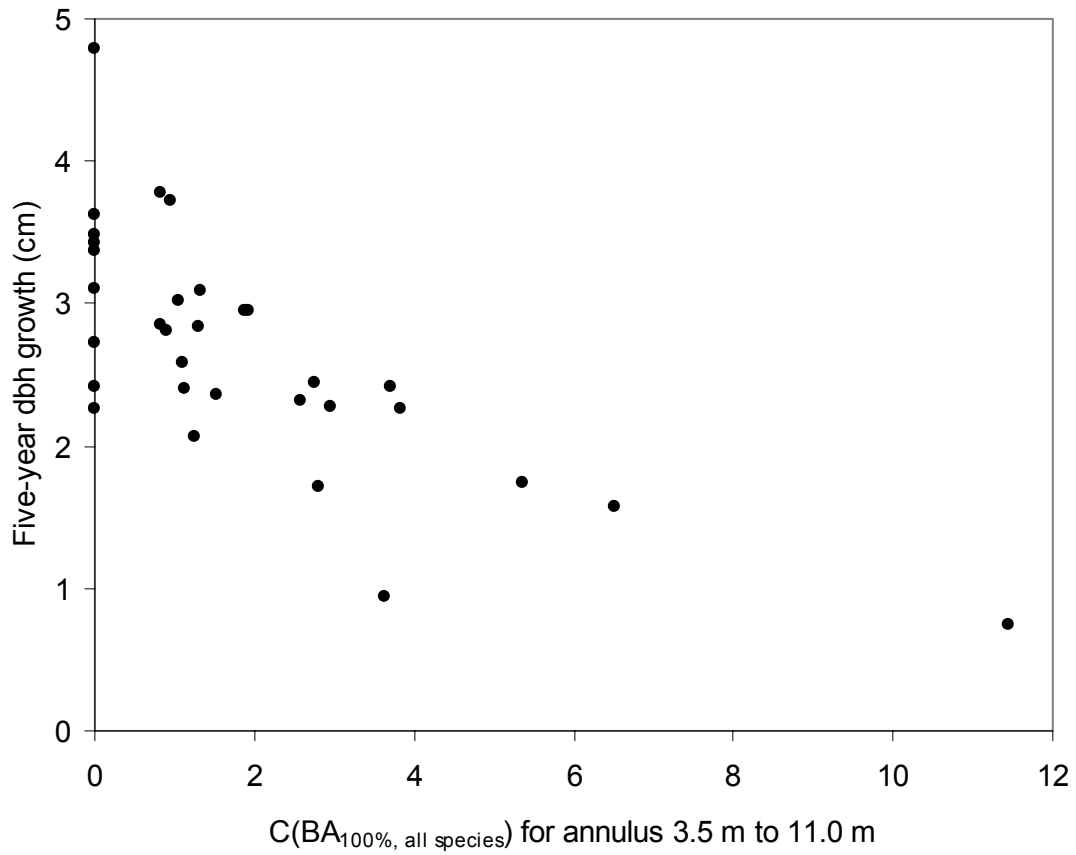


Figure 2.4. Plot of 5-yr diameter at breast height (dbh, 1.37 m) growth versus the competition index (C), where C is calculated by the formula: $C = \frac{\sum BA}{BA_i}$, where BA_i is the basal area of the subject tree, and $\sum BA$ is the sum of the basal areas of the trees that are taller than the subject tree regardless of their species ($BA_{100\%, \text{all species}}$) and are located in the annulus from 3.5 m to 11.0 m away from the subject tree.

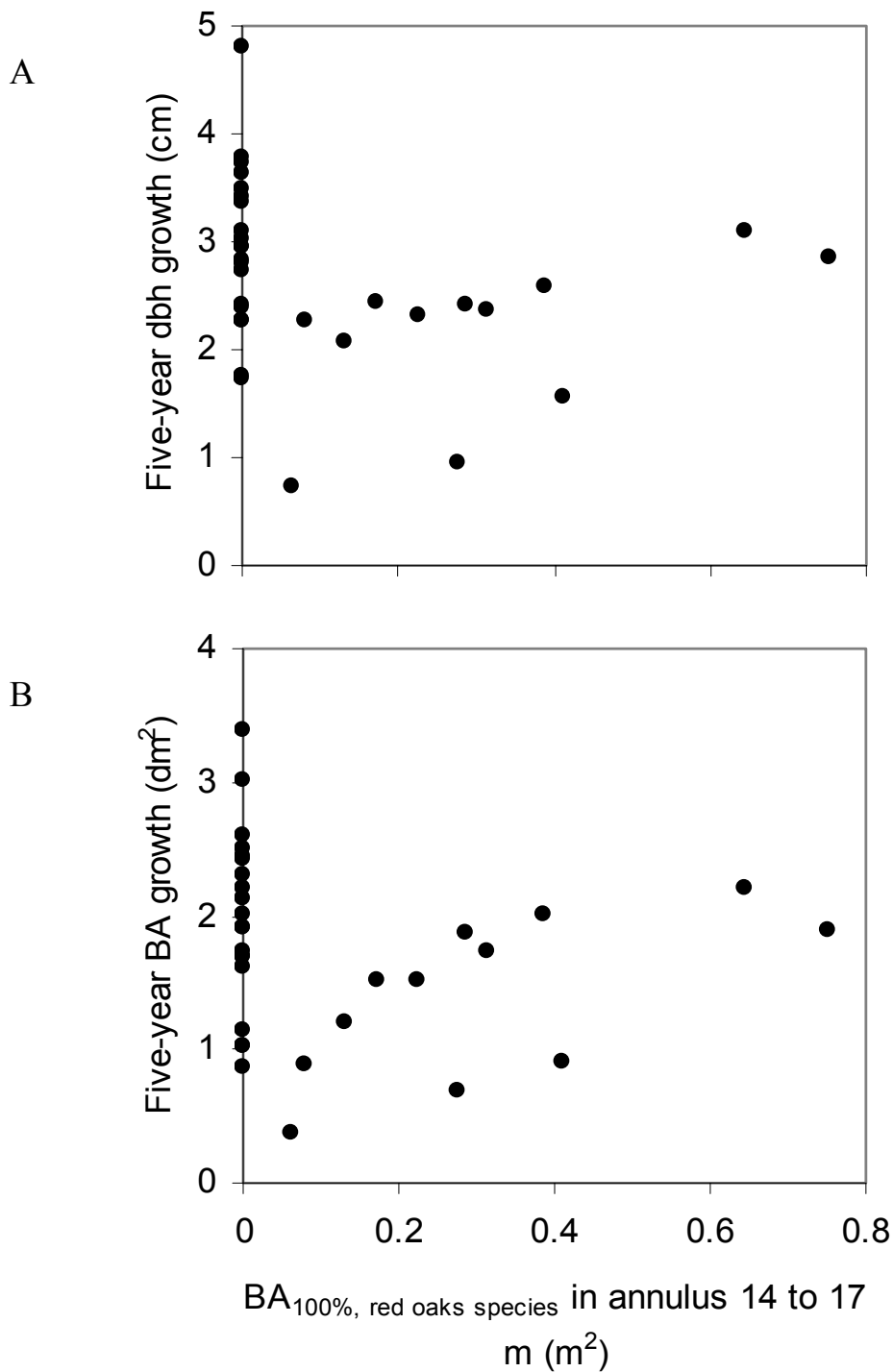


Figure 2.5. Scatterplots of the dependent variables (a) 5-yr diameter at breast height (dbh, 1.37 m above ground) growth of the subject trees and (b) 5-yr basal area (BA) growth of the subject trees against the basal area of the red oaks equal in height or taller than the subject tree and located between 14.0 and 17.0 m away.

number of available data points to twelve. A similar trend, where the growth increased with the increase in the basal area in the 14.0 to 17.0 m annulus, was also observed with the independent variable representing the trees from all species that were taller than the subject tree ($BA_{100\%,\text{all species}}$). In this case however, the coefficients of determination were not as high – 0.18 for ΔD ($P=0.11$, $n=15$) and 0.23 for ΔBA ($P=0.07$, $n=15$).

2.3.4 Multiple Regression Models with Individual Tree Variables, Distance-independent, and Distance-dependent Variables

The selected multiple linear regression model for ΔD had two independent variables and achieved a coefficient of multiple determination (R^2) value of 0.71 (Table 2.8):

$$\ln(\Delta D) = 2.67121 - 0.09731 C(BA_{100\%, \text{ all species, 3.5-11.0m}) + 0.03193 \text{ CRSCORE}$$

where

$\ln(\Delta D)$ is the natural logarithm of the tree 5-yr diameter growth; and

CRSCORE is the crown class score determined as described in Meadows et al.

(2001)

The model that was selected for the 5-yr basal area growth had an R^2 of 0.82 and three independent variables:

$$\ln(\Delta BA) = 3.55145 + 0.02405 \text{ INIDBH} - 0.09763 C(BA_{100\%, \text{ all species, 3.5-11.0m}) + 0.02670 \text{ CRSCORE}$$

where

$\ln(\Delta BA)$ is the natural logarithm of the tree 5-yr growth in basal area; and

INIDBH is the initial tree diameter, i.e., tree diameter 5 full growing seasons ago

Table 2.8. Selected multiple linear regression models. The models were obtained after selection from among all individual tree variables, distance-dependent and distance-independent variables, and the competition indices (C). Variables were included in the model if they were significant at the 0.15 level

Dependent variable	Independent variable	Parameter estimate	Standardized parameter estimate	P-value	R ²
ln(ΔD) ^a	Intercept	2.67121	0	<0.0001	0.71
	C(BA _{100%} , all species, 3.5-11.0m) ^c	-0.09731	-0.61765	0.0001	
	crscore ^d	0.03193	0.28790	0.0451	
ln(ΔBA) ^b	Intercept	3.55145	0	<0.0001	0.82
	INIDBH ^e	0.02405	0.47786	<0.0001	
	C(BA _{100%} , all species, 3.5-11.0m)	-0.09763	-0.49556	0.0002	
	CRSCORE	0.02670	0.19253	0.0929	
ln(ΔBA) (INIDBH excluded)	Intercept	4.93931	0	<0.0001	0.75
	C(BA _{100%} , all species, 3.5-11.0m)	-0.13050	-0.66230	0.0001	
	CPA ^f	0.00365	0.41600	0.0002	

^aln(ΔD) is the natural logarithm of the tree 5-yr growth in diameter at breast height (1.37 m above ground)

^bln(ΔBA) is the natural logarithm of the tree 5-yr growth in basal area

^cC(BA_{100%}, all species, 3.5-11.0m) is the competition index calculated by the formula $C = BA_i^{-1} * \left(\sum BA_{j,k,p} \right)$, where BA_i is the basal area of the subject tree, and $\sum BA_{j,k,p}$ is the sum of the basal areas of the trees that satisfy conditions j , k , and p , where $j=100\%$ indicates the minimum height of the trees relative to the height of the subject tree (100% meaning that they are at least as tall as the subject tree), k represents the species and takes the values “all species”, and p represents an annulus between 3.5 m and 11.0 m from the subject tree (see Figure 2.1 for graphical explanation). Annulus is the space between two concentric circles

^dCRSCORE is the crown class score (Meadows et al. 2001). Calculation explained in detail in Methods section

^eINIDBH is the dbh of the tree five years earlier

^fCPA is the crown projection area

Another multiple regression model constructed for the dependent variable ΔBA was one where neither the initial diameter nor the basal area of the subject tree were allowed to be included in order for the equation to be more useful in predicting potential response to disturbances or silvicultural treatments. Exclusion of the initial diameter and basal area of the harvested trees resulted in less variance being accounted for, but reflects the competitive environment around the subject tree that is modified or influenced through silvicultural treatments. The resulting model had an R^2 of 0.75 and was

$$\ln(\Delta BA) = 4.93931 + 0.00365 CPA - 0.13047 C(BA_{100\%, \text{ all species, 3.5-11.0m}}),$$

where

CPA is the crown projection area.

Histograms, stem and leaf plots, boxplots, and test statistics (Shapiro-Wilk, Kolmogorov-Smirnov, Cramer-von Mises, and Anderson-Darling) of the error terms all indicated that they were normally distributed. Plots of the residuals against each of the predictor variables and plots of the predicted against the observed values suggested the regression functions were adequate.

2.4. Discussion

2.4.1. Individual Tree Variables

Simple linear regressions of ΔD with individual tree variables as the independent variables indicated that factors affecting the crown attributes, as accounted for by the crown class score had the highest influence on ΔD among the individual tree based variables. The score was classified as an individual tree variable in the present study, but its value for each tree is affected by the height and position of the crown relative to the neighboring trees. Therefore, crown class score could be considered to represent an estimate of the amount of above ground competition

exerted on the subject tree by the immediate neighbors. The crown class score is determined by observation, making it fairly fast and convenient to estimate in the field. Simplifying it by estimating only the amount of direct sunlight from above and from the sides, and not considering the relative crown size and crown balance, only marginally reduced the variance accounted for in both ΔD and ΔBA . However, because crown size and balance reflect tree growth potential, it is possible that their importance may increase if growth is modeled over a longer period of time than 5 yr. This relationship is partially supported in earlier findings of Holsoe (1948), who found a high correlation index coefficient (0.93) between the 10-yr BA growth and crown diameter of red oaks. Once the crown class score was included in the multiple regression model tested in this study, none of the other individual tree variables significantly contributed to the model, suggesting that they may account for some of the same competitive effects as included in the crown score.

In the simple linear regression models, crown class score did not perform as well for ΔBA as it did for ΔD as judged by the amount of variance accounted for. In contrast, tree height, crown projection area, and crown diameter accounted for just over 40% of the variation in ΔBA , which was around 30 percentage points higher than in the models for ΔD . A comparison of the performance of the individual tree variables in the ΔD and ΔBA models demonstrates how different the results for these two dependent variables are, despite the fact that the calculation of ΔBA is actually based in large part on ΔD . The small amount of the variance in ΔBA accounted for by the crown class score compared to that accounted for by the other individual tree variables suggests that in dominant or codominant red oaks, crown size and tree height that had more influence on the 5-yr growth in basal area. If more red oaks from the intermediate and some of the suppressed crown classes had been included in the selected trees, perhaps crown class score

would then be an even more useful variable in the Δ BA model. Individual tree variables and indices incorporating estimated crown parameters are reported to perform well in models of the 5-yr basal area growth of individual trees in some conifer species (Biging and Dobbertin 1992). Biging and Dobbertin (1992) also determined that such individual tree variables and indices performance was generally better for shade-tolerant species.

The simplified form of the crown class score containing only the sum of the score for direct sunlight from above and from the sides performed only slightly worse than the full crown class score in accounting for the variation in Δ BA. This seems to indicate that over the studied period of time the portion of the crown exposed to direct sunlight was an important factor affecting Δ BA and that crown size may also explain variation through the amount of exposure to sunlight or related factors (e.g., CO₂ assimilation). The high degree of association between Δ BA and the independent variables tree diameter and tree basal area 5 yr earlier, both of which accounted for nearly half of the variability in Δ BA, was a result of the fact that basal area growth is accreted on an already accumulated diameter and basal area.

Although crown class score was not as significant as other crown based variables in the simple regression for Δ BA, crown class score was the only significant variable in addition to initial tree diameter in the multiple regression models with only individual tree variables. Moreover, as indicated by the standardized parameter estimates, both variables had the same relative importance in the model. Thus, these two variables complemented each other in accounting for the variability in Δ BA than any other combination of individual tree variables. This result demonstrates how in modeling considering the predictor variables as a whole, rather than individually, may reveal additional information and relationships. Initial size upon which

new basal area is formed and the exposure to sunlight (or related factors) were the primary above ground factors related to increase in basal area growth.

2.4.2. Distance-independent Variables

None of the plot-level distance independent variables explained any significant proportion of the variability in ΔD or ΔBA , suggesting that in fairly heterogeneous stands local factors and crowding were more important to individual tree growth than were plot level variable. In contrast, Wimberly and Bare (1996) found that when they added distance-dependent variables to their model that already included distance-independent variables only a small (<0.01) increase in the adjusted coefficient of multiple determination occurred. In their classification of the variables, however, they included initial tree dbh and crown class in the distance-independent category, while in the current study they are classified as individual tree based variables. Similarly, Daniels et al. (1986) found that several distance-independent competition indices based on tree size to mean size ratios, including crown ratio, which they classified as distance-independent measure, performed similarly with the best distance-dependent indices in a loblolly pine (*Pinus taeda* L.) plantation. In a study of several conifer species, Biging and Dobbertin (1995) were also able to achieve similar model performance with their distance-independent indices that included crown parameters.

2.4.3. Distance-dependent Variables

The crowding of the subject trees, estimated through the basal area within concentric circles and annuli around them, revealed that trees that are equal in height or taller than the subject trees and are located in the annulus from 3.5 to 11.0 m and 2.0 and 11.0 m (for ΔD and ΔBA respectively) from the subject tree may have the highest negative influence on crop tree 5-yr radial growth. When basal area of only the red oaks within the same height category and

within these same annuli was used as a predictor variable, the variance in radial growth accounted for decreased only marginally. This result suggests that intragenus competition from other red oaks, which were more numerous in the upper canopy than any other species, was most crucial for crop-tree 5-yr radial growth. Other studies have also found that in mixed upland hardwood stands, the canopy red oaks become highly competitive and exhibit strong dominance over other tree species while maintaining low mortality. Oliver (1978a) found that the oaks, which were initially inconspicuous, start to dominate the overstory around 40 yr after stand establishment. Sometimes the oaks outgrow the other species so much that even-aged stands may appear to be uneven-aged (Oliver 1978b). Because oaks tend to spread their crowns once they are above the general canopy, their major competitors usually become other red oaks (Hibbs, 1981, 1983). Such growth pattern dynamics results in a need of thinning only after the competition becomes intraspecific (Hibbs and Bentley 1984), which for northern red oak in New England is reported to be around age 45 yr. Kittredge (1988) found that 5-yr basal area growth of overstory northern red oaks is negatively related to the basal area of neighboring oaks with crowns in the same stratum. In some instances, southern red oaks have also been suggested to have similar development pattern. Clatterbuck and Hodges (1988) noted that in mixed cherrybark oak – sweetgum stands in minor river bottoms in Mississippi cherrybark oak tends to overtop the initially faster-growing sweetgum by the age of 20-25 yr.

The smaller coefficients of determination in the models using the basal areas of trees of all heights (i.e., including suppressed trees) compared to models using only overstory trees, suggests that trees from the lower strata were not necessarily competitors of the upper stratum red oaks. Therefore, it is likely that the competition for light and other aboveground resources (e.g., CO₂, physical growing space), rather than for belowground resources, was critical in the

examined bottomland hardwood sites. An observational experiment (Kelty 1984) similarly reported lack of negative relationship between understory presence and growth of overstory trees (mostly northern red oaks) on two adjacent mixed hardwood stands that had not been treated since establishment. In a designed experiment involving plots where the understory was actually removed, Kelty et al. (1987) similarly failed to demonstrate negative understory effect on northern red oak growth. Kittredge (1988) also reported that accounting for the amount of understory does not contribute to a better red oak basal area growth model in mixed hardwood stands in New England. In areas with lower precipitation, however, the understory does appear to have some impact on the growth of the overstory (Rogers and Brinkman 1965, Bower and Ferguson 1968).

A visual comparison of the performance of the distance-dependent variables (Figures 2.2 and 2.3) reveals that regardless of which one is used, the highest coefficient of determination with ΔD and ΔBA is achieved with the basal areas of the trees located within part of or the whole of the 2.0 to 11.0 m annulus. The distance of 2.0 to 11.0 m corresponded to 0.4 to 2.4 times the quadratic mean crown radius of the unsuppressed trees. If a circle with radius 11.0 m is drawn around the crop tree, the circle will likely confine all immediate neighbors. This result would have the practical implication that thinning the trees taller than the crop tree within a distance of 2.4 times the crown radius would allow for elimination of the main competition influence over the next 5-yr period and for free space between the crowns of adjacent trees of 0.4 times the mean crown radius. This distance would likely be sufficient for the trees not to compete severely through mutual shading and crown abrasion and still not waste much growing space between their crowns. A consideration during any thinning in hardwood stands with some oak component however, should be the possibility of epicormic branching. Creating large openings may result in

the proliferation and survival of epicormic branches, which degrade wood quality, on the less vigorous trees of susceptible species. Many of the red oaks are indeed susceptible to epicormic branching, including cherrybark and water oak (Meadows 1995).

Nearly all scatterplots of tree basal area within specific annuli versus ΔD or ΔBA indicated a decrease, whether significant or not, in tree radial growth with an increase in annuli basal area. The same was true for the scatterplots where the dependent variables were plotted against the competition index (equation (1), Figure 2.4). In cases where there were trees present in the 14.0 to 17.0 m annulus that were equal to or greater in height than the subject tree (twelve of the instances), however, ΔD and ΔBA actually increased with an increase in basal area of the trees in this annulus (Figures 2.5a and 2.5b). Considering the crown radius of the unsuppressed trees averaged 4.5 m, the trees in this annulus are confined at a distance between 3.1 and 3.8 times this mean crown radius. This places these trees where the indirect (second-order) neighbors would be relative to the crop tree. Thus, the trees confined in the 14.0 to 17.0 m annulus may be close enough to compete with the crop tree immediate neighbors, but too far to compete with the crop tree itself. They may therefore have an indirect positive impact on crop tree growth. Such propagation of competitive effects has been reported in other plant species. Harper (1977) summarizes a study by Yoda et al. (1957), where the authors reported the presence of a negative correlation between the weights of individual maize (*Zea mais* L.) plants and their first, third, and fifth-order neighbors in the crop row, but positive correlation with the weights of the second and fourth-order neighbors. Similarly, the positive correlation between the second-order neighbors basal area and the growth of the crop tree may be through their negative influence on the immediate neighbors (i.e., on the main competitors). Trees in natural stand in the current study, had a larger number of first, second, third, and higher order neighbors compared to the row crop

plants in the study by Yoda et al. (1957). Thus, competitive effects in the forest were likely spread over more first, second, and third-order neighbors resulting in a lack of detection of a measurable relationship between the dependant variables and beyond third-order neighbors.

In conclusion, the results indicated that 5-yr radial growth of selected red oak crop trees in the studied bottomland sites may be significantly negatively influenced by the amount of taller competitors located between 0.8 and 2.4 times the mean crown radius away, and especially by the red oak component in them. Radial growth may be positively affected however, by the indirect neighbors through their negative influence on the immediate neighbors. Radial growth was positively associated with the crown condition as quantified by the crown class score (Meadows et al. 2001), by crown size, and by tree height. The growth in basal area was significantly and positively related to initial tree diameter and initial basal area, while diameter growth was not significantly related to these initial stem attributes.

CHAPTER 3

GEOSTATISTICAL SPATIAL ANALYSIS IN BOTTOMLAND HARDWOOD FORESTS

3.1. Introduction

Many biological phenomena have properties that cannot be analyzed with common statistical techniques normally used to reveal relationships and make inferences. Rossi et al. (1992) provided an example from a study by Hangeveld (1979) of the importance of also knowing the spatial dependence among sample locations that allowed previously undetected features of the biology and ecology of a species to be determined. Spatial dependence can be thought of as similarity of sample values located close to each other in space as a result of underlying spatially continuous processes. Rossi et al. (1992) indicated that obvious and important spatial characteristics of the data are not revealed if the data are described only by standard statistical analysis based on mean, variance, coefficient of variation, and frequency distribution. A set of statistical tools often employed for spatial analysis is geostatistics. Geostatistics is the branch of applied statistics that is concerned with the detection, modeling, and estimation of spatial dependence, or continuity (Isaaks and Srivastava 1989, Rossi et al. 1992) that may commonly underlie many biological and environmental processes. Although geostatistics was initially used most extensively in mining geology (Matheron 1963), the variogram, one of its most well known tools, was reportedly used first in forestry as early as 1926 (Langsaeter 1926, as reported by Matérn 1986, p.51).

Geostatistics is intended for use with spatially continuous variables and is often used to provide unbiased estimation of values at unsampled locations that are distributed among the sampled locations. Trees, however, are discrete objects, so their attributes are quite different

from the attributes of variables having a continuous spatial aspect of their spatial distribution. Nevertheless, tree growth, and consequently size, is a reflection of spatially continuous factors, which may include soil characteristics, competition, and seed dispersal. Soil characteristics (e.g., fertility, moisture, depth) may vary continuously with elevation, distance from a stream, parent material, etc., while competition likely decreases with the increase in intertree separation distance. Continuity in seed dispersal might result in higher concentration of regeneration in close proximity to the parent tree, especially for heavy seeded species, possibly resulting in higher genetic similarity of adjacent trees. By not assuming independence among the samples, geostatistical analysis methods strengthen the more traditional studies of competition and may be particularly suited and their use well justified for forestry research.

Forestry research has indeed recently been taking more extensive advantage of the advances in geostatistics. Geostatistical techniques were used in forestry to model tree size and growth in natural old growth ponderosa pine (*Pinus ponderosa* Dougl.) stands and evaluate temporal variation of spatial patterns (Biondi et al. 1994). With the help of geostatistical techniques, Grushecky and Fajvan (1999) studied the spatial dependence and heterogeneity in an Appalachian hardwood stand, in which diameter-limit and shelterwood cuttings had been applied. Various aspects of geostatistical spatial analysis were also used in other forestry related studies to summarize tree-ring data (Meko et al. 1993); characterize rainfall spatial distribution in tropical forests (Molicova and Hubert 1994); examine spatial autocorrelation in boreal forested landscapes (Hyppanen 1996); estimate spatially continuous variables of interest to forest management (Gunnarsson et al. 1998); determine spatial dependence of spectral reflectance in forest ecosystems (Treitz 2001); characterize leaf area index at various scales (Burrows et al.

(2002); and examine the spatial variation and autocorrelation in throughfall and find minimum distances for independence of the throughfall sample collectors (Loescher et al. 2002).

A number of issues are yet to be explored, however, including questions related to potential presence of any spatial statistical structures in data from relatively undisturbed natural forest stands. An intriguing aspect of exploring stands that have been developing with little or no human interference since harvest is the spatial relationships that result from a stand's development. Once trees have become established on a particular site and in the absence of major disturbances, their survival and their relative dimensions and spatial distribution are largely the consequence of two counteracting processes: growth and competition. Growing trees occupy portions of the soil and aboveground space, from which they extract and sometimes deplete resources necessary for their and their neighbors growth and survival. Unequal sharing of the limited resources or competition, acts in conjunction with growth processes, and, in part, results in specific tree spatial distributions. Geostatistical analysis methods can provide a unique insight and perspective of the relative spatial tree distribution in regard to their size, which resulted from the action of the two opposing forces (growth and competition) over the life of the stand.

A review of the literature did not reveal any studies in bottomland hardwood stands that made use of the capabilities of geostatistical tools and methods. Moreover, a clear and meaningful biological interpretation of spatial dependence in forest stands is yet to be found.

Consequently, the objectives of this study were to (1) determine intertree distances over which tree dimensions are likely spatially dependent, (2) quantify the proportion of variability in tree growth, and therefore tree size, that can be attributed to the spatial distribution of the trees, and (3) contrast the extent of spatial dependence determined through the spatial distribution of

tree basal area (BA) and crown projection area (CPA). To answer these research objectives, geostatistical analysis was employed for plots in natural hardwood stands on major and minor stream bottoms located in the states of Louisiana, Arkansas, and Mississippi.

3.2. Materials and Methods

3.2.1. Study Areas and Collected Data

The current study was carried out in four natural bottomland hardwood stands located in Louisiana, Arkansas, and Mississippi (Table 3.1). The selected stands had little or no anthropogenic disturbance since stand initiation and had a large proportion of red oak species. One of the stands was on a major stream bottom and was located in central Louisiana's St. Landry Parish within an abandoned and older portion of the Mississippi River floodplain. The last silvicultural operation in the stand was carried out some 25 years earlier and involved removal of a limited number of trees. The remaining three stands were located on minor stream bottoms. The stand in northern Louisiana was in Jackson Parish on Cypress Creek bottom and was subjected to removal of a small number of pine (*Pinus* spp) trees 12 years earlier. The Arkansas site was located in Drew County on Hungerrun Creek and it has remained uncut since establishment. The last stand was at a site in Oktibbeha County, Mississippi on the Noxubee River and has not been cut either. All sites had either clay loam or silt loam soils (Table 2.1), were well stocked with significant proportion of the basal area in red oaks (Table 2.2), and the stands were established over 40 yr ago.

To examine for presence and degree of spatial dependence in the natural bottomland hardwood stands studied, three plots were established at each of the four sites for a total of twelve plots. Plot selection procedures involved randomly selecting from the pool of predetermined potential plots and are described in more detail in section 2.2.1. The plots were 80

Table 3.1. Forest stand locations and geographic coordinates of the plot centers at each study site (Map Datum WGS 84)

Location and plot number	Latitude	Longitude
Central Louisiana		
1	30°40'.149	91°59'.915
2	30°40'.206	92°00'.061
3	30°40'.239	91°59'.954
Northern Louisiana		
1	32°22'.432	92°41'.992
2	32°22'.644	92°41'.950
3	32°22'.394	92°42'.065
Arkansas		
1	33°41'.584	91°52'.188
2	33°41'.470	91°52'.150
3	33°41'.540	91°52'.151
Mississippi		
1	33°17'.554	88°54'.997
2	33°17'.490	88°55'.250
3	33°17'.405	88°55'.310

m on the side. Sides of the plots were orientated to the cardinal directions.

Only the trees with diameter at breast height (dbh, 1.37 m) greater than 10.0 cm were measured. For each, tree the dbh, species, location on the local plot coordinate system, and crown class were recorded. The crown classification used was developed by Kraft (1884) (as cited by Assmann 1970), and later modified to its current form by Smith et al. (1997). Additional measurements that were recorded included the total height and the radius of the vertical crown projection in the four cardinal directions. Height and crown radii were not measured on suppressed trees.

Diameter tapes were used for the dbh measurements, while a laser hypsometer-rangefinder and a digital angle encoder (Laser Technologies Inc., Centennial, CO, USA) were used to map tree locations within plots. During the mapping procedures the horizontal distance from locations within the plot and the angle from North were measured to each tree. These measured distances and angles were later transformed to Cartesian coordinates (to the nearest 0.01 m). The edges of the vertical crown projections were determined with a densitometer (GRS, Arkata, CA, USA), unless severe crown overlapping occurred, to ensure vertical viewing. The distance from the center of the bole to the projected crown edge was measured with the laser hypsometer-rangefinder or a measuring tape. Diameters were measured to the nearest mm, horizontal angles to the nearest 0.01° , and distances to the nearest cm.

3.2.2. Geostatistical Analysis

Although geostatistics is often employed for creating krigged maps where values at intermediate locations are estimated, this was not part of the current project because all plot trees of interest were mapped. Kriging, or “optimal prediction” (Cressie 1993), refers to a method of finding the best linear unbiased estimators of the values of a stochastic process at unsampled

locations (Isaaks and Srivastava 1989). Geostatistical analysis was used in the current study to determine the spatial relationship among plot trees. Because the primary interest was in the spatial dependence that may be present in bottomland hardwood stands, the focus of this study was on finding common relationships in the tree spatial distribution that have general applicability. A basic introduction to the geostatistical tools used in the current study is presented next with additional details available in the Appendix. For more information the reader can refer to the texts by Isaaks and Srivastava (1989), Cressie (1993) and Goovaerts (1997).

A basic principle in geostatistics is that samples located closer in space are more related and therefore more similar than distant ones (i.e., they are more continuous). The spatial continuity is determined by the semivariogram (also called variogram), which is a statistical model of structural spatial dependence. The semivariance function is estimated for certain distance and direction by the formula:

$$\hat{\gamma}(h) = \frac{1}{2n(h)} \sum_{s_i - s_j = h} (y_i - y_j)^2 \quad (1)$$

where $\hat{\gamma}(h)$ is the semivariance estimate; h is the separation vector; $n(h)$ is the number of pairs separated by vector h ; s_i and s_j are the locations of points i and j , and y_i and y_j are the values of variable y at these locations. As the distance between the samples increases, so usually does the difference between the sample values, which results in a larger semivariance. The distance at which the variogram levels off is called the range, which indicates the distance of spatial dependence.

The pairing of the values of two different variables y and z at different locations is used for construction of cross-semivariograms (also called cross-variograms):

$$\hat{\gamma}_{yz}(h) = \frac{1}{2n(h)} \sum_{s_i - s_j = h} (y_i - y_j)(z_i - z_j) \quad (2)$$

where $\hat{\gamma}_{yz}(h)$ is the cross-variogram estimator of the two variables y and z and the other parameters are as in equation (1).

Initial analysis of the data involved plotting tree locations and examining their distribution on the graph. Trees were also plotted by crown class and by basal areas. These are simple but important initial steps in spatial analysis, as some of the most effective tools for spatial description of data are visual ones (Isaaks and Srivastava 1989). Spatial continuity was examined by constructing isotropic variograms and cross-variograms for each plot. The variables used were the tree basal area (BA) and crown projection area (CPA) of the individual trees. Both variables have special significance in forestry. Because CPA is related to the leaf area (Kuuluvainen 1991, Bartelink 1997), CPA is indicative of a tree's growth potential. The BA represents the realization of this growth potential. The models considered in fitting the variogram were linear, linear to sill, spherical, exponential, and Gaussian (for definitions and equations the reader can refer to Journel and Huijbregts (1978, pp. 161-195) and Cressie (1993, pp. 61-63)). The selection criteria used was the minimal residual sum of squares. The recommendations of Journel and Huijbregts (1978) were followed regarding the lag and search distances (the distance between the most distant pairs of samples). The lag distances used were 4 m, which allowed for a sufficient number of tested pairs (about 30 or more) for each lag distance. The maximum search distance used was 40 m, which corresponded to half the plot width (Liebhold et al. 1993).

3.3. Results

Trees of different basal area size classes appeared to be fairly regularly dispersed on the study plots (Figure 3.1). There were, however, some exceptions. On plot 1 in Mississippi the

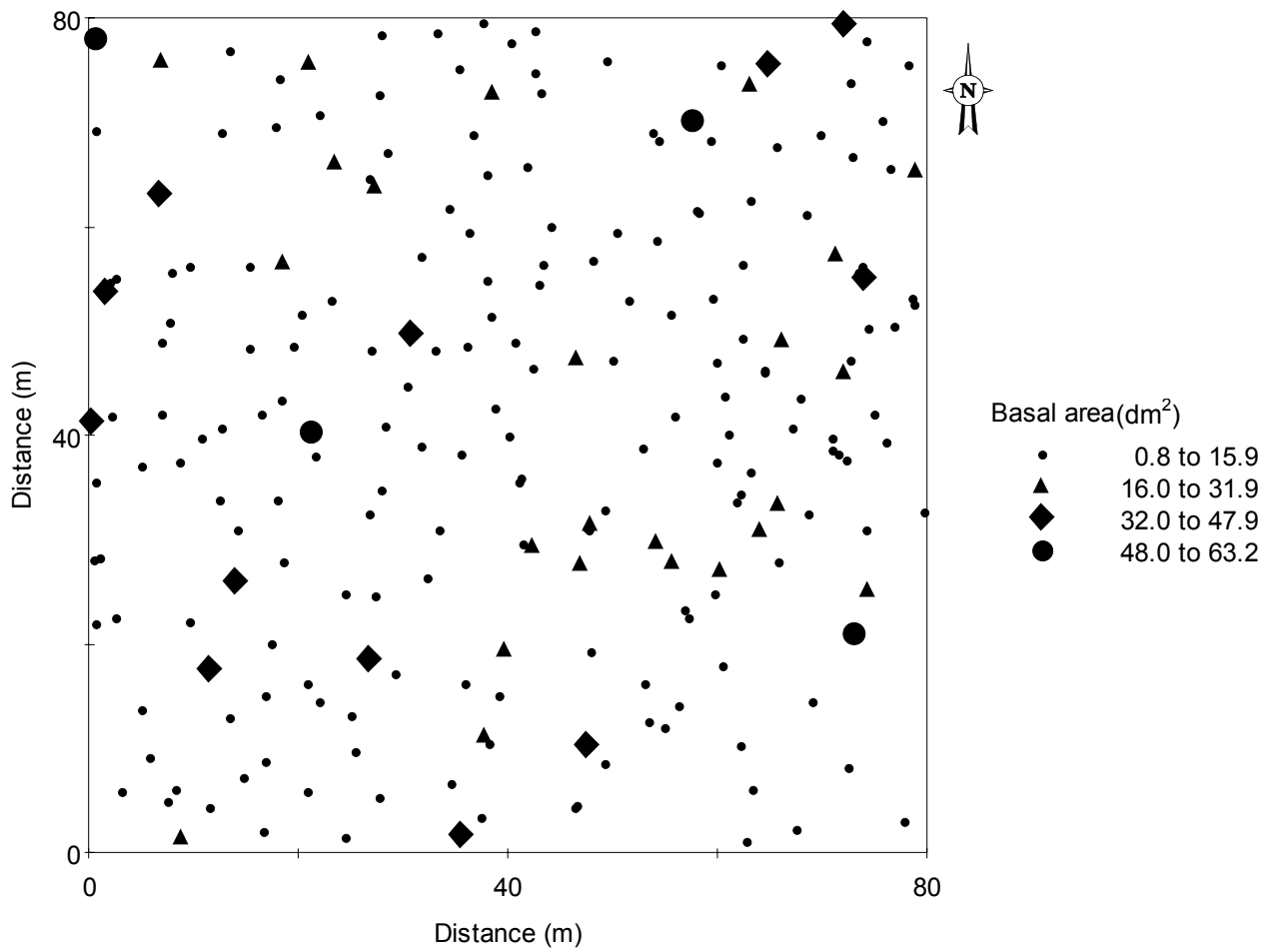


Figure 3.1. Typical tree distribution plot map illustrating relatively regular size distribution across a sample plot (plot 3 in central Louisiana) with trees represented as different symbols according to their basal area category.

larger trees were concentrated mostly in the west-southwestern part of the plot (Figure 3.2), while on plot 2 in the same stand (Figure 3.3), the larger trees were concentrated in the southeastern quadrant. A three-dimensional plot map, with the vertical axis representing the basal area in different areas within the plot (Figure 3.4a) confirms the spatial separation of the larger and smaller trees on plot 1. Such spatial separation was similarly confirmed for plot 2. The denser portions of these two plots were occupied by smaller trees, which were mostly sweetgum. The observed spatial separation in these 2 plots was in contrast to tree distribution found on the remaining plots (e.g. Arkansas plot 3, Figure 3.4b). Construction of separate variograms for the different portions of plots 1 and 2 in Mississippi was considered, but resulted in too few tree pairs for most of the lag distances. Therefore, comparisons were kept at the whole plot level.

The range of the variograms using the BA of all plot trees, regardless of their relative tree size or position in the canopy, averaged 4.5 m (Table 3.2). Two plots were not considered in this average as a result of the obtained pure nugget-effect variograms, which are models lacking spatial structure that appear as a horizontal line (Liebhold et al. 1993). These were plots 1 and 2 in the central Louisiana stand. Two additional plots were not considered because the variogram range extended beyond the studied search distance of 40 m (plot 3 in northern Louisiana with variogram range of 128.5 m and plot 1 in Mississippi with 117.7 m). A variogram range extending beyond the search distance is not reliable, because it makes assumptions regarding tree relative spatial distribution and relative size distribution over distances that are not examined. On the average, 95% of the variability in tree basal area could be accounted for by the spatially structured variance and could be modeled as spatial dependence (the mean $C_1/(C_0+C_1)$ in Table 3.2), but the model variograms fitted the sample variogram relatively poorly, as indicated by the coefficient of determination.

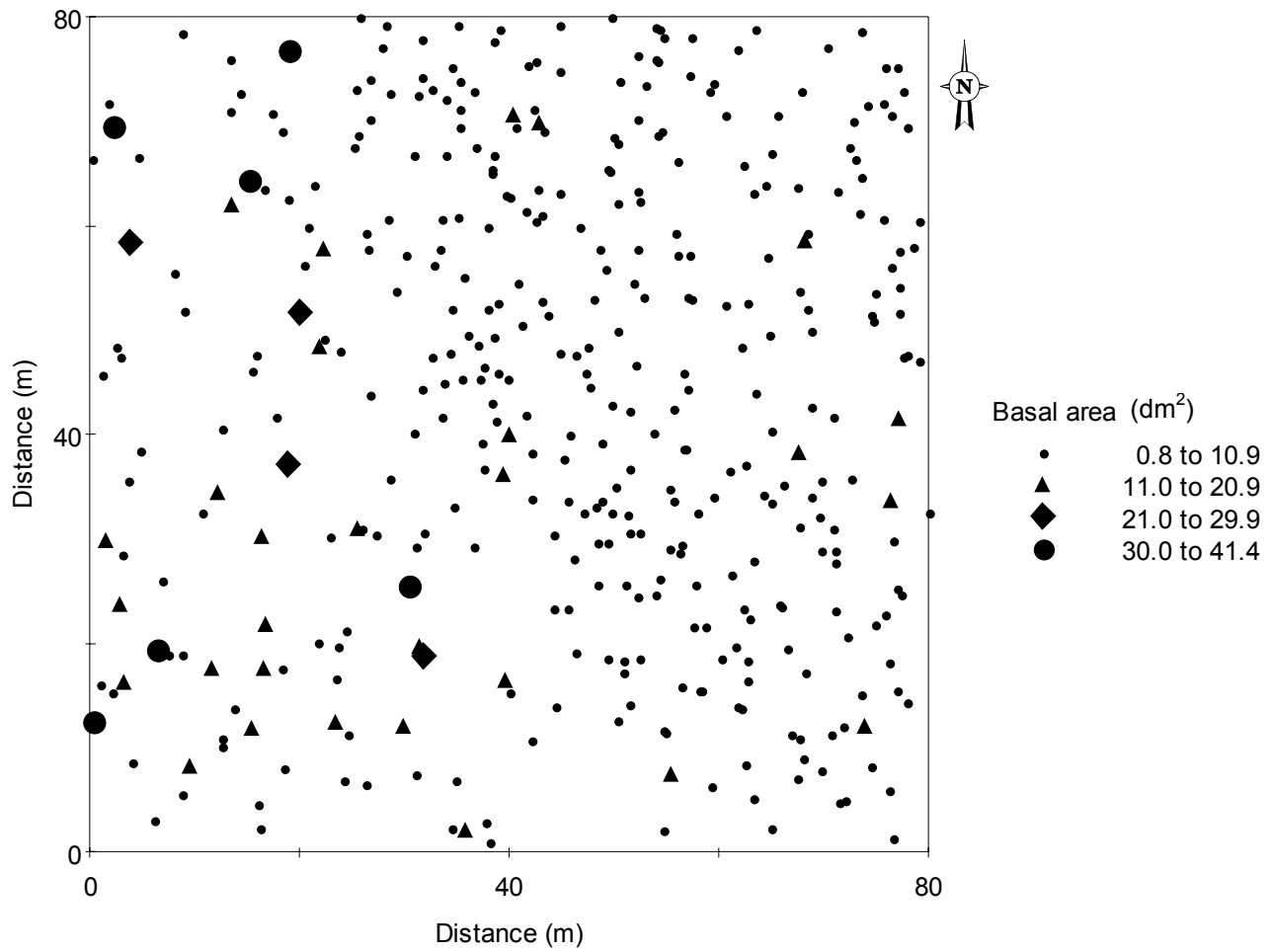


Figure 3.2. Tree distribution on plot 1 in the state of Mississippi with trees represented as different symbols according to their basal area category. Nearly all of the larger trees are located on the west-southwestern part of the plot.

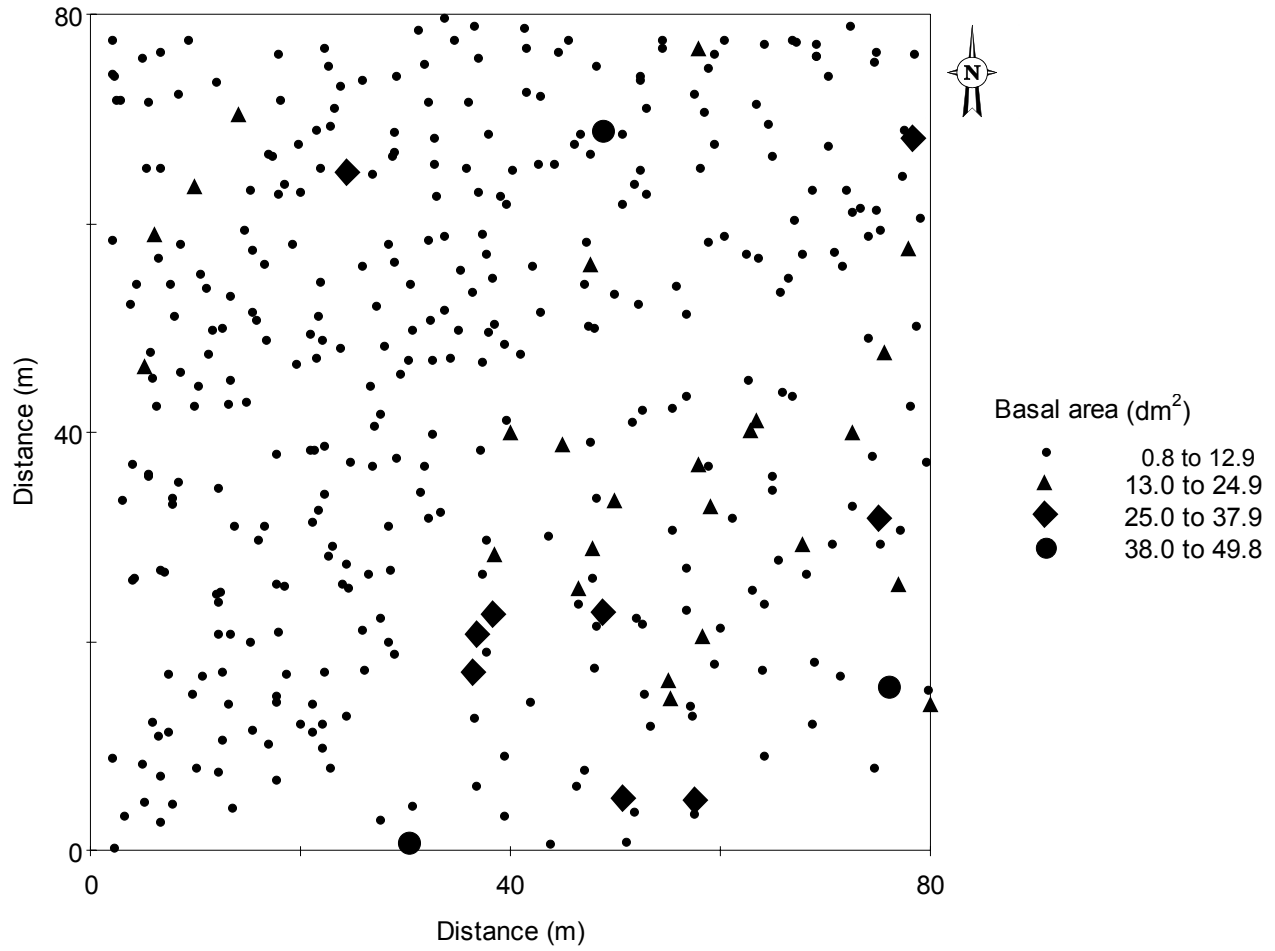


Figure 3.3. Tree distribution on plot 2 in the state of Mississippi with trees represented as different symbols according to their basal area category. Most of the larger trees are in the southeastern quadrant.

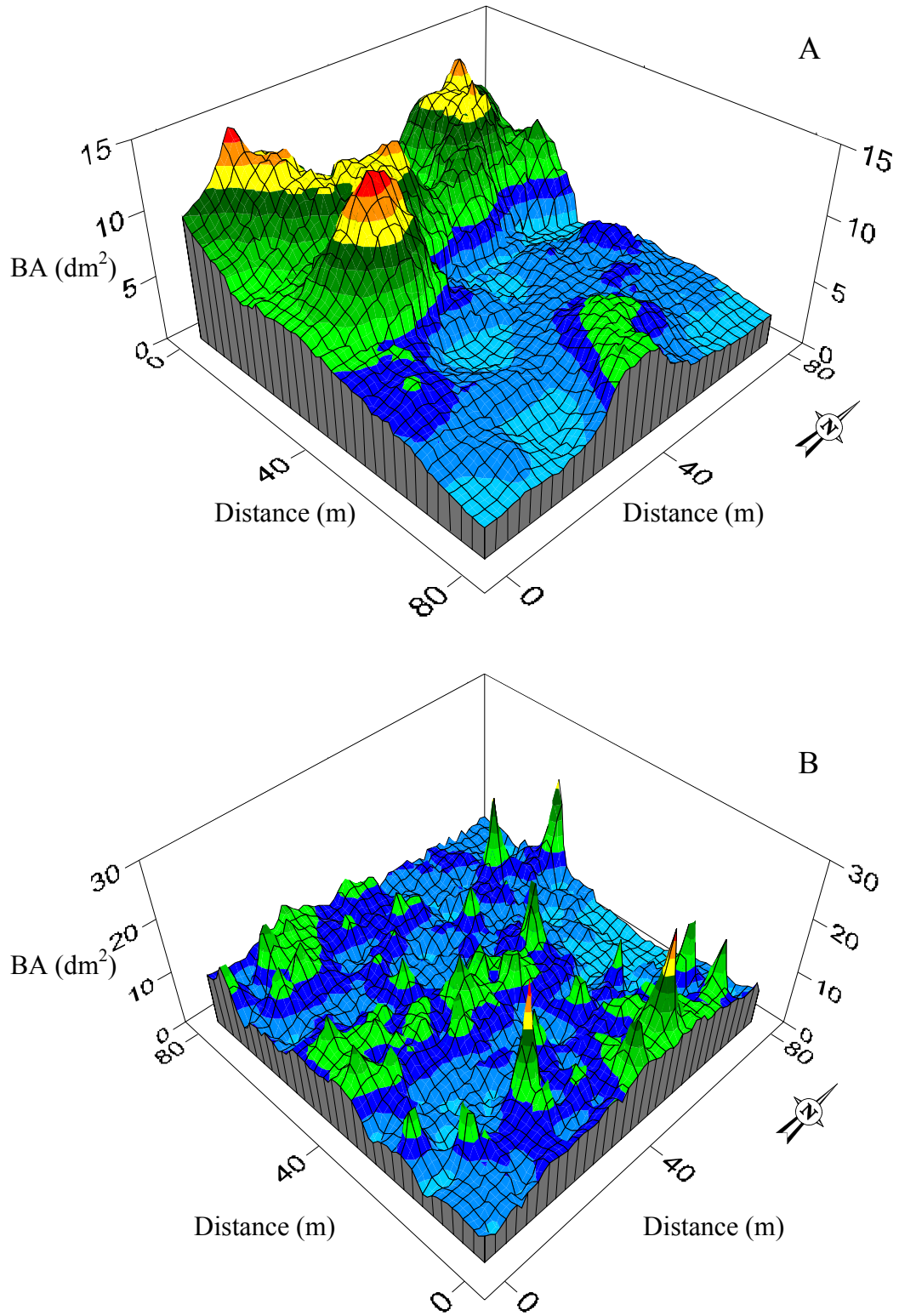


Figure 3.4. Three-dimensional maps obtained through kriging of a plot where tree basal area is disproportionately distributed (A, plot 1 in Mississippi) and a plot where tree basal area (BA) is more regularly distributed throughout the plot area (B, plot 3 in Arkansas).

Table 3.2. Spatial dependence on twelve hardwoods study plots from variograms of tree basal area for trees larger than 10.0 cm in diameter

Location and plot number	Variogram range ^a (m)	$C_1/(C_0+C_1)^b$	r^2 ^c
Central Louisiana			
1	-----Pure nugget effect ^d -----		
2	-----Pure nugget effect-----		
3	2.6	1.00	0.00
Northern Louisiana			
1	4.2	0.95	0.17
2	6.4	0.97	0.57
3	N/M ^e	N/M	N/M
Arkansas			
1	3.6	0.91	0.28
2	6.7	0.85	0.36
3	4.7	0.92	0.90
Mississippi			
1	N/M	N/M	N/M
2	2.2	1.00	0.00
3	5.3	1.00	0.45
Mean	4.5	0.95	0.34

^aVariogram range is the distance after which spatial dependence is no longer observed

^b $C_1/(C_0+C_1)$ represents the amount of variance that can be modeled as spatial dependence, where:

C_0 is nugget variance

C_1 is structural variance

$(C_0+ C_1)$ is the sill or the value of the semivariance at which the variogram levels off

^c r^2 is the coefficient of determination of the variogram

^dPure nugget effect is observed when there is no spatial dependence found at the studied scale

^eNot Meaningful. These plots were excluded because the variogram range extends beyond the search distance of 40.0 m

After this initial analysis, the suppressed trees were removed from the data. This reduced the variability in basal area at small separation distances. Excluding the suppressed trees resulted in BA variogram range that extended to greater distances (Table 3.3), i.e., the unsuppressed tree basal area appeared to be more continuous (Figures 3.5a, 3.5b, 3.6a, and 3.6b). The range of the variograms using the crown projection area (CPA) and the range of the cross-variograms employing both BA and CPA were commensurate with that of the BA variogram range (Table 3.3). The BA variogram range was ranked and plotted (Figure 3.7) to examine their values on the 12 plots. On the first 9 plots the variogram range was more similar and extended between 11.0 and 20.4 m. Although the range on the 10th plot was 30.4 m (average of 17.6 m for the first 10 plots), it appeared to be more similar to the first 9 than to the last 2 plots. On the remaining 2 plots (Mississippi plots 1 and 2) the spatial dependence extended well beyond the 40.0 m search distance.

The variogram range associated with CPA was between 11.4 m and 31.0 m for the study plots (Figure 3.8), and averaged 18.5 m (Table 3.3), excluding three plots whose variogram range extended beyond the selected 40 m search distance (plot 3 in northern Louisiana and plots 1 and 2 in the Mississippi stand; Figure 3.9).

The extent of spatial dependence was also explored with cross-variograms of the BA and CPA (Table 3.3, Figure 3.10). Although not perfectly correlated, the coefficient of determination between BA and CPA was fairly high and ranged from 0.43 to 0.80 for the different plots. The spatial dependence on the plots, as determined by the cross-variogram range, ranged from 11.2 m to 27.2 m and averaged 18.5 m. The variogram range exceeded the search distance of 40 m on four plots – plots 1 and 2 in the Mississippi stand, plot 3 in Arkansas and plot 3 in northern Louisiana, which were therefore not taken into account.

Table 3.3. Parameters of plot basal area (BA) variograms, crown projection area (CPA) variograms, and the cross-variograms for the unsuppressed trees on the twelve plots used in this study

Location and plot number	QMCR ^a (m)	BA Variograms			CPA Variograms			Cross-variograms			
		Range (m)	r ² ^c	C ₁ /(C ₀ +C ₁) ^d	Range (m)	r ²	C ₁ /(C ₀ +C ₁)	Range (m)	r ²	C ₁ /(C ₀ +C ₁)	
Central Louisiana											
1	4.6	14.1	0.74	0.80	17.3	0.67	0.50	14.0	0.78	0.87	
2	5.1	15.7	0.59	1.00	12.4	0.64	1.00	20.6	0.68	0.69	
3	5.6	18.2	0.51	0.58	11.5	0.55	1.00	11.7	0.64	1.00	
Northern Louisiana											
1	4.7	16.5	0.79	0.96	11.4	0.90	0.94	15.1	0.87	1.00	
2	4.6	17.3	0.93	0.94	27.4	0.92	0.93	27.2	0.92	0.99	
3	3.9	30.4	0.91	0.67	N/M ^e	N/M	N/M	N/M	N/M	N/M	
Arkansas											
1	4.9	15.1	0.86	0.98	11.8	0.73	0.79	11.2	0.70	0.77	
2	4.9	20.4	0.86	0.73	23.2	0.80	0.64	27.2	0.81	0.60	
3	4.6	11.0	0.85	0.98	20.8	0.86	0.90	77.6	0.61	0.51	
Mississippi											
1	3.6	N/M	N/M	N/M	N/M	N/M	N/M	N/M	N/M	N/M	
2	3.5	N/M	N/M	N/M	N/M	N/M	N/M	N/M	N/M	N/M	
3	4.4	16.9	0.88	0.91	31.0	0.90	0.78	20.7	0.90	0.98	
Mean ^e	4.5	17.6	0.79	0.86	18.5	0.77	0.83	18.5	0.77	0.82	

^aQMCR is the quadratic mean crown radius of the unsuppressed trees

^cr² is the coefficient of determination for the variogram model

^dC₁/(C₀+C₁) is the amount of variance that can be modeled as spatial dependence, where:

C₀ is nugget variance

C₁ is structural variance

(C₀+ C₁) is the sill, which is the value of the semivariance at which the variogram levels off

^eNot meaningful. These plots were excluded because the variogram range extends beyond the search distance of 40.0 m

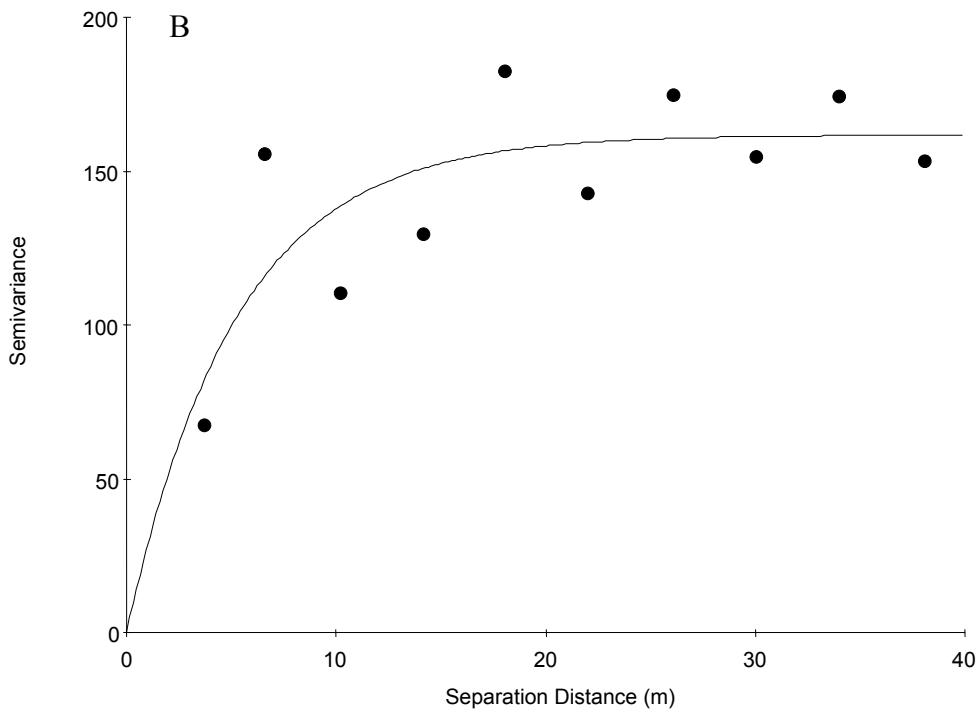
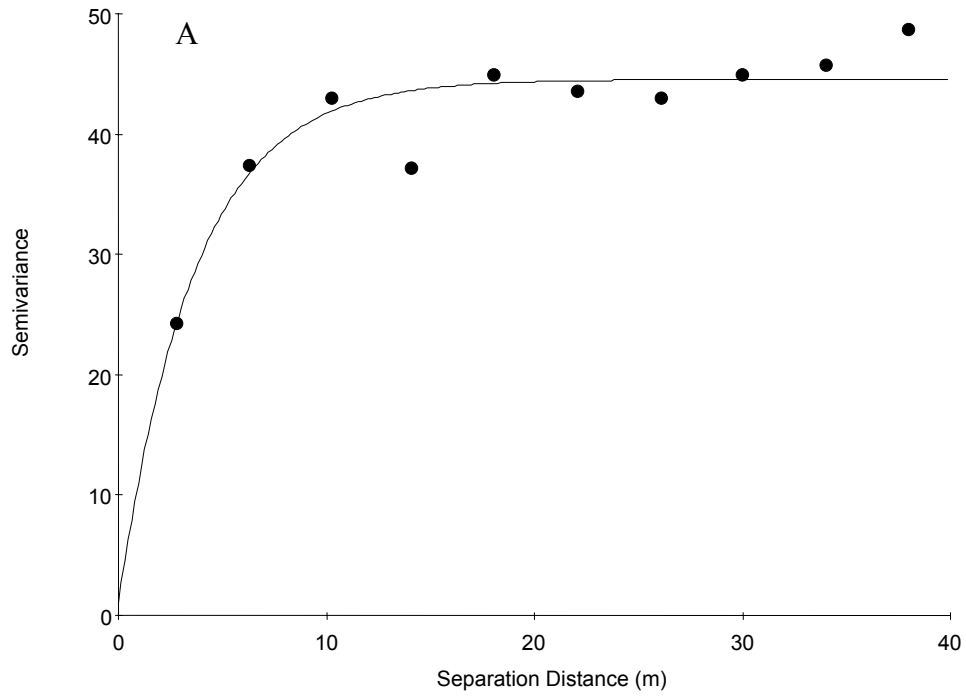


Figure 3.5. Isotropic variograms of the basal area of the unsuppressed trees for plot 3 in Arkansas (A) and plot 2 in central Louisiana (B) with variogram range of 11.0 and 15.7 m respectively.

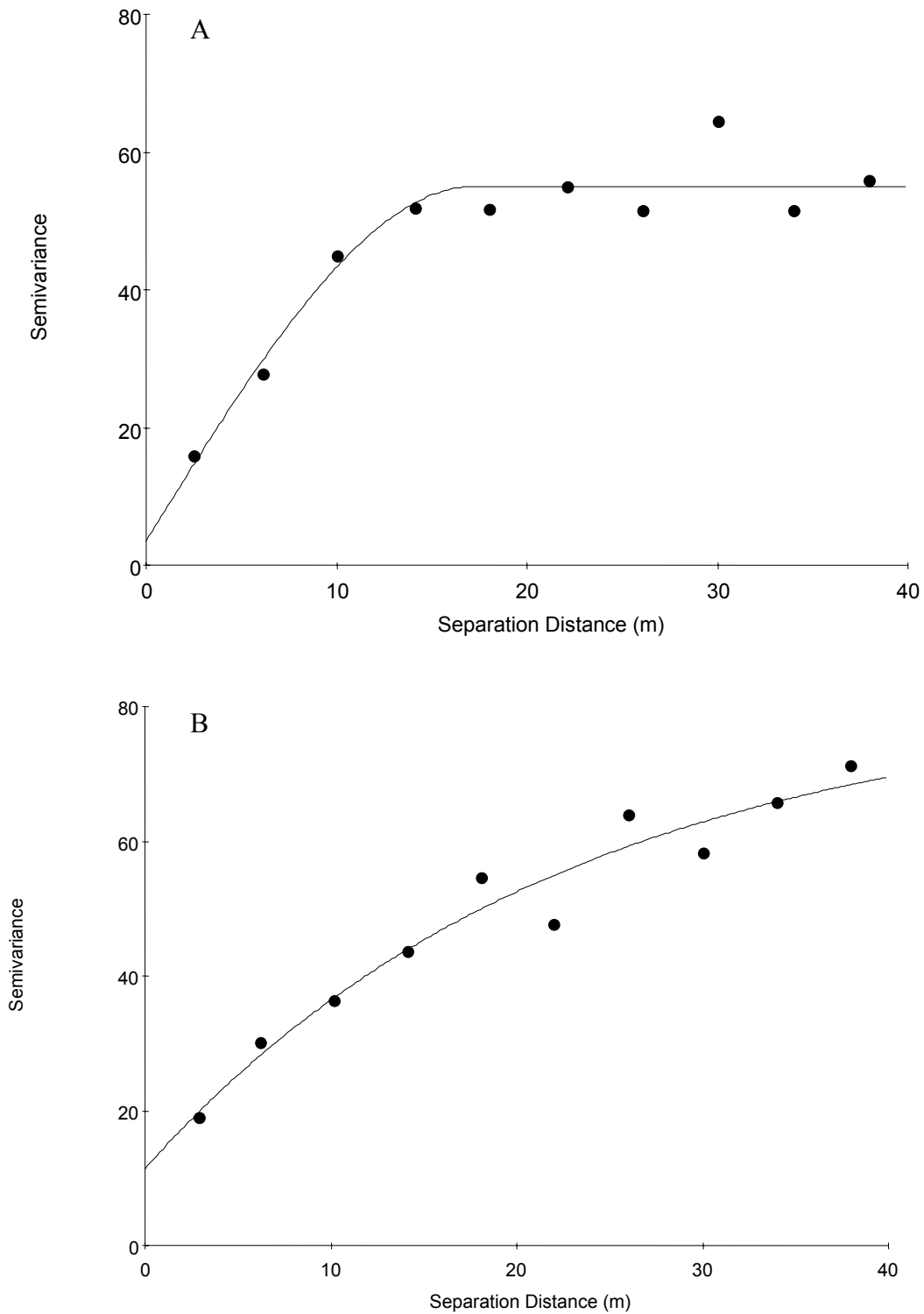


Figure 3.6. Isotropic variograms of the basal area of the unsuppressed trees for plot 2 in northern Louisiana (A) and plot 2 in Mississippi (B) with a variogram range of 17.3 and 67.9 m (which is beyond the maximum search radius of 40.0 m) respectively

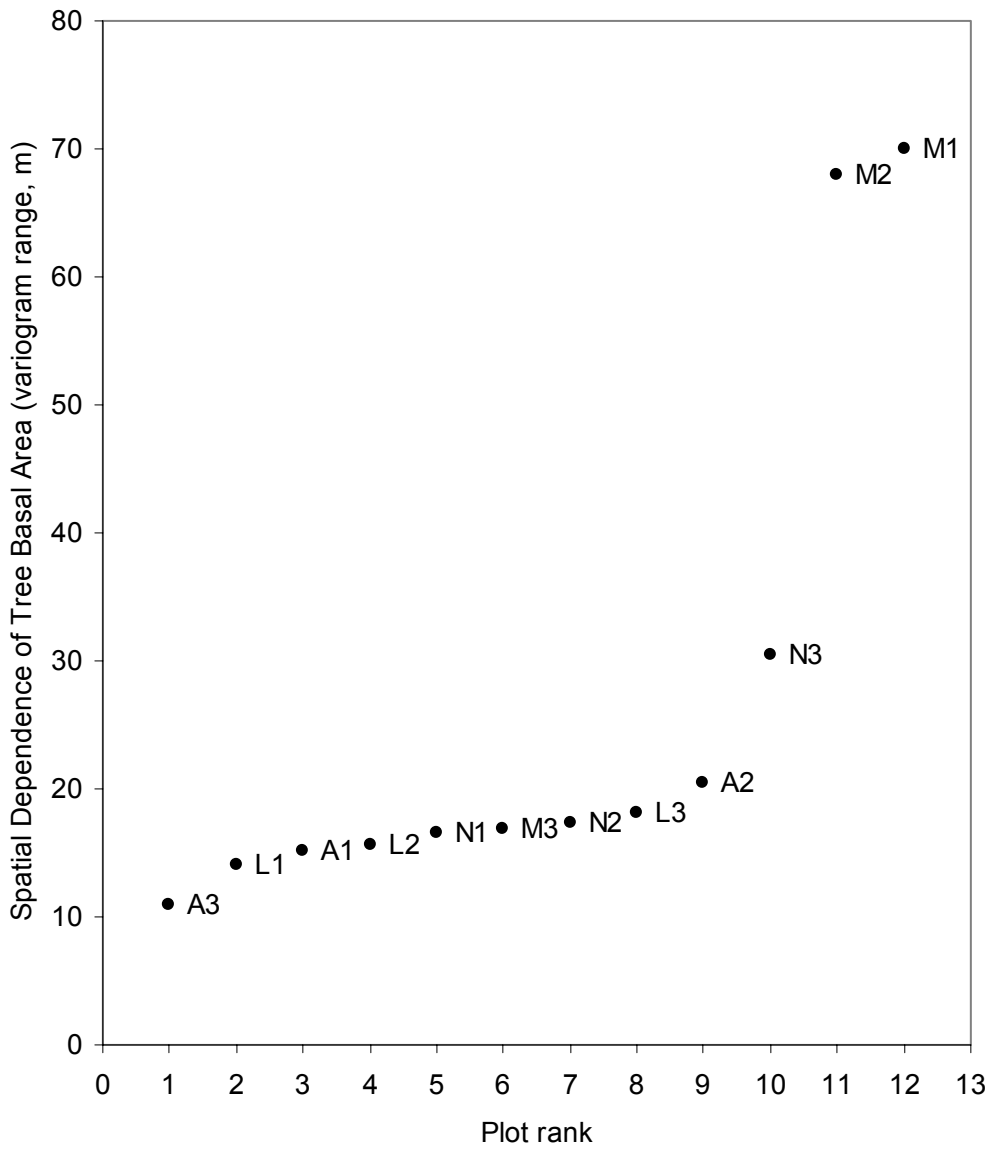


Figure 3.7. Plot rank according to spatial dependence based on unsuppressed tree basal area variogram range values for Arkansas (A), central Louisiana (L), northern Louisiana (N), and Mississippi (M) stands followed by plot number.

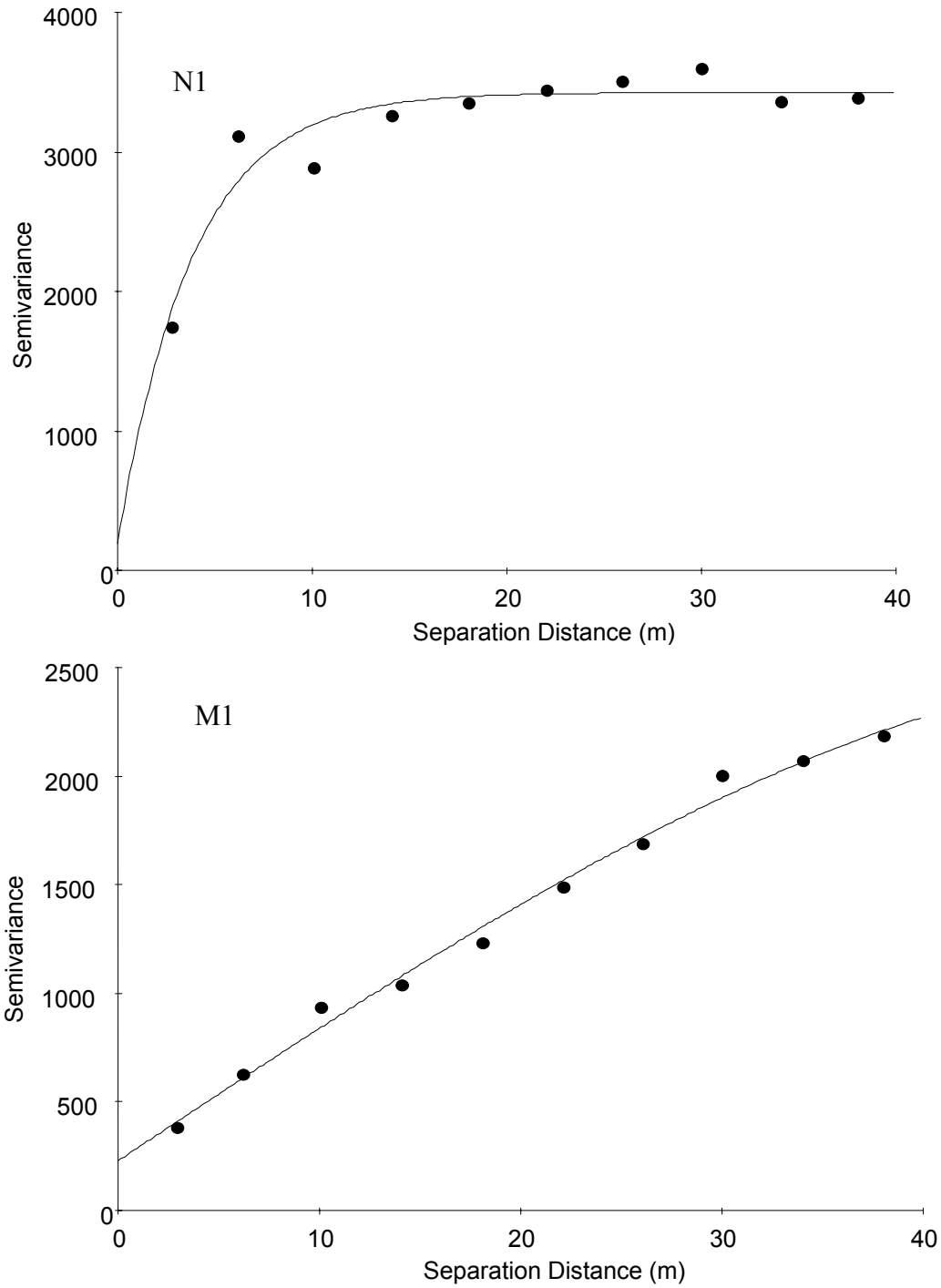


Figure 3.8. Isotropic variograms of the crown projection area for the plot with the least spatial dependence (range=11.4 m), plot 1 in northern Louisiana (N1), and the plot with the most spatial dependence (range=55.8 m, which is beyond the maximum search radius of 40.0 m), plot 1 in the Mississippi stand (M1)

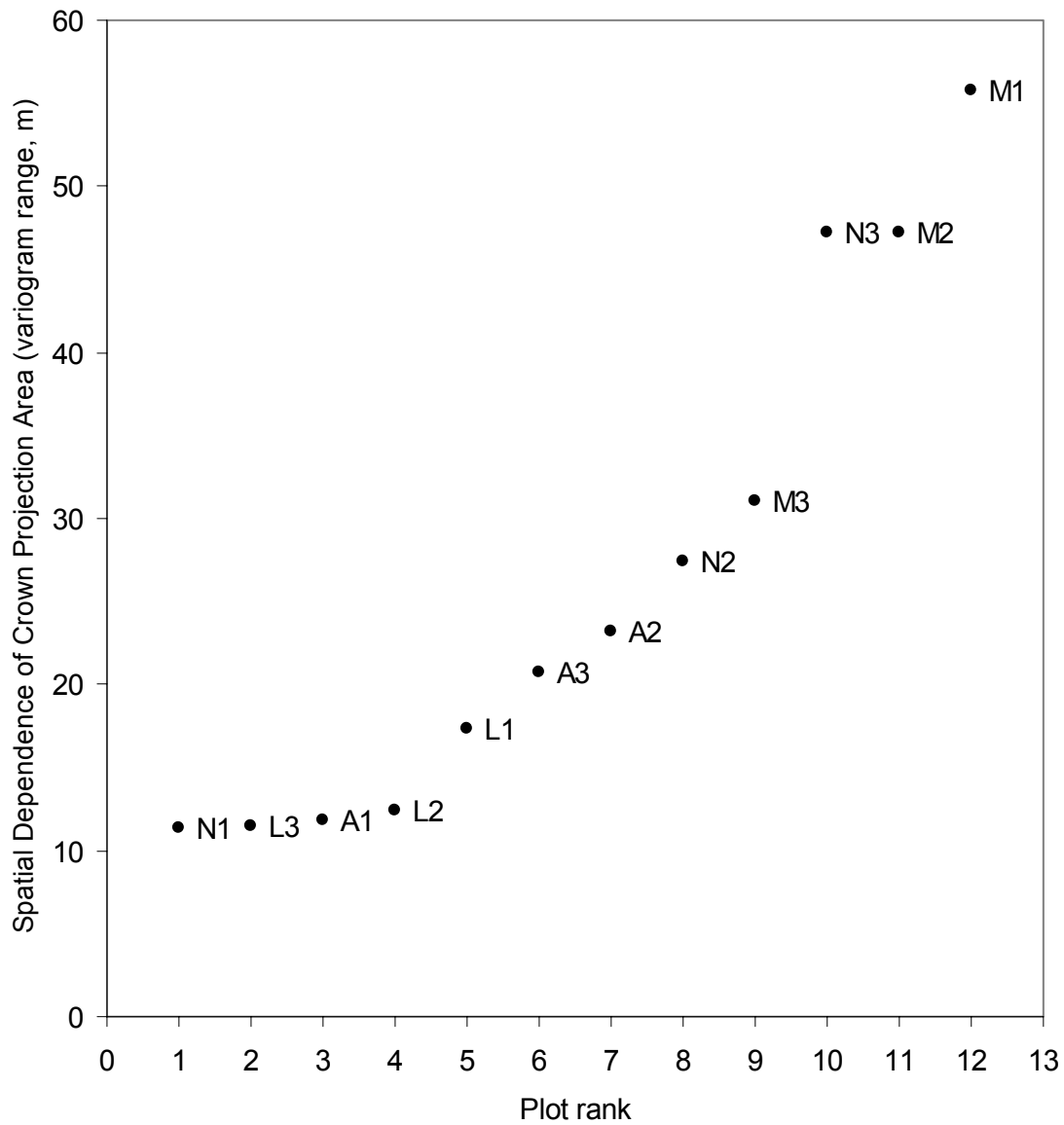


Figure 3.9. Plot rank according to spatial dependence based on unsuppressed tree crown projection area variogram range values for Arkansas (A), central Louisiana (L), northern Louisiana (N), and Mississippi (M) stands followed by plot number.

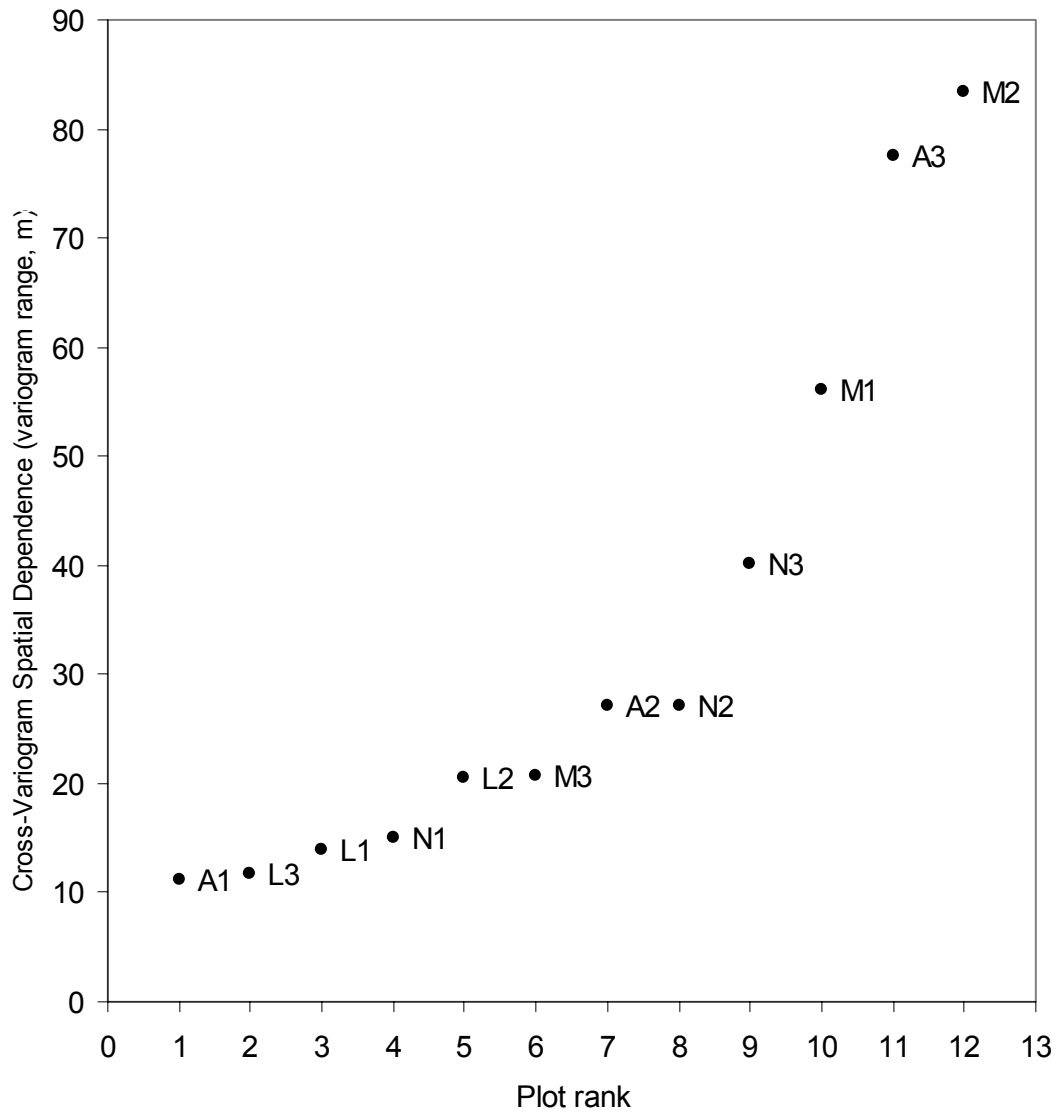


Figure 3.10. Plot rank according to spatial dependence based on the cross-variogram range of tree basal area and crown projection area of the unsuppressed trees for Arkansas (A), central Louisiana (L), northern Louisiana (N), and Mississippi (M) stands followed by plot number.

The proportion of variance that could be modeled as spatial dependence was relatively high and averaged 0.95 for the BA variograms which used all trees. The r^2 averaged 0.34. After excluding the suppressed trees from the data this proportion averaged 0.86 for the BA variograms, 0.83 for the CPA variograms, and 0.82 for the cross-variograms (the mean of $C_1/(C_0+C_1)$ in Table 3.3). The average r^2 was between 0.77 and 0.79.

3.4. Discussion

3.4.1. Spatial Continuity of the Basal Area of Trees from All Crown Classes

The average spatial dependence determined by the variograms based on the BA of all trees (including the suppressed), was 4.5 m and was equal to the quadratic mean crown radius (QMCR) of the unsuppressed trees. The spatial dependence on the plot with most spatially continuous basal area was three times as large as the spatial dependence on the plot with the least continuous basal area. Expressed as mean crown radii on the respective plot, the variogram range on the eight plots with spatial continuity above covered distances from 0.5 to 1.4 times the QMCR of the unsuppressed trees. Four plots were excluded from the above determination: two had variogram range exceeding the maximum search distance and on another two there was no spatial continuity at the studied scale (pure nugget effect).

Short variogram range (e.g., Mississippi plot 2) and pure nugget effect variograms (e.g., central Louisiana plots 1 and 2) result from pairing of trees that are located close to each other, but are very dissimilar in size. On the other hand, the presence of mostly similarly sized trees (e.g., on about half of Mississippi plot 1) resulted in a very high level of spatial continuity that extended well beyond the maximum search distance (e.g., Mississippi plot 1 and northern Louisiana plot 3).

The average spatial continuity in tree basal area (of the trees from all crown classes) was 4.5 m and might be a result of similar growth conditions at this scale. It could also result from simultaneous tree establishment within canopy gaps, similar competitive abilities among trees (if trees are genetically similar), or simply an adequate resource base. One might expect that a competitive effect would start from under the center of the crown and extend outward to some distance, probably to the edge of the crown or even farther. Therefore, it is interesting that trees at distances less than the mean crown radius had similar basal areas, rather than being dissimilar due to competition and suppression from one of the trees. When resources are limited, one tree usually becomes dominant over time to the eventual elimination of others in the sphere of influence. In contrast, when resources are not limited, the multiple trees in a sphere of influence may be able to coexist. Growth differences and other indicators of vigor within the groups may help managers to decide when trees in close proximity can be left and when the trees should be removed. Removing noncompetitors within a group may only serve to reduce stand volume without much positive effect on the residual trees. Trees within a group with similar basal areas possibly act as “trainer” trees (a tree that by its shading and abrasive action accelerates the natural pruning of an adjacent tree), rather than as competitors. .

3.4.2. Spatial Continuity of the Basal Area and Crown Projection Area of the Unsuppressed Trees

Exclusion of the suppressed trees and use of only the intermediate, codominant, and dominant trees resulted in a more extended variogram range. The spatial continuity, as determined from the average range of the two types of variograms and the cross-variograms, extended to distances from 17.6 m to 18.5 m (Table 3.3, Figure 3.11), which was 3.9 to 4.1 times the QMCR. This would be far enough to encircle the first and second order upper canopy neighbors (i.e., the immediate and the indirect neighbors), assuming their crown size is average

(Figure 3.12). The spatial dependence on the plots where it extended beyond the maximum search radius of 40.0 m (Table 3.3) was not used in determining average variogram range.

For comparison, a study in Appalachian hardwood stands (Grushecky and Fajvan 1999), where either diameter limit harvests or shelterwood seed cuts were applied, showed that spatial dependence of the residual canopy trees extends between 7.5 and 11.5 m. This distance corresponded to twice the average crown radius in the stand they studied. The 7.5 m variogram range value was interpreted by Grushecky and Fajvan as average crown diameter, or “intratree dependence”, while the larger range was called “intertree dependence” (i.e., the mean width of crown groups). Similar findings were reported by Cohen et al. (1990), who found spatial dependence to extend to twice the mean crown radius in Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) forest stands in the Pacific Northwest region of the United States. Biondi et al. (1994), however, found the spatial dependence determined by variograms of the basal area, stem diameter, and 10-year periodic basal area increment in an old-growth stand of ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws. Var. *scopulorum*) to be a constant 30 m, which was equal to the average diameter of the groups of pine that were present on the study area.

The extension of spatial dependence as far as the second order neighbors in the current study presents the challenging question of whether any of the factors discussed in previous studies describe the processes responsible for such a result. If the observed spatial continuity is influenced or caused by genetic similarity as a result of poor seed dispersal, root sprouting, or other factors, then the individual species would tend to be aggregated. This could be tested by some spatial point pattern techniques. Possible competitive effects may be another possible factor, as propagation of competitive effects beyond the first order neighbors has been reported for some plant species. Yoda et al. (1957) (cited by Harper 1977) detected presence of negative

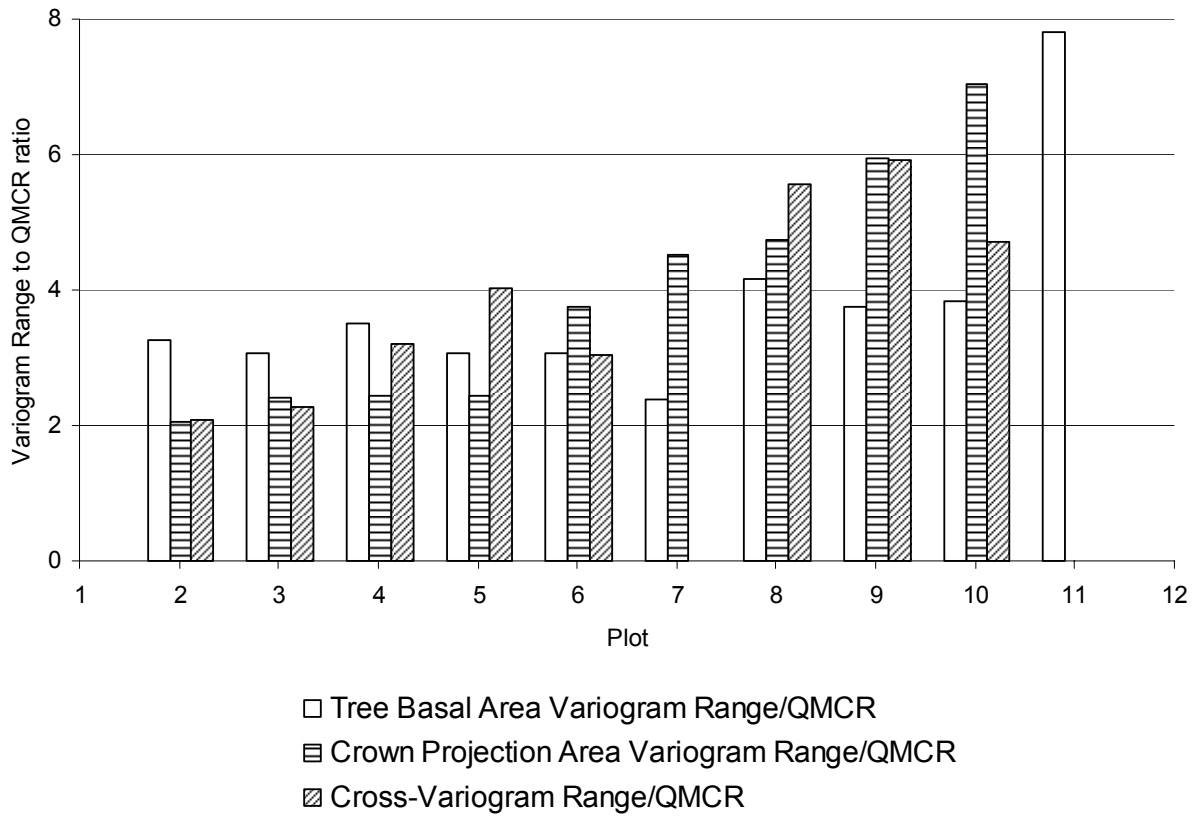


Figure 3.11. Ratio of tree basal area variogram range to the quadratic mean crown radius (QMCR), crown projection area variogram range to QMCR, and cross-variogram range to QMCR for the unsuppressed trees. The plots are ordered consecutively from small to large crown projection area variogram range. The ratio expresses the spatial dependence in QMCR units. Plots on which the variogram range extended beyond the search distance (the maximum distance at which trees are paired) are excluded.

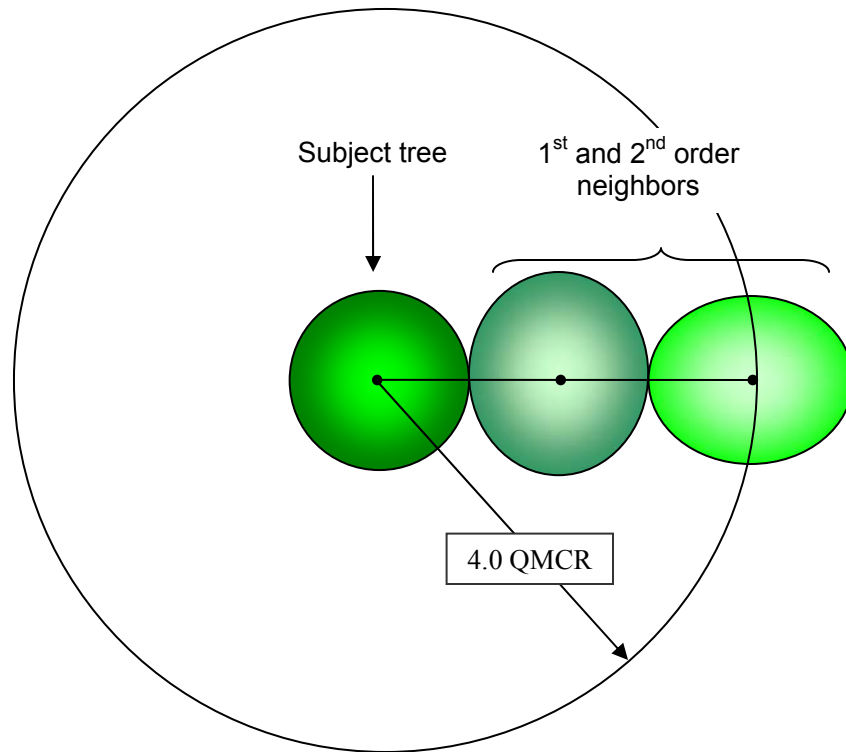


Figure 3.12. Representation of the zone of spatial dependence. According to the average range of the variograms of the basal area, crown projection area and the cross-variograms spatial dependence was present up to a distance of 4.0 times the quadratic mean crown radius (QMCR) of the unsuppressed trees. This distance is represented as a circle surrounding a subject tree and its first and second order neighbors in one direction. The trees are assumed to be unsuppressed and to have a crown radius equal to the QMCR.

correlation between the weights of individual maize (*Zea mais* L.) plants and their first, third, and fifth order neighbors, and positive correlation with the second and fourth order neighbors. If such competitive effects existed in the stands from the current study, the trees that are currently in the overstory have probably already outcompeted the trees that used to be their first order neighbors at earlier stages of stand development. If their current first and second order overstory neighbors have also overtopped their past first order neighbors, then the trees left in the upper canopy would be those that were previously second, forth, etc. order neighbors in the earlier stages of stand development. Stated differently, in the forest stand conditions studied, there exists the possibility that on the average, former first and third order neighbors were eliminated and only the presently more similar-in-size second and fourth order neighbors remain in the overstory. Oliver (1978a, 1978b, 1980) and Hibbs (1981, 1983) indicated that some oak species tend to outgrow some other initially faster growing competitors, but the oaks can eventually overtop them. Thus, rapid initial height growth does not necessarily guarantee the tree an interspecific competitive advantage over the long-term. The stand development pattern indicated by Oliver (1978a, 1978b, 1980) and Hibbs (1981, 1983) would be consistent with the one discussed in this study, where trees that in the past were first order neighbors are eventually eliminated from the overstory.

Despite the impression that thinning and release is necessary in some young mixed stands in which oaks appear to be in the process of being suppressed, such silvicultural activity may actually not be necessary. Avoiding unnecessary silvicultural operations would result in economic savings, as well as decrease in the probability of residual tree damage and proliferation of epicormic branches on some of the residual trees that have been stressed. Depending on the degree of crowding around trees that will be kept through the rotation and depending on their

vigor, thinning operations may not necessarily be needed until the stand is fairly mature. Even then, thinning may not be very beneficial, as overstory trees may not “invest” in much crown expansion at older ages.

Some studies report spatial continuity in important soil factors at distances that may impact tree growth at the observed scale (Bringmark 1989, Lechowicz and Bell 1991, Bekele 2001). Others speculate that spatial dependence of tree attributes may represent competition, soil attributes, topography, and soil parent material depending on the scale (e.g., Kint et al. 2003).

The results from the geospatial analysis utilized in this study indicated that some fairly complex intertree interactions may exist in the studied bottomland hardwood stand conditions. Further geospatial analysis of stands at different development stages and ages would provide additional insight into the spatial distribution and spatial dependence that may be present and might be influencing the direction of stand development. Such future research would certainly provide a clearer understanding of the spatial aspect of stand development and its management implication and should eventually be tied to an economic analysis for decision making.

CHAPTER 4

SPATIAL POINT PATTERN ANALYSIS IN FOUR BOTTOMLAND HARDWOOD FOREST STANDS IN THE SOUTHEASTERN U.S.

4.1 Introduction

4.1.1. Previous Work

The spatial distribution patterns of individual organisms are of frequent interest in ecological studies (Dale 2000). Early documented observations in the tropics (Wallace 1853, 1878) indicated how highly dispersed conspecific trees appear. Black et al. (1950) similarly observed that population densities of many Amazonian forest tree species are quite low with less than one individual per hectare. Janzen (1970) reported that adult tropical conspecific trees are not found in the immediate neighborhood of other adults where most seeds fall. Janzen then hypothesized that this results in tree distribution being more dispersed than clumped. He attributed this overdispersion to the effect of host-specific plant parasites and predators which exterminate the seeds and seedlings mostly at the places with higher density (i.e., near the seed producing adult trees). Connell (1971) also proposed that high degree of dispersion is likely a defense against predators on the seeds and seedlings.

The development of spatial point pattern analysis techniques allowed many of the early observations and conjectures based on less sophisticated methods to be tested statistically. Condit et al. (2000) presented empirical data indicating that larger conspecific trees are indeed less aggregated than smaller ones, supporting the notion of herbivores playing an important role in reducing conspecific aggregation at a young age in tropical species. They found that conspecific trees of nearly all of the 1768 tropical species examined are clumped. Moreover,

conspecific trees of rare species are reported as being more aggregated than those of common species (Hubbell 1979, Condit et al. 2000). Lieberman and Lieberman (1994) similarly found that conspecific trees of tropical species appear most often clumped or random and rarely overdispersed. This is confirmed by a study of canopy species in a dry evergreen forest in Thailand, where the trees of each species they studied are significantly clumped at most quadrat sizes (Bunyavejchewin et al. 2003). Other studies have also found clumping to be predominant among conspecific trees in tropical forests (Pires et al. 1953, Poore 1968, Ashton 1969, Lang et al. 1971, Forman and Hahn 1980, Pemadasa and Gunatilleke 1981, Newbery et al. 1986, Sterner et al. 1986, He et al. 1997).

Analysis of the spatial pattern of distribution of trees of nontropical species has not been as extensive. In the studies that have been done however, aggregation is also the most common type of conspecific spatial distribution pattern found. Cooper (1960) and White (1985) both documented that ponderosa pines (*Pinus ponderosa* Dougl. ex Laws.) are clumped. Moer (1993) similarly observed clumping of canopy trees in a number of conifer species in northern Idaho. In contrast to the high degree of dispersion Janzen (1970) found in young conspecific trees, Dovčiak et al. (2001) determined that the smaller seedlings of white pine (*Pinus strobus* L.) are found farther from the seed source tree than the older seedlings. Based on this finding, Dovčiak et al. (2001) suggested that the conditions near the parent trees facilitate seedling establishment and survival; otherwise, the large seedlings would have also been present away from the tree. Aldrich et al. (2003) found that trees of the same upland hardwood species from temperate forests are also aggregated, although some degree of overdispersion was observed for distances beyond 55 m. For most other distances, however, Aldrich et al. (2003) found that conspecific trees of all species are aggregated.

Tree spatial pattern is a crucial attribute of forest habitat reflecting initial dispersal patterns, intra- and interspecific competition, and the influence of microenvironment and interaction with animals. Spatial pattern affects the distribution of leaves, litter fall, nectar, fruits, and seeds (Doak et al. 1992, Dale 2000). Many of the early studies used techniques that have limited, or have had inferior, capabilities for detecting patterns of spatial distribution (i.e., quadrat methods, kernel estimation methods, and nearest neighbor analysis), especially in comparison to some new methods now available. Some more recently developed and more complex techniques examine second order effects (i.e., the $L(t)$ and $L_{12}(t)$ functions based on Ripley's K), which are described in general spatial statistics texts (e.g., Diggle 1983, Bailey and Gatrell 1995, Cressie 1991, Dale 2000). Additionally, most of the available studies investigate the spatial distribution patterns of trees from a single species, very often in isolation, and seldom examine more than one site. Use of a single study site is a problem indicated by several other authors (Lieberman and Lieberman 1994, He and Duncan 2000).

Although much is known about species composition in bottomland hardwood forests of the southeastern United States, a significant gap exists in our knowledge about their inter- and intraspecific spatial distribution patterns. The current study examines the spatial distribution pattern in a number of bottomland hardwood stands spread across a fairly substantial geographic area. This research also evaluates the pattern of (1) all plot trees regardless of their species, (2) three common and commercially important tree species – cherrybark oak (*Quercus pagoda* Raf.), water oak (*Q. nigra* L.), and sweetgum (*Liquidambar styraciflua* L.), and (3) the interspecific (bivariate) spatial patterns of each of the possible pairs of the three selected species. Bivariate spatial pattern analysis can reveal the presence of spatial aggregation (positive association) or segregation (negative association) between paired species (Lotwick and Silverman 1982,

Goreaud and Pélissier 2003). Comparison between stands was not emphasized in this analysis, as the stand differences were not of interest. The interest was in underlying overall general spatial distribution patterns that may be present in bottomland hardwood forests.

A better understanding of the distribution patterns in bottomland hardwood forest communities is critical for advancement of their sustainable silviculture and management. Knowledge of tree spatial distribution patterns has a potential to provide further insight into intra- and interspecific competitive relationships within species- rich bottomland hardwood forests. Crop tree selection and thinning decisions will be enhanced through this knowledge.

4.1.2. Introduction to Some Aspects of Spatial Point Pattern Analysis

The following brief introduction to some aspects of spatial point pattern analysis presents theory and concepts used in this study. The purpose is to familiarize those readers without background in this type of spatial statistical analysis with the methodology used. An effort is made to tailor the terminology to forestry, so the standard terms found in point pattern texts are slightly modified here. The term event (plant, animal, or other study object) is referred to here as tree or point. The term point, as it is used in this study, differs from its meaning in point pattern literature, which uses it to designate any location among events. The term intensity (number of events on a particular region) is referred to as tree density (number of trees per unit area) in this study.

One of the oldest point pattern statistics is the nearest neighbor index developed by botanists Clark and Evans (1954). This index is presently a part of a set of statistical analysis tools called spatial point pattern analysis. Unlike other forms of spatial analysis (e.g., geostatistics), where the interest is in the spatial behavior of the object's attributes, point pattern analysis focuses almost entirely on the spatial patterns of tree locations. The purpose of point

pattern analysis, as related to tree distribution, is to determine if there is any systematic arrangement of the tree locations or if they are distributed at random. If they are not randomly distributed they can be either aggregated (also referred to as clumped or clustered), or overdispersed (also referred to as hyperdispersed or regularly dispersed). Combinations of the different distribution patterns are also possible (i.e., trees can be randomly spatially distributed at a certain scale), while at other scales they may exhibit aggregation and at still other scales they can be overdispersed. If it is found that trees are not randomly distributed, the interest usually shifts to determining the spatial scales at which the systematic patterns are exhibited (Bailey and Gatrell 1995, Dale 2000). More formal definitions of the terms spatially random, aggregated, and overdispersed are provided below.

Spatial point pattern analysis describes first order (global) and second order (local) properties. The first order properties represent the pattern of the distribution across the mapped region (the contiguous sampling area). First order properties describe how the density varies in the area (i.e., the geometric center of the spatial distribution, its spread the deviation of the X and Y coordinates from their mean, and average density). The second order properties refer to the spatial patterns in subregions of the mapped area. Analyses of second order properties include the nearest neighbor distance analysis, which assesses the distance from each tree to its nearest first, second, ..., k^{th} order tree neighbor, and the K function (Ripley 1977, 1981), also referred to as Ripley's K. Ripley's K function is also referred to as index of spatial pattern (Rebertus et al. 1989). A transformation of the K function, called L function, and the approaches based on the K function are considered to be the best currently available techniques for univariate and bivariate point pattern analysis (Andersen 1992, Dale 2000).

Univariate spatial patterns are those of one type of points (e.g., conspecifics or different species that are combined for the analysis). The bivariate point patterns are concerned with the spatial distribution of individuals from one species in relation to those of another species.

The K function is determined by the equation

$$\hat{K}(t) = \frac{A}{n^2} \sum_i \sum_j \frac{I_t}{w_{ij}}, \quad (1)$$

where A is the plot area, n is the number of trees on the plot, t is a distance used as a radius of a circle around each tree, within this circle the trees are counted, I_t is an indicator function which is 1 if $d_{ij} \leq t$ and 0 if $d_{ij} > t$ (d_{ij} is the distance between the i th and j th trees), and w_{ij} is the weight. The purpose of assigning weights is for edge correction. Their use reflects the uncertainty that, for a tree close to the edge of the plot, there may be another tree outside the plot boundary that is closer to it than any of the mapped trees within the plot. The weights are calculated with the equations:

$$w_{ij} = 1 - \cos^{-1}(e/d_{ij})/\pi \quad (\text{Getis and Franklin 1987}); \quad (2)$$

$$w_{ij} = 1 - [\cos^{-1}(e_1/d_{ij}) + \cos^{-1}(e_2/d_{ij}) + \pi/2]/2\pi; \quad \text{and} \quad (3)$$

$$w_{ij} = 1 - [2\cos^{-1}(e_1/d_{ij}) + 2\cos^{-1}(e_2/d_{ij})]/2\pi \quad (\text{Haase 1995}), \quad (4)$$

where e is the distance from tree i to the nearest boundary, and e_1 and e_2 are the distances between tree i and the two nearest boundaries. Equation (2) is utilized when the distance d_{ij} is greater than the distance e between tree i and the nearest boundary. Equation (3) is used when the distance from tree i to the nearest plot corner (in a rectangular plot) is smaller than the distance d_{ij} . Otherwise, when the distance from tree i to the nearest plot corner (in a rectangular plot) is larger than the distance d_{ij} , equation (4) is used.

The L function also represents the spatial pattern at various scales and is based on a transformation of the K function proposed by Besag (1977) that linearizes $K(t)$, stabilizing its

variance, and results in $L(t)$ having an expected value of zero under the assumption of homogeneous Poisson process (a type of stochastic process):

$$\hat{L}(t) = \sqrt{\frac{\hat{K}(t)}{\pi}} - t. \quad (5)$$

Plotting $L(t)$ against t allows for examination for presence of spatial patterns. The spatial distribution pattern of the trees when $L(t)=0$ is termed complete spatial randomness (CSR). Under CSR tree distribution follows “a homogeneous Poisson process over the study region” (Bailey and Gatrell 1995, p.96). A homogeneous Poisson process is characterized by a Poisson probability distribution function, where each tree has an equal probability of occurring anywhere on the study region, and its position is independent of the position of any other tree. Values of $L(t)>0$ suggest aggregation (i.e., the trees appear to be more clumped than what may be expected under CSR), while an $L(t)<0$ indicates overdispersion (i.e., the trees are more scattered or regularly spaced than what might be expected under CSR). The significance of the difference of $L(t)$ from 0 is examined through comparison with confidence envelopes (normally 95%) constructed through Monte Carlo simulations. The term envelope is used instead of interval (or limit) in point pattern theory and literature to emphasize that unlike intervals, they are obtained through simulations. The Monte Carlo approach is the accepted method for testing the significance of the observed values of $L(t)$ (Besag and Diggle 1977, Diggle 1983, Cressie 1993, Dale 2000). The Monte Carlo procedure places n points (i.e., the same as the observed number of trees) at random in the plot with area A (i.e., the same as the area of the studies plot), as the placement of each point is independent of the placement of the previous ones. The procedure is then repeated a number of times (for example 100 times). Then the results from the observed actual tree locations in the field are compared with the results from the simulations.

For the bivariate (interspecific) spatial pattern analysis the function $L_{12}(t)$ (where 1 represents the first species and 2 represents the second species) proposed by Lotwick and Silverman (1982) is used. $L_{12}(t)$ is a transformation of the $K_{12}(t)$ function:

$$\hat{L}_{12}(t) = \sqrt{\frac{\hat{K}_{12}(t)}{\pi}} - t \quad (6)$$

where the $K_{12}(t)$ function is a generalization of the $K(t)$ function for a bivariate process and its calculation is presented in detail in several texts (Lotwick and Silverman 1982, p. 407; Diggle 1983, p. 107-108; Upton and Fingleton 1985, p. 253-254). $K_{12}(t)$ is calculated as follows:

$$\hat{K}_{12}(t) = \frac{n_2 \tilde{K}_{12}(t) + n_1 \tilde{K}_{21}(t)}{n_1 + n_2} \quad (7)$$

where n_1 and n_2 are the number of individuals from species 1 and 2, and \tilde{K}_{12} and \tilde{K}_{21} are determined by the formulas:

$$\tilde{K}_{12}(t) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} \frac{I_{t,12}}{w_{ij}} \quad (8)$$

$$\tilde{K}_{21}(t) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} \frac{I_{t,21}}{w'_{ij}} \quad (9)$$

where $I_{t,12}$ and $I_{t,21}$ are indicator functions equal to 1 if $d_{ij} \leq t$ and $b_{ij} \leq t$ respectively and equal 0 if $d_{ij} > t$ and $b_{ij} > t$ respectively (d_{ij} is the distance between the i th tree of species 1 and the j th tree of species 2, b_{ij} is the distance between the i th tree of species 2 and the j th tree of species 1), and w_{ij} and w'_{ij} are the weight associated with species 1 and 2 respectively.

Plots of $L_{12}(t)$ against t are used to represent the spatial association between species pairs at various scales. Similar to the interpretation of $L(t)$, when $L_{12}(t) = 0$ the two species are considered to be spatially independent of each other. If $L_{12}(t) > 0$, then the two species are positively associated (presence of positive dependence or aggregation) with each other, which is

interpreted in ecology as an attraction effect (Goreaud and Pélissier 2003). For values of $L_{12}(t) < 0$, the two groups are considered to be negatively associated (presence of negative dependence or segregation) with each other, interpreted in ecology as a repulsion effect (Goreaud and Pélissier 2003). The degree of aggregation and segregation is proportional to the magnitude of the difference from 0. Monte Carlo simulations are used to evaluate the significance of the difference of $L_{12}(t)$ from 0. During the simulation procedure each of the two types of points (species) is distributed independently of the other species.

4.2. Materials and Methods

4.2.1. Study Areas and Measurements

The study was carried out in four naturally regenerated bottomland hardwood stands. The stands are located in central Louisiana, northern Louisiana, southern Arkansas, and central Mississippi (Table 2.1 and 2.2). The sites of the selected stands included both minor and major stream bottoms (according to a Meadows and Hodges (1997) classification). Three plots, 80 m on each side and minimum 10% red oak basal area were established in each stand to assess tree spatial distribution patterns. Plot selection procedures involved random selection from the pool of preselected potential plots. The orientation of the plot sides corresponded to the four cardinal directions. Only trees with diameters at breast height (dbh, 1.37 m above the ground) larger than 10.0 cm were measured. The collected data included tree dbh, species, and location on the plot using a local coordinate system. The slope on all plots was less than 1%. All plots had some red oak component in their composition (13 to 73% of basal area). The instruments used for mapping of tree locations were a laser hypsometer-rangefinder for the distances and a digital angle encoder for the horizontal angles (Laser Technologies Inc., Centennial, CO, USA). Mapping was carried out by measuring the angle from north and the horizontal distance to each tree from a

point on the plot. These polar coordinates were converted to Cartesian coordinates (to the nearest 0.01 m) for the analysis. Tree diameters were measured with diameter tape to the nearest mm, distances to the nearest cm, and horizontal angles to the nearest 0.01°.

4.2.2. Data Analysis

In the current study both $L(t)$ and Monte Carlo simulations were used to examine whether the spatial distribution pattern of (1) all trees, regardless of species, within each plot and (2) the three species, cherrybark oak, water oak, and sweetgum on each plot, conformed to CSR at scales up to a $t=40$ m. This distance was equal to half the length of the plot side as recommended by Diggle (1983) and Haase (1995). The minimum number of random simulations required to construct 95% confidence envelopes to test for CSR is 19, because the confidence interval is equal to $[s/(s+1)]100$ (%), where s is the number of simulations (Leemans 1991). Generally, more simulations are done, which result in the somewhat smoother confidence envelopes, but too many simulations can take a lot of computing time. Two software packages were used at first to compare their performance and consistency in the results: SPPA v.2.0 (Peter Haase) and the Microsoft Excel add-in SpPack (George Perry, Perry 2004). It should be noted that SpPack, despite being an Excel add-in, does not use the Excel random number generator, but rather its own generator (L'Ecuyer 1999, Perry 2004). When 100 or fewer simulations are generated, SPPA constructs the upper and lower confidence envelopes by using the maximum and minimum of the simulated values for each distance t , instead of calculating a 95% envelope. If 101 or more simulations are used, then the actual 95% confidence envelopes are constructed. SpPack did not have this limitation. After determining that the results from both packages were the same, the SpPack was chosen due its slightly faster execution speed. The number of simulations used was 101 for all Monte Carlo tests.

The $L_{12}(t)$ function and Monte Carlo simulations were used to examine the spatial independence between the pairings of the 3 species (cherrybark oak and water oak, cherrybark oak and sweetgum, and water oak and sweetgum) on each of the plots. The 95% confidence envelopes were generated under the hypothesis of independence of the spatial distribution of the different species (after Diggle 1983, Goreaud and Pélissier 2003, Perry 2004).

4.3. Results

The number of trees ranged from 309 to 614 per ha (Table 4.1). Tree distribution, when all species were combined, differed significantly from random at some scale on 11 plots: 6 plots had trees that were significantly aggregated, 3 plots had trees that were significantly overdispersed, and 2 plots had trees that were both aggregated and overdispersed at some scale (Table 4.2). Departure from CSR was not detected for any scale (i.e., the $L(t)$ function was enclosed within the confidence envelopes for all distances) on one plot (Figure 4.1a). In contrast, aggregation ($L(t)$ above the upper envelope) was detected at scales of 0.0 to 1.5 m and 9.0 to 40.0 m (Figure 4.1b), and overdispersion ($L(t)$ below the lower envelope) was detected at distances between about 1.0 and 5.5 m (Figure 4.1c). For the remaining distances, the pattern was random. With the exception of the 3 plots in the Mississippi forest stand, the remaining plots that exhibit aggregation were quite consistently aggregated at the shorter distances – from 0.5 m to just over 1 m. On some plots aggregation was also detected at larger distances. On plots 1, 2, and 3 in Mississippi, aggregation was found only at distances greater than 2.5, 4.0, and 7.0 m respectively and in all 3 plots the scale of aggregation extended up to the maximum examined distance of 40 m. Overdispersion at the small distances occurred starting from about 2.5 m and extending to 5 m. Four of the 5 plots exhibiting overdispersion were those with largest quadratic mean tree diameters (QMD, diameter of the tree with mean basal area) (Tables 4.1 and 4.2).

Table 4.1. Quadratic mean diameter (QMD) at breast height (1.37 m), number of trees from 3 selected species and total number of trees from all species on the twelve 0.64 ha sample plots

Location and plot number	QMD (cm)	Sweetgum	Cherrybark oak	Water oak	All species
		(trees/ha)			
Central Louisiana					
1	34.3	84	69	17	309
2	33.0	177	22	53	378
3	34.7	109	67	33	347
Northern Louisiana					
1	28.6	206	30	30	519
2	26.1	233	58	33	578
3	26.0	239	36	14	594
Arkansas					
1	30.6	136	72	72	434
2	27.9	105	38	61	405
3	30.7	113	119	48	394
Mississippi					
1	24.8	386	39	17	614
2	27.9	389	16	3	595
3	27.5	281	17	3	544

Table 4.2. Distance intervals at which trees of all species combined are completely spatially randomly (CSR) distributed, significantly aggregated (AG), or overdispersed (OD) based on the 95% confidence envelope calculated for the $L(t)$ function. Distance intervals not listed have trees that are randomly dispersed and an asterisk appears in that column. If tree distribution is CSR at all measured scales the word “All” appears. All distances are in meters

Location and plot number	AG	CSR	OD
Central Louisiana			
1		*	3.2-3.7, 4.5-4.9
2		*	1.0-5.5
3	0.8-1.2	*	1.9-5.8, 6.1-6.4, 6.9-8.0
Northern Louisiana			
1	0.9-1.1	*	
2	0.3-1.5, 9.0-40.0	*	
3		*	4.4-5.0
Arkansas			
1		All	
2	0.5-1.5, 6.5-6.7, 10.3-12.9, 15.3-16.1	*	
3	0.4-0.8	*	2.7-4.9
Mississippi			
1	4.0-40.0	*	
2	7.0-40.0	*	
3	2.5-40.0	*	
12 plots AG=8 CSR=1 OD=5			

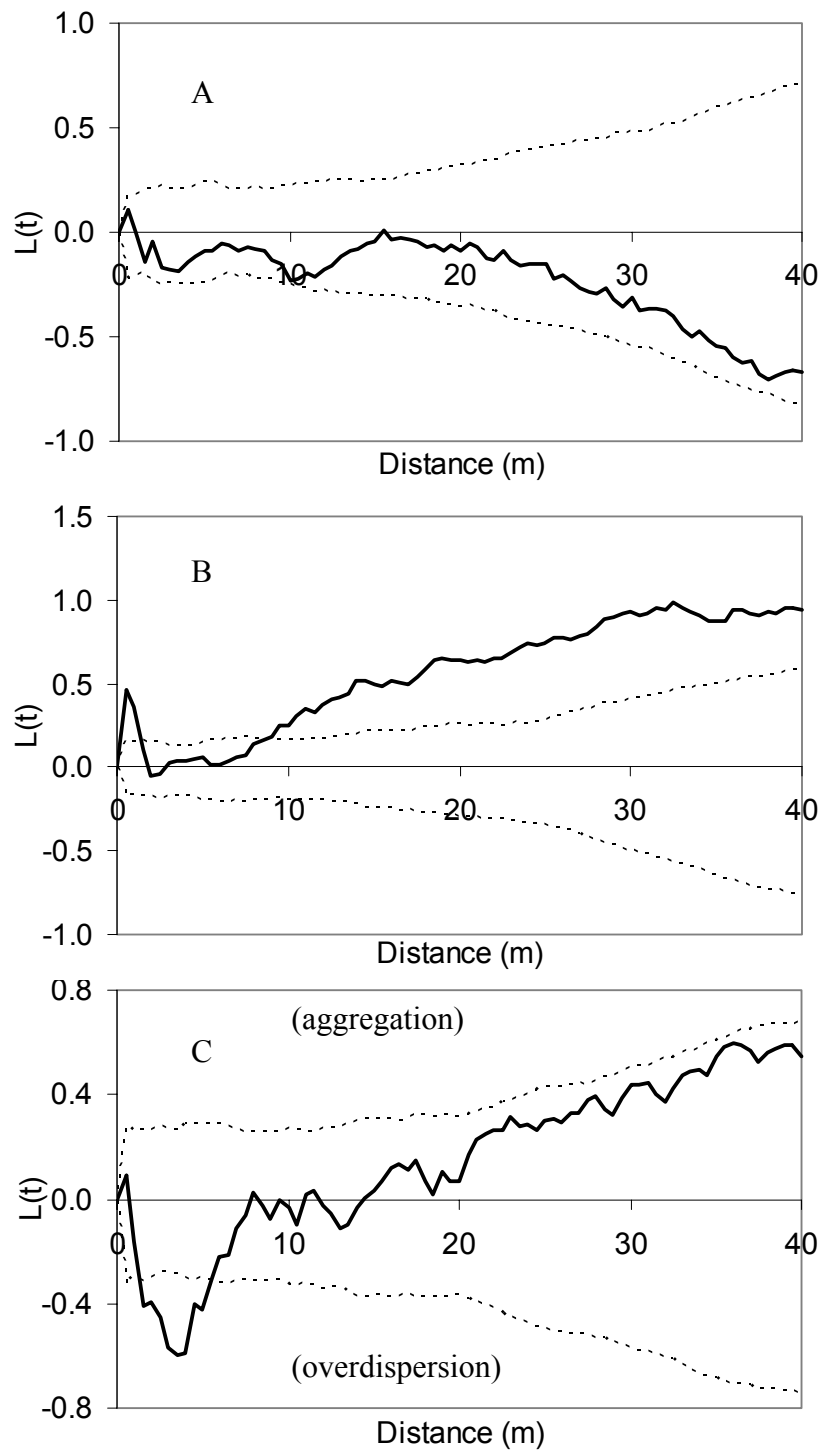


Figure 4.1. Representative sample plots of the spatial distribution patterns of all tree species according to the $L(t)$ function, which is an index of spatial pattern (thick line) against distance t . Complete spatial randomness (A) on the entire plot is present when $L(t)$ is within the 95% confidence envelope (thin lines). Aggregation at a certain distance is present when $L(t)$ extends above the upper 95% confidence envelope (B). Overdispersion is observed when $L(t)$ is below the lower envelope (C).

The $L(t)$ function for cherrybark oak, water oak, and sweetgum, when the species are examined individually, indicated that aggregation and CSR were the most common (Figure 4.2 shows 3 typical plots; see Table 4.3 for details). Cherrybark oak exhibited aggregation on 6 of the 12 plots and complete spatial randomness (CSR) on the other 6 plots. The aggregation started at distances from 5 m on 4 plots and from 12 m on 2 plots, and sometimes extended to distances up to 40.0 m. The spatial distribution of water oak was similar to that of cherrybark oak. Two of the 12 plots contained only 2 water oaks trees; consequently they could not be used for calculating $L(t)$. Of the remaining 10 plots, the spatial distribution of water oaks was not significantly different from the distribution expected under CSR on 6 plots, while on the remaining 4 plots the water oak trees were aggregated. Aggregation in water oak on 3 of the plots was detected at distances starting at 6.0, 10.0, and 15.0 m, while on the fourth plot aggregation started at a smaller distance. Sweetgum was aggregated on all 12 plots. Additionally, sweetgum aggregation commonly started at distances that were mostly shorter than those observed in the oaks – generally from less than 5.0 m. There were no plots on which sweetgum was distributed randomly for all examined distances. Although overdispersion appeared to be present on one of the plots, it was only at very large distances (37.8-40.0 m).

The $L_{12}(t)$ function indicated that segregation was a more common pattern in the bivariate spatial distribution of the pairs of examined species (cherrybark oak, water oak, and sweetgum) than aggregation (Figure 4.3 shows 3 representative plots, Table 4.4 shows the specific patterns and scales for all plots). There were 10 plots with a sufficient number of cherrybark oak and water oak pairs to perform the bivariate spatial analyses for these two species. On 6 of these plots, significant segregation between the two species was apparent, while aggregation was detected on one plot. On the remaining 3 plots the spatial distribution of each of the two species

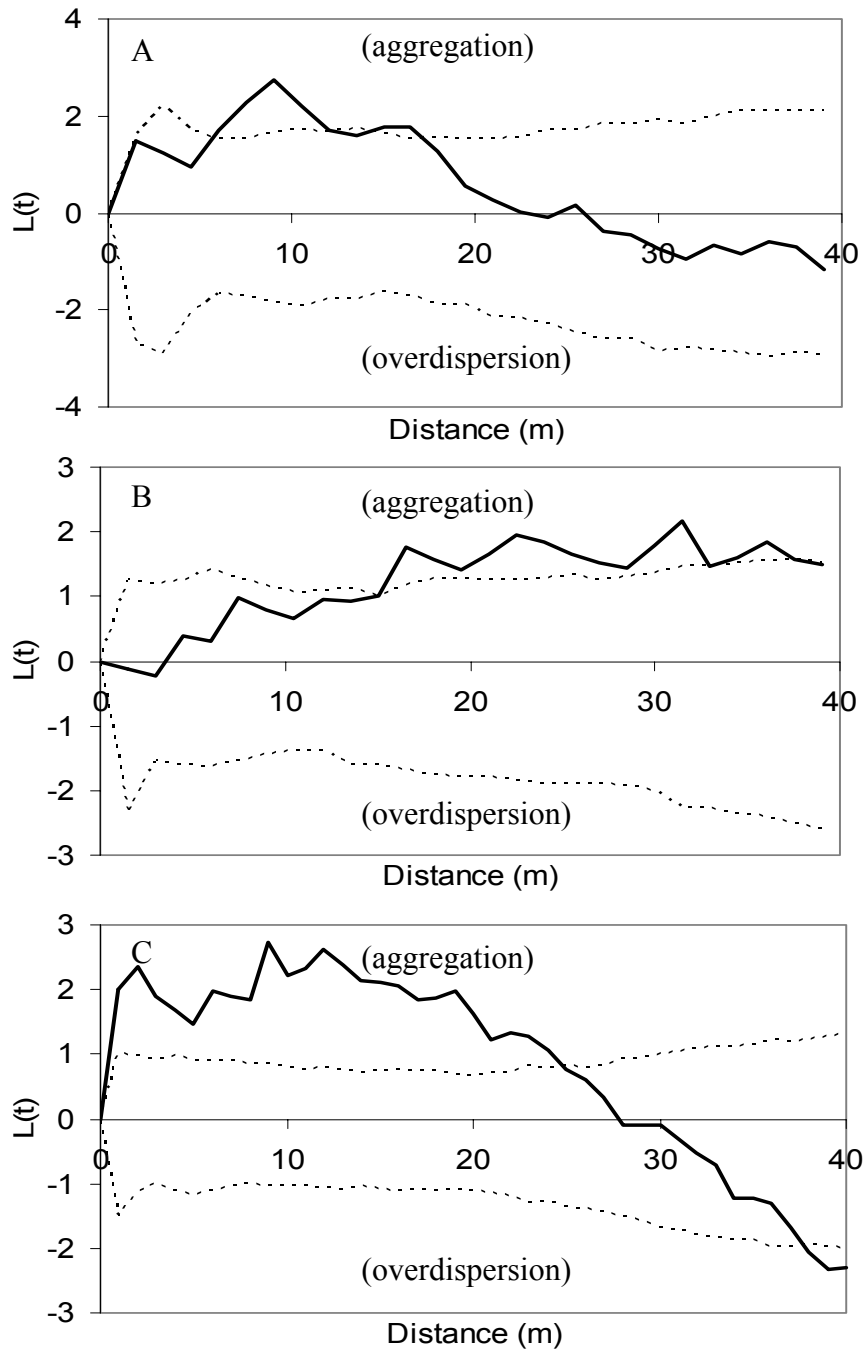


Figure 4.2. Representative sample plots of the spatial distribution patterns of cherrybark oak (A), water oak (B), and sweetgum (C) according to the $L(t)$ function, which is an index of spatial pattern (thick line) against distance t . Spatial aggregation is present when $L(t)$ is above the 95% confidence envelope (thin lines). Overdispersion is observed when $L(t)$ is below the lower envelope.

Table 4.3. Distance intervals at which trees of selected species are completely spatially randomly (CSR) distributed, significantly aggregated (AG), or overdispersed (OD) based on the 95% confidence envelope calculated for the (*Lt*) function. Distance intervals not listed have trees that are randomly dispersed and an asterisk appears in that column. If tree distribution is random at all scales the word “All” appears. All distances are in meters

Location and plot number	Cherrybark oak			Water oak			Sweetgum		
	AG	CSR	OD	AG	CSR	OD	AG	CSR	OD
Central Louisiana									
1		All			All		0.0-1.5, 17.5-32.0, 35.5-40.0	*	
2	12.0-40.0	*			All		0.0-0.5, 7.0-40.0	*	
3		All		6.0-30.0	*		0.0-1.5, 3.5-37.5	*	
Northern Louisiana									
1		All			All		5.0-40.0	*	
2	5.5-12.0, 14.5-17.0	*		0.0-2.5, 16.5-17.5	*		0.0-40.0	*	
3	5.0-11.0	*			All		2.7-40.0	*	
Arkansas									
1	12.0-14.5, 16.0-26.0	*		15.0-38.0	*		2.0-13.0, 14.5-16.5	*	
2		All		10.0-40.0	*		0.0-25.0	*	37.8-40.0
3	5.5-40.0	*			All		0.0-3.5	*	
Mississippi									
1	5.0-10.0, 25.0-40.0	*			All		2.0-40.0	*	
2		All		N/A ^a	N/A		3.0-40.0	*	
3		All		N/A	N/A		1.0-40.0	*	
12 plots AG=6 CSR=6 OD=0				10 plots AG=4 CSR=6 OD=0			12 plots AG=12 CSR=0 OD=1		

^aN/A represents a state of rarity (<9 individuals per plot) concerning water oak

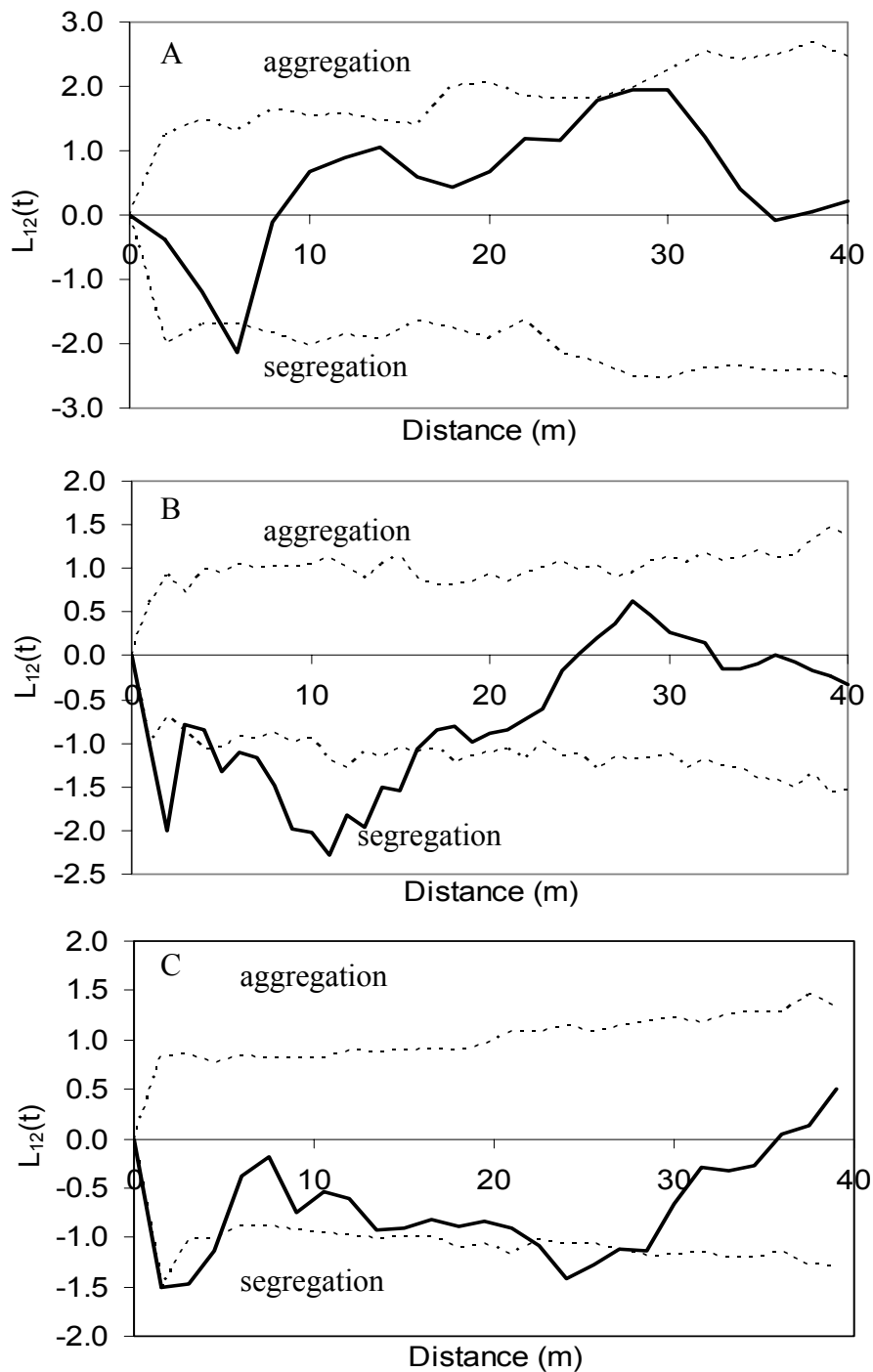


Figure 4.3. Representative sample plots of the interspecific spatial distribution patterns of cherrybark oak and water oak (A), cherrybark oaks and sweetgum (B), and water oak and sweetgum (C) according to the $L_{12}(t)$ function, which is an index of spatial independence (thick line) against distance t . Spatial aggregation is present when $L_{12}(t)$ is above the 95% confidence envelope (thin lines). Spatial segregation between the two populations is observed when $L_{12}(t)$ is below the lower envelope. When $L_{12}(t)$ is within the envelope the two populations are considered to be distributed spatially independently of each other.

Table 4.4. . Distance intervals at which trees from two selected species pairs are distributed independently (ID) of the other species, exhibit significantly interspecific aggregated (AG), or interspecific segregated (SG) based on the 95% confidence envelope calculated for the (*Lt*) function. Distance intervals not listed have an independent interspecific spatial distribution and an asterisk appears in that column. If tree distribution is random at all scales the word “All” appears. All distances are in meters

Location and plot number	Cherrybark oak vs. water oak			Cherrybark oak vs. sweetgum			Water oak vs. sweetgum		
	AG	ID	SG	AG	ID	SG	AG	ID	SG
Central Louisiana									
1		All			*	1.0-3.0, 4.5-15.8	16.5-22.5, 28.5-30.0	*	
2		* 21.0-30.0			All		22.7-40.0	*	
3		* 7.8-10.5, 13.1-15.5, 20.7-22.5			*	3.8-4.3, 7.0-8.5, 9.4-10.6	7.6-30.0	*	
Northern Louisiana									
1		All		26.3-28.2, 28.6-30.0	*			All	
2		* 5.1-6.4		30.3-40.0	*			* 7.8-40.0	
3		All			*	14.2-36.5		* 6.2-30.0	
Arkansas									
1		* 2.0-3.4, 6.2-34.2			All			* 1.0-4.0	
2		* 17.7-21.3		14.5-30.2	*	3.0-6.7		* 1.5-4.7, 22.4-27.0	
3		* 2.7-7.0, 9.5-10.6			*	0.0-5.6		All	
Mississippi									
1	19.0-30.0	*		10.0-40.0	*		0.0-4.0, 6.6-30.0	*	
2	N/A ^a	N/A	N/A		*	3.5-25.2	N/A	N/A	N/A
3	N/A	N/A	N/A		*	6.2-30.0	N/A	N/A	N/A
10 plots AG=1 ID=3 SG=6			12 plots AG=4 ID=2 SG=7			10 plots AG=4 ID=2 SG=4			

^aN/A represents a state of rarity (<9 individuals per plot) for water oak

was independent from the distribution of the other. Segregation in a wide range of scales was frequently detected in the other two species combinations as well, with the cherrybark oak and sweetgum being segregated at some scale on 7 of the 12 plots, aggregated on 2 plots, and distributed independently of each other on 2 plots. Both segregation and aggregation were detected at different scales on one plot in Arkansas (Table 4.4). The pairing of water oak and sweetgum resulted in the detection of segregation on 4 plots and aggregation on another 4 plots. On the remaining two plots there was no spatial association present between water oak and sweetgum.

4.4. Discussion

The purpose of point pattern analysis in terms of tree distribution is to examine if tree locations follow some systematic arrangement or if they are distributed at random. If the null hypothesis that tree distribution is completely spatially random at all scales is rejected, the interest shifts to determining if the pattern is aggregated or overdispersed and at what scales. As the focus is diverted to the scale at which these systematic arrangements occur, one should keep in mind that at scales that are not mentioned the trees are distributed randomly. Because a category of trees (e.g., trees from the same species or the same group of species) may exhibit rather different scales of their dispersion on different sites, the issue of most interest and importance then becomes whether there is either aggregation at any scale or overdispersion at any scale. In some cases, this may be the only common feature of their pattern across different sites.

4.4.1. Point Pattern Analyses When All Tree Species Are Combined

Point pattern analysis of all species revealed presence of aggregation on most plots, but also some overdispersion. On only one plot were the trees distributed randomly at all scales.

Four of the 5 plots that exhibited overdispersion at some distance were the plots with the largest quadratic mean tree diameters (QMD, diameter of the tree with average basal area ranged from 24.8 to 34.7 cm) compared to the rest of the plots. These were all plots in central Louisiana and plot 3 in Arkansas. The fifth plot, plot 3 in northern Louisiana, was an exception, as the mean tree diameter was among the smallest. The 8 plots where aggregation was observed were primarily the plots where tree QMD was the smallest compared to the rest of the plots. Thus, in these bottomland hardwood stands, increasing average tree size seemed to be associated with a shift of tree spatial distribution from aggregation to overdispersion. Condit et al. (2000) presented empirical data indicating that larger trees are indeed less aggregated than smaller ones. The shift from aggregation to overdispersion with increasing tree size is in agreement with the results from other studies (Moeur 1993, Ward et al 1996). Moeur (1993) indicated that between-tree competitive interactions appear to drive spatial patterns of forest trees from clustering or aggregation toward regularity (overdispersion). Ward et al. (1996) detected a shift toward overdispersion of the spatial pattern of all size classes above 10 cm in diameter, over a period of 50 years or more. Differences in the spatial pattern from plot to plot could result from different tree mortality dynamics. Pélissier (1998) indicated that large clumps of vegetation are found in areas disturbed by treefalls that create relatively large gaps, while in areas with standing tree mortality there are no large gaps and this leads to more regularity in the tree spatial distribution.

4.4.2. Intraspecific Point Pattern Analysis for Cherrybark Oak, Water Oak, and Sweetgum

The analysis of the spatial patterns of conspecifics in the current study revealed that there were some fundamental differences in the spatial patterns of the two oak species and the pattern for sweetgum. In the plots where trees of these species were sufficient for analysis, cherrybark oak and water oak spatial distributions were either equivalent to CSR, or aggregated at distances

beyond 5 m in nearly all cases (with the exception of 1 plot where aggregation began at less than 1 m). In contrast, sweetgum trees were generally clumped on all 12 plots and aggregation was usually present at smaller distances. Aggregation in sweetgum may be a result of its propensity to regenerate from root sprouts (Harlow and Harrar 1958) and its relatively narrow crown compared to the red oaks.

It is evident that for the three chosen species, overdispersion was not a common intraspecific spatial pattern. This is in agreement with the findings in a number of studies. Aldrich et al. (2003) similarly found that, out of 23 tree species in a temperate hardwood forest in Indiana, most exhibit aggregation, while only 4 species exhibit overdispersion and that was at distances of greater than 55m. Rebertus et al. (1989) found that *Quercus laevis* (turkey oak) on unburned Florida sandhills is slightly clumped to randomly dispersed. Other studies with hardwood species include the research by Call and Nilsen (2003) conducted in low-elevation hardwood forests in Virginia, which concluded that the invasive tree-of-heaven (*Ailanthus altissima* Miller) has a tendency to be aggregated at a scale of 4-12 m on 2 sites and random on the remaining 4 sites. Another species, black locust (*Robinia pseudoacacia* L.), appeared to be clumped on all sites at a minimum distance of 1 m and maximum of 25 m.

Some studies involved with coniferous species (Harrod et al. 1999, Dovčiak et al. 2001), found clumping in stands of ponderosa pine. Through stand reconstruction, Harrod et al. (1999) determined that an even larger degree of aggregation existed in historical ponderosa pine stands.

Studies in other geographic regions have obtained similar results regarding intraspecific tree spatial patterns. A large study encompassing many tropical forest conditions on two continents by Condit et al. (2000) indicated that clumping occurs in nearly all of the 1768 tree species studied. From these species, 1490 are significantly aggregated at scales of 0 to 10 m

(considering 95% confidence limits), 1759 were aggregated at scales of 10 to 20 m, and 1730 were aggregated at scales of 20 to 30 m. Aggregation is the prevailing pattern whether all trees >1cm dbh were considered, or only the trees with dbh > 10 cm were included. Even when only large trees (dbh>30 cm) were included, aggregation was again observed for most species, although aggregation intensity weakens with the increase in the minimal dbh threshold used. Other research reporting aggregated patterns of spatial distribution among conspecifics include Couteron and Kokou (1997), Goreaud and Pélissier (1999), Bunyavejchewin et al. (2003), and Goreaud and Pélissier (2003). Results from a smaller number of studies do find some cases where aggregation and CSR are not the dominant patterns among conspecifics. Penttinen et al. (1992) found both Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth.) to be overdispersed. Other species for which such shift from aggregation to overdispersion with increase in tree size is reported include sand pine (*Pinus clausa* Vasey) (Laessle 1965), *Dacrycarpus dacrydioides* (Kahikatea) (Duncan 1991), and Torrey pine (*Pinus torreyana* Parry ex Carr) (Wells and Getis 1999).

4.4.3. Interspecific Point Pattern Analyses for Cherrybark Oak, Water Oak, and Sweetgum

Aggregation was not a predominant spatial distribution pattern in the bivariate spatial pattern analysis of species pairs composed of cherrybark oak, water oak, and sweetgum, although some bispecific aggregations did occur. The prevailing distribution pattern between the cherrybark oak and water oak species pair and between the cherrybark oak and sweetgum species pair was segregation. While with the water oak and sweetgum species pair there was an equal number of plots indicating presence of either aggregation or segregation (i.e., positive or negative spatial association), segregation was still a relatively frequent spatial pattern.

The prevalence of aggregation of conspecific trees, and of segregation between trees from different species, may indicate a higher level of interspecific competition relative to intraspecific competition. Such patterns may result from the competitive exclusion of one of the species from the habitat on which the other species is better suited to thrive. For microhabitats where both species are equally well adapted, factors like initial density, height growth pattern, crown growth dynamics (Clatterbuck and Hodges 1988), and stand disturbance history will likely also exert an influence on the future bivariate spatial distribution patterns. This underlines the importance of examining more than just one plot in studies of tree spatial patterns. Some suggest that repulsion between individual trees of two different species is not a result of competitive interspecific interaction (Duncan 1991, 1993), but simply a way of avoiding such competition. Assuming fairly homogeneous site conditions (most of the sites in the current study lacked topographic variability and the slope was always less than 1%), adequate seed availability, and adequate growing conditions for all three species, it can be argued that habitat partitioning is likely a result of severe interspecific competitive interactions at an early stage of stand development. This argument is supported by Jiří et al. (2004), who found higher mortality of common beech (*Fagus sylvatica* L.) in dense patches of silver fir (*Abies alba* Mill.), which would result in interspecific spatial segregation in the future stand composition. An example of bivariate spatial pattern affected by disturbances was presented by Rebertus et al. (1989), who determined that after repeated fires a segregated pattern emerges between turkey oak (*Quercus laevis* (Walt.) and longleaf pine (*Pinus palustris* (Mill.). The oaks are left in clumps that are well separated from pines. The pines cause substantial oak mortality in their neighborhood by creating “hot spots” – areas of greater fire intensity and temperature.

The interspecific tree spatial segregation reported in the current study contrasts with the findings of a number of other studies. Martens et al. (1997) found strong aggregation of trees from two species at scales of 2 to 4 m on a semi-arid woodland in New Mexico. An overall positive spatial association was also found between *Ailanthus altissima* (Mill.) and *Robinia pseudoacacia* (L.) on 4 out of 6 plots at minimum distances of 2.0 and 9.0 m (Call and Nilsen 2003). Lack of interspecific spatial aggregation was presented by Duncan (1991) for a mixed *Podocarp* stand in New Zealand, where no spatial dependence between two studied species is present on the studied plot.

With the development of spatial point pattern analysis techniques, many of the earlier observations (Wallace 1853, 1878, Black et al. 1950, Janzen 1970) of high degrees of dispersion of forest trees has gradually given way to the statistically supported view that conspecific trees species actually appear to be clumped. The validity of this notion has been corroborated for both tropical, upland temperate, and now with the current study for bottomland temperate forests. Some of the reasons for the observed high frequency of aggregation in plant communities could be the patchiness of the suitable habitat (e.g., soil nutrient variability in patches, Hall 1971), or better light conditions when trees regenerate in canopy gaps (Williamson 1975, Newbery et al. 1986). Other possible reasons include the lack of good seed dispersal and survival of seeds at large distances from the seeding trees (Poore 1968, Ashton 1969), seedling germination being most successful near adult plants (Hubbell 1979, Sterner et al. 1986, Eccles et al. 1999), spatial variation of fire intensity (Rebertus et al. 1989) and other endogenous and exogenous stand disturbances, and positive interactions between plants (Eccles et al. 1999). At a small scale, aggregation among conspecifics may also arise as a result of stump or root sprouting. One of the

species in the current study, sweetgum, does produce root sprouts, which may explain its observed aggregation at small scales.

Random pattern in tree distribution may be related to either homogeneous site conditions (Brereton 1971) or to heterogeneous site conditions associated with the ability of a species to tolerate and thrive in a wide range of environmental conditions (Williamson 1975). Cases of overdispersion may result where competition leads to regularity in the spacing through interspecific repulsion (Cooper 1961, Laessle 1965) and is sometimes observed at a later stage in stand development following the clumped and random distributions (Greig-Smith 1952, Moeur 1993, Ward et al. 1996, Aldrich et al. 2003). Evidence from the current study suggests that, as average tree size increases, the spatial distribution pattern of the trees as a whole, regardless of their species, may shift from aggregation to overdispersion. Interspecific competition among cherrybark oak, water oak, and sweetgum may have been intense and resulted in segregation, possibly after occupation of a limited resource by the more competitive species on a particular microsite. Spatial distribution of cherrybark oak and water oak was characterized by CSR and mostly large clumps, while sweetgum always exhibited aggregation at smaller scales. The aggregation of sweetgum at these scales is possibly as a result of root sprout regeneration and narrow crowns allowing more trees to be packed in a smaller area. Any interpretations and conclusions from spatial point pattern analysis, however, need to take into account that (1) forests are complex multidimensional in nature and are being simplified to a pattern of points in this type of analysis and (2) there are numerous possible variables that can affect spatial interactions among individual organisms to result in the observed pattern of spatial distribution including time (Barot et al. 1999, Bazzaz 1990).

CHAPTER 5

SUMMARY AND CONCLUSIONS

The bottomland hardwood forests of the southeastern U.S. are a valuable renewable natural resource and a source of multiple ecological, aesthetic, and economic benefits. The importance of these forests and their ecosystems underlines the importance of their sustainable and successful conservation, management, and use. Sustainability requires a good understanding of the basic processes, relationships, and dynamics occurring within these forests. Basic knowledge regarding the origin, succession, species-site associations, silviculture, and management has been accumulating over the last several decades. However, the present day availability of efficient, accurate, and affordable instruments for mapping tree locations, coupled with the development and improvement of statistical analysis methods, makes it possible to gain a more detailed insight into bottomland hardwood forests structure and dynamics from several different perspectives. A key component of this insight is the understanding of growth and spatial relationships among trees and species in these forests.

This study examined a number of characteristics of bottomland hardwood forests that are associated with tree spatial distribution and attempted to reveal some underlying relationships that had led to the current tree distribution patterns and radial growth of individual subject trees (crop trees). The trees whose 5-yr radial growth was studied were crop trees from species belonging to the red oak subgenus – mostly cherrybark oak, but also water oak, and Nuttall oak. In addition to modeling 5-yr radial growth, some additional spatial relationships were described. These included the (1) spatial continuity (dependence) of tree basal area and crown projection area, (2) spatial distribution patterns of all trees on the study plots, regardless of their species, (3) spatial pattern of three selected species (cherrybark oak, water oak, and sweetgum), and (4)

interspecific (among trees from different species) spatial pattern of the pairs of these three species. The analysis examined the intraspecific (among trees from the same species) and interspecific competitive interactions on the studied plots.

The results from the growth analysis indicated that a relatively new crown class score rating system proposed by Meadows et al. (2001) could account for as much as 41% of the variation in the 5-yr diameter growth of selected crop trees from the red oak group. However, crown class score did not perform as satisfactory in accounting for the variation in basal area growth (30% of the variance accounted for) over the same period. Other tree attributes, crown projection area and tree height, accounted for more of the variation in basal area growth. In contrast, plot-level characteristics (i.e., distance-independent characteristics), were unable to account for any significant portion of the variability in 5-yr diameter or in 5-yr basal area growth of individual red oak crop trees. Some distance-dependent variables, however, performed better in terms of variance accounted for. In the studied stands, the basal area of trees taller than the selected crop trees and located within 2.4 mean crown radii of unsuppressed plot trees had the highest negative correlation with crop tree 5-yr radial growth. This variable accounted for nearly half of the variation in 5-yr diameter growth and a quarter of the variation in 5-yr tree basal area growth. It is likely that such trees are among the most influential competitors of the selected crop trees and are generally the ones that are to be considered for harvesting during thinning operations. If species from the non-red oak group are excluded, the correlation with crop tree radial growth decreased only slightly, suggesting that it was the red oaks that exerted the strongest competitive effects. This finding confirms results obtained with other red oak species from more northern latitudes. Another interesting finding was that crop tree radial growth was positively associated with the basal area of red oaks located between 3 and 4 times the mean

crown radius (i.e., the indirect neighbors) and taller than the crop tree. It is possible that such indirect neighbors did not interfere with the crown of the crop tree, while they probably did compete with the direct competitors of the crop tree thus having an indirect positive influence on crop tree growth.

Multiple linear regression models constructed with variables from among all independent variables achieved coefficients of multiple determination of 0.71 and 0.82 for the 5-yr growth in diameter and basal area, respectively (the dependent variables were log transformed). The model for growth in diameter contained two variables: a competition measure and the crown class score. The competition measure was the ratio between (1) the basal area of the trees that are taller than the subject tree and located between 3.5 and 11.0 m away from the subject tree and (2) the basal area of the subject tree. For the basal area growth model there were three selected variables: the first two were the same as in the model for growth in diameter and the third variable was the initial tree diameter. When the initial tree diameter and initial tree basal area were not allowed in the model, so the model reflected only variables that can be influenced through silvicultural treatments, the variance accounted for decreased from 0.82 to 0.75.

The geostatistical analysis performed in the second part of the study showed that spatial continuity of the unsuppressed trees extended to a distance equal to 4 times the mean crown radius. This result was fairly consistent whether the variable that was used to calculate the experimental variograms was tree basal area or crown projection area, or whether a cross-variogram of these two variables was utilized. In this study, spatial continuity may represent a distance that encompasses an overstory tree and its first and second order neighbors. As indicated in studies with other plant species, competitive effects can extend as far away as the fifth order neighbors and can result in similar plant size with the second and fourth order

neighbors, but dissimilar size with the first, third, and fifth order neighbors. In the study stands, it is therefore hypothesized, that current first order neighbors might represent what in an earlier stage of stand development could have been second order neighbors. Competition, growth, and stand development may be what caused the removal of these competitors or their delegation to a suppressed crown class. Thus, some highly competitive trees may extend their effect on other trees farther from their immediate neighbors – by negatively influencing their growth they may be beneficial to their indirect or second order neighbors. Such speculation appears to be confirmed by this study in the analysis of growth of individual crop trees. There was an apparent positive relationship between crop tree 5-yr radial growth and the basal area of the trees that are just beyond its direct neighbors (i.e., between about 3 and 4 average crown radii away).

A number of available studies investigated the spatial distribution point patterns of forest trees, but such analyses are often carried out for the species in isolation. Additional limitations of previous studies include usually examining one site and the use of small plots relative to the size of the trees, especially the studies done outside of the tropics. The current study used data from 12 plots of 0.64 ha each located in 4 stands that are distant from each other. The analyses were carried out for 3 individual species, but also for 3 bispecific combinations and for the combined species. Spatial point pattern analysis indicated that, overall, trees in the studied stands were most often aggregated and sometimes overdispersed, while complete spatial randomness (CSR) was much less common (CSR detected on only one of the plots). The results supported the notion that as trees grow and capture resources that were previously available to other individuals their spatial pattern shifts from aggregated to overdispersed.

The univariate (intraspecific) spatial pattern analysis of the individual species cherrybark oak and water oak was characterized by CSR and aggregation, with aggregation usually

occurring at distances of 5 m or more. In contrast, sweetgum was much more aggregated and this aggregation occurred at shorter distances than with the oaks. Aggregation appears to be a fairly common univariate spatial pattern in many individual species from both temperate and tropical regions.

The bivariate (interspecific) pattern analysis between the three species – cherrybark oak, water oak, and sweetgum indicated that trees from different species are often spatially segregated. One exception was the pair water oak-sweetgum, where trees were overdispersed or aggregated on an equal number of plots. This suggested that there could be a negative association between the species. These findings are in contrast to most studies examining between-species patterns. Such studies, all of them using different species from the ones in the current study, often do not find presence of interspecific spatial segregation between tree species. Species spatial segregation supports the theory of habitat partitioning. If each species had an equal chance of initial establishment, it can be argued that because all three studied species could grow across the studied plots, then the better adapted species for particular microsite perhaps outgrew (outcompeted) the other species at earlier stages of stand development; this could have resulted in partitioning of the available site according to microsite variability. Although the observed habitat partitioning may reduce interspecific competition at later stages of stand development, the partitioning is indeed a likely outcome of a severe interspecific competition in the past. Although some interspecific aggregations were observed, they were generally not as prevalent as segregation, especially in the combinations that contained cherrybark oak.

As spatial point pattern analysis techniques were refined, earlier observations contending that high degree of dispersion in forest trees existed were gradually replaced by the results of numerous studies demonstrating quite the opposite notion in tropical and temperate forests.

Likely causes for the prevalence of aggregated patterns for intraspecific distributions include habitat patchiness, gap dynamics, sprouting, lack of adequate seed dispersal and high survival rate far from the seeding trees, and even fire intensity effects. On the other hand, a factor that possibly leads to random pattern could be the lack of heterogeneity in site conditions.

Overdispersion may result when competition leads to regularity in tree spacing through interspecific competition. Therefore, overdispersion is often considered a later stage in stand development.

Some of the conclusions based on results from the spatial point pattern analysis may initially seem to contradict conclusions from the analysis of crop tree radial growth. Regression analysis indicated that red oaks may exert the most negative influence on the 5-year radial growth of selected crop trees, suggesting strong intraspecific and intragenus (between trees of the same genus) competition. Point pattern analysis, however, indicated that intraspecific competition may not be as strong as interspecific competition, because individual species appeared to be mostly aggregated while pairs of species exhibited mostly spatial segregation. However, it is important to take into account that the observed patterns of spatial distribution were likely a result from lifelong developmental patterns within stands. Additionally, trees of nearly all sizes were included in the point pattern analysis. Crop tree growth, on the other hand, is modeled for only the previous 5 yr and only overstory trees were used in the radial growth models. Thus, the different types of examined trees in the two analyses make it clear that the results from them do not contradict.

The analyses in the studied mixed bottomland hardwood stands suggested an existence of a complex web of influences. Regression analysis of growth indicated that in these conditions, the effects of tree competition were detectable as far as the second order neighbors.

Geostatistical analysis demonstrated that spatial dependence extended to distances that were commensurate with those found in the radial growth analysis. In addition, over 80% of the variation in tree basal area and crown projection area could be modeled as spatial dependence. Other spatial characteristics in these stands were revealed by the use of point pattern analysis techniques. Analyses of effects among conspecific trees (trees from the same species); among individual trees from pairs of the species cherrybark oak, water oak, and sweetgum; and among individual trees when all species are combined suggest that over the long term, strong interspecific competition may have resulted in segregation of the trees from selected species, while weaker intraspecific competition may have led to within-species aggregations at different scales for different species. Strong intragenus competition, however, had a strong short term (5 yr) influence on radial growth of individual red oak crop trees. The smaller and suppressed trees in the vicinity of overstory red oak crop trees were not a likely source of competition in the studied stands. This suggests that under the studied conditions, understory and midstory removal might not be necessary to increase short term radial growth of the overstory. Although intraspecific competitive effects might be weaker than interspecific effects at earlier stages of stand development and result in higher probability of conspecific aggregations, the presence of tall vigorous conspecific trees and trees from the same subgenus may still impede the short term growth of red oaks. Therefore, thinning efforts may be most beneficial if they concentrate on tree removal only from the upper canopy stratum. It should be recognized, however, that in some instances coexistence of certain aggregations of vigorous conspecific trees may occur. Under such circumstances, tree vigor and condition may be a more important consideration than proximity to neighboring overstory trees with respect to deciding if the tree should be removed. The crown class score can be used as an indication of such tree condition and vigor. Future

research efforts focused on identification of conspecific aggregations and following their temporal attributes, in addition to spatial development attributes, may provide further insight into the processes and conditions that drive stand development and determine such outcomes. Additional understanding could also be gained by examining the patterns of distribution among more than two species and by linking tree aggregations to microsite and growth related factors.

Findings of this study regarding the competition among individual plants and the spatial and temporal forest dynamics may be very useful in predicting changes in the abundance of tree species resulting from stand succession (Huston 1991). The relationships explored and found in this study might also be useful in development and improvement of individual-based forest competition and succession models similar to and including JABOWA (Botkin et al. 1972), FORET (Shugart and West 1977), and SORTIE (Deutschman et al. 1999).

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APPENDIX

AN INTRODUCTION TO SOME GEOSTATISTICAL METHODS

A basic principle in geostatistics is that samples located closer in space are more related and similar than distant ones, or in other words, they are more continuous. Spatial continuity is concerned with the relationship between the values of a variable at one location and the values of the same or a different variable at another location. Spatial continuity is often classified as structural and stochastic (Rossi et al. 1992). The former involves variability across many sample locations and is what geostatistics is mainly concerned with, while the latter deals with small-scale correlation at distances less than the separation distance between samples. The semivariogram (also referred to as variogram), a statistical model of structural spatial dependence, is the most often used tool in geostatistics for characterizing spatial continuity (Isaaks and Srivastava 1989). The variogram measures the degree of similarity among the values of a variable when the samples are at consecutive distances (lags) away from each other and in a specified direction from each other. The semivariance function is thus estimated for each lag distance and direction by the formula:

$$\hat{\gamma}(h) = \frac{1}{2n(h)} \sum_{s_i - s_j = h} (y_i - y_j)^2 \quad (1)$$

where $\hat{\gamma}(h)$ is the variogram estimator (estimate of the semivariance); h is the separation vector; $n(h)$ is the number of pairs separated by vector h ; s_i and s_j are the locations of points i and j , and y_i and y_j are the values of variable y at these locations. Although the theoretically correct name is semivariogram, because the value is divided by two, in the literature this is frequently shortened to simply variogram, and will be used similarly here. Normally, a certain amount of tolerance for the separation distance and direction is required, because there will rarely be another sample located at the exact separation distance. As the distance between the samples increases, so usually does the difference between the sample values, which results in a larger semivariance.

When plotted for different distances, the semivariance values form a line called the sample (or experimental) variogram (Figure A.1), where the semivariance level tends to increase with separation distance up to some particular distance, after which it levels off, or at least does not fluctuate as much. The sample variogram can be approximated by a model variogram calculated using the least squares method or other methods as a fit criterion. The ordinate at which the model variogram levels off (by convention this is at 95% of the distance from the abscissa axis to the asymptote) is referred to as the sill (designated as $C_0 + C_1$ in Figure A.1). The distance (the abscissa) at which the sill is reached is called the range (designated as A in Figure A.1). The sill represents the variance of the random variable as well as the average maximum variogram value achieved at large separation distances, while the range represents the distance up to which the samples appear to be spatially dependent. In geostatistics the intercept of the model variogram and the ordinate axis (designated as C_0 in Figure A.1) is referred to as the nugget effect or nugget variance and represents the random component of the spatial structure. (The term traces its origins to gold mining and refers to the discontinuity obtained when golden nuggets were found outside of the spatially continuous seams of ore (Liebhold et al. 1993)). The main reasons for the occurrence of nugget effects are either the presence of spatial variability below the minimum lag distance, or errors in the measurements of spatial locations, or both. The distance between the sill and the nugget variance is called the structural variance (designated as C_1 in Figure A.1) and the ratio between the structural variance and the sill represents the amount of variance that can be modeled as spatial dependence (Rossi et al. 1992). According to its direction, a variogram can be (1) isotropic (omnidirectional) when the spatial dependence is a function of the distance between the samples only, and (2) anisotropic (directional) when the spatial dependence is also a function of the direction.

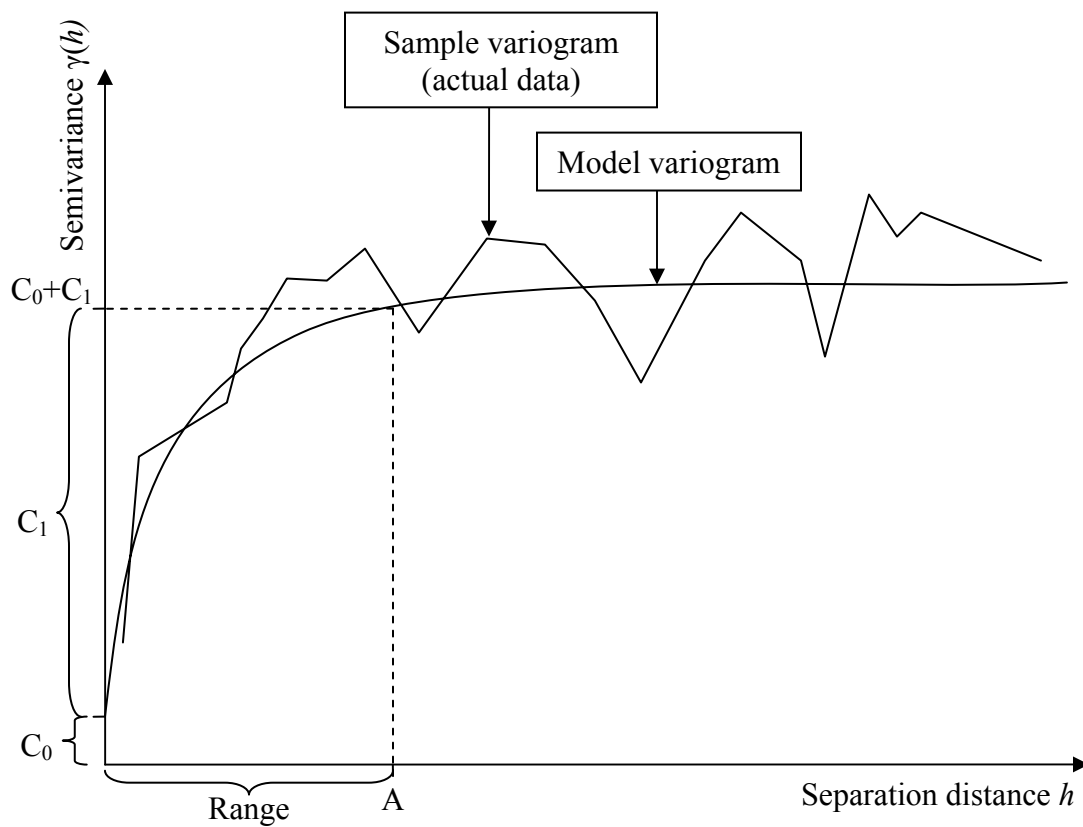


Figure A.1. Sample diagram illustrating variogram parameters. The abscissa of the point where the model variogram levels off is the range (A) and the ordinate of the same point is the sill (C_0+C_1). The nugget variance is the intercept (C_0) and the difference between the sill and the nugget variance is the structural variance (C_1).

The notion of the variograms, where the pairing is between values of the same variable y at different locations, can be extended to pairing the values of two different variables y and z at different locations to find how they co-vary spatially. This is done through the cross-variogram estimated by the following function:

$$\hat{\gamma}_{yz}(h) = \frac{1}{2n(h)} \sum_{s_i - s_j = h} (y_i - y_j)(z_i - z_j) \quad (2)$$

where $\hat{\gamma}_{yz}(h)$ is the cross-variogram estimator of the two variables y and z and the other parameters are as in equation (1).

Because the variogram is rather susceptible to influence by outliers, a less erratic function that can be used to aid in determining the range and anisotropy is the madogram (Deutsch and Journel 1992). It is determined as in formula (1), except that the exponent is replaced with one. This allows for some previously outlying observations to appear less inconsistent with the general trend. The madogram however, is used for confirming the range and nugget effect of the variogram (Goovaerts 1997), rather than being used by itself.

VITA

Luben D. Dimov obtained his Master of Science degree in forestry in 1998 from the University of Forestry in Sofia, Bulgaria (no intermediate awarding of Bachelor's degree). During his studies at the University of Forestry he was involved in research projects related to forest ecology, silviculture, and management of uneven-aged mixed forests. He spent a year of work and training experience in plant nursery production in Thetford, England, through the support of the University of Forestry and the International Plant Propagator's Society. Luben gained additional research experience in the Department of Biology at the University of Zagreb, Croatia, under the auspices of the Central European Exchange Program for University Studies, where he was involved in oak tissue culture research. While attending the School of Renewable Natural Resources at Louisiana State University he was involved in a wide range of research activities including work related to the spatial aspects of tree growth and distribution in bottomland hardwood forests and the ecology and silviculture of natural hardwood stands and plantations. Luben gained some teaching experience by lecturing in the undergraduate classes in forest ecology and silviculture and management of hardwoods, as well as in the graduate class research methodology. He satisfied the requirement for a split minor in experimental statistics. He attended and presented at a number of professional meetings and was actively involved with recruiting activities at the School of Renewable Natural Resources at Louisiana State University.