To the Graduate Council:

I am submitting herewith a dissertation written by Thomas W. Doyle entitled "Competition and Growth Relationships in a Mixed-Aged, Mixed-Species Forest Community." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

H. H. Shugart, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

The Graduate School

COMPETITION AND GROWTH RELATIONSHIPS IN A MIXED-AGED, MIXED-SPECIES FOREST COMMUNITY

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Thomas W. Doyle

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ABSTRACT

The purpose of this research was to investigate the nature and extent of intertree and interspecies competition in a mixed-aged, mixed-species mesic hardwood forest in southern Appalachia. The study focused on competition and growth relationships as influenced by community structure and development, climatic conditions and species interaction.

Sampling involved coring and mapping study trees and neighbors above 2.54 cm dbh on circular .08 ha plots. Study plots were selected to maintain site homogeneity and species complement with respect to pure and mixed stands of tulip-poplar, Liriodendron tulipifera L., and white oak, Quercus alba L. Each plot was centered about subject tree pairs composed of pure and mixed associations of these two species. Measurements of diameter, crown class and core orientation were taken along with tree azimuth and distance from plot center. Cores were crossdated and measured to determine age, sapwood basal area and ring width for years 1930 to 1981.

A computer program was written to recreate plot and tree configurations in order to calculate and test newly proposed competition measures along with established indices. These indices were evaluated on their performance under different competitor selection criteria and assumptions. Paired tree comparisons were employed to examine competitive intensity between trees in intra- and inter-specific associations.

Forest structure dictated the primary competitive influence in these mesic, mixed-aged, mixed-species stands. While horizontal spacing and density of trees has been emphasized in the design of most competition indices, vertical stratification and differential resource partitioning of light proved most significant. New competition indices, sapwood basal area and a crown-area estimate, demonstrated the highest correlations of all measures evaluated. Success of these indices was attributed to their strong relationship to leaf area and a tree's structural position and expanse to intercept available light. Increased spatial and positional variation in stand structure through time accounted for stronger competitive relations in latter growth years. The relationship between competition and annual growth was strengthened in years of climatic extremes, such as drought years. Differences in competitive ability by species was demonstrated. White oak proved more drought tolerant and a more intense competitor. Results indicated that both intra- and interspecific association can give rise to greater competitive interaction depending on the species, stand and site conditions involved.

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CHAPTER I

INTRODUCTION

Plants in close proximity to one another modify their immediate environment in ways that may result in restricted growth and development (Milthorpe 1961). This interactive process has been defined as competition. Though not fully understood, competition and the mechanisms by which plants exert stress upon one another may be both direct and indirect, biotic and abiotic. It is thought that competition occurs when the supply of resources shared between two or more individuals falls below their combined demands (Clements et al. 1929). These resources include those factors or elements necessary for growth and survival, namely light, water, carbon and nutrients. While competition may indirectly represent the struggle under limiting conditions, there is also evidence to support antagonistic reactions whereby certain plant species retard the growth and establishment of other individuals or species through chemical inhibition (Rice 1974). Because of the complex and pervasive interactions involved on both the individual tree and species level, competition remains a difficult plant growth process to examine directly.

Competition among trees is generally measured as a function of growth, or the lack thereof, from what might otherwise be expected under open-grown conditions. Most forest and crop yield studies evaluate competition from mean growth performance in relation to mean spacing and density (Harper 1961, Harper 1977). This approach

works favorably where individuals are artificially planted into evenly distributed and maintained growing units, as in monocultures. In unmanaged stands, however, the proximity, size and species of competing individuals may vary greatly from the mean stand condition and composition. This shortfall has warranted the development of spatially explicit and size-weighted expressions known as competition indices.

Competition indices represent an attempt to incorporate those factors and dimensions which best describe a tree's ability to exploit the available resources relative to its neighbors. In general, they consider the size, number and distance of neighboring trees, but vary in mathematical design and detail, ranging from simple competitor density values to elaborate crown geometry estimates. Four major types are recognized: (1) stand density measures, (2) influence-zone overlap indices, (3) distance-weighted size ratios and (4) growing-space polygons. Relative size indices (Spurr 1962, Curtis 1971, Glover and Hood 1979) assume that the distribution of resources and growth is proportional to the individual tree's dbh or basal area with respect to its competitors or a site maximum. Zone overlap models (Staebler 1951, Newnham 1966, Opie 1968, Gerrard 1969, Bella 1971, Keister 1971) evaluate competition from the sum or percent of presupposed open-crown overlap shared between competing individuals. Distance-weighted size ratios (Hegyi 1974, Monserud and Ek 1977) define the competitive effect as the sum of ratios of subject tree and competitor size times the inverse distance between them. Growing-area

polygons (Brown 1965, Moore et al. 1973, Adlard 1974, Pelz 1978) represent geometrical designs to calculate non-overlapping crown area of subject trees as limited by the proximity and size of neighboring trees. Samples of the most successful of these indices have been incorporated into this study and are discussed more fully in the methods section.

An unresolved problem with implementing any competition index arises with determining which neighbors are actual competitors and to what degree (Liu 1982). It is hypothesized that there exists about every tree a relatively circular area wherein the tree vies for resources essential to its growth (Aaltonen 1926, Rogers 1935). This area is referred to in some studies as the tree's influence zone (Opie 1968). Competition is then determined by the extent to which surrounding trees encroach on each other's space. The radius of the encroachment zone depends mostly on the type of index employed. Stand density and relative size measures generally employ a fixed radius approach, assuming that all competitors lie within a net distance regardless of tree size (Hegyi 1974). Zone overlap indices specify competing neighbors as those whose influence zone intersects with that of the subject tree, based on crown spread of open-grown trees the same size (Staebler 1951). This approach allows large trees to be potential competitors even though they may stand more than a fixed distance from the study tree. Designating competitors that limit individual crown area, as in the polygon models, differs based on the concept and subjectivity of the originator. Other less

noted selection methods include angular dispersion criteria (Newnham 1966), quadrant searches (Lin 1974) or choosing the first nth nearest neighbors (Thompson 1956, Prodan 1968, Liu 1981).

Competition may not be equal for trees of different age, size, or species, nor for the resources they demand. Light, for example, is essentially a vertically distributed resource whose interception is related to individual crown area and forest canopy structure. However, competition indices and competitor selection are almost exclusively based on horizontal stem spacing and size. While crown architecture dictates the quantity and quality of light absorption, root development influences water and nutrient uptake. This involves below-ground processes of which little can be observed or measured directly. Competition models assume that the above-ground condition also adequately describes the below-ground processes and conditions as well. Stiell (1970) found crown competition to be related to crown size and position, while root systems overlapped and were widely dispersed indicating that root competition is highly diffuse. It is not known to what degree the balance between the shoot and root systems, or the lack of methodology to account for their differences, affect the ability to better account for growth loss due to competition.

In the same manner that individual trees may be differentially positioned to exploit the pool of available resources, so might species characteristics intensify or ameliorate structural positioning to some degree. Several attempts have been made to include species

weightings in competition indices mainly as an effort to reduce unexplained growth variation (Bella 1971). However, this approach has yet to be applied in determining whether plants of the same or different species compete more or less intensively with one another.

Most of the research on inter- and intra-specific competition has focused on agronomic crop plants where yield is evaluated in monocultures and mixed species plantings under controlled environmental conditions (Harper 1977). Competition theory states that intra-specific competition should be more intense than inter-specific competition because individuals of the same species are more likely to demand and use the same resources than are neighboring individuals of different species (Miller 1967). While this idea has much logical appeal, there is reason to believe that competition may be more intensive between tree species than within species. Plants, unlike animals, with few exceptions are sessile and similarly rely on light, water and nutrients for growth. Some tree species are likely to use any of these essential resources more efficiently than another species, therefore exerting more competitive force from differential exploitation of a single limiting resource than the combined demands on all common resources (Tillman 1982).

The evaluation of competition-growth relations is further complicated by the confounding influence of other growth regulating factors, such as tree history, genetic attributes, microsite conditions, climatic fluctuations and chance events (Major 1951, Bella 1971). The degree of success of any individual may well be predetermined by

the fortuitous timing and circumstances of its early establishment (Ross and Harper 1972). While tree size is generally used as a measure to gauge potential growth, it may more aptly constitute the cumulative competitive and climatic effects under which it has developed over its life history (Bella 1971). Explaining the variation in growth not accounted for by major growth-limiting factors, climate and competition, presents a formidable task of accounting for less observable differences of genetic expression, site condition and past history.

Competition may restrict growth to such a degree as to induce tree death. Mortality, whether due to competition or other cause, changes the forest environment and competitive conditions in ways that may bring about increased growth. The degree or ability of individuals to respond to competitive release depends primarily on the extent of disturbance, proximity and position to the opened environment, as well as tree history. Because of the dynamic nature of forests, competition is neither static in time nor space.

Research Outline and Objective

The purpose of this study was to implement a multilevel field design to examine the nature and extent of competitive interactions in a mixed-aged, mixed-species forest community. Analyses focused on competition-growth relationships on the individual, species and community levels of organization and function. Sampling methodology introduces a combined stand-level tree coring and stem-mapping design

that allows for explicit spatial and temporal assessments. Competitive interrelations with stand structure and development and under varying climatic conditions were explored. A computer program has been developed to recreate plot and tree configurations in order to calculate and test newly proposed competition measures along with other established indices. In addition, these indices were evaluated on their performance under different competitor selection criteria and assumptions. Study plots were selected to maintain site homogeneity and species complement with respect to pure and mixed stands of tulip-poplar, Liriodendron tulipifera L., and white oak, Quercus alba L. Paired tree comparisons were employed to investigate the competitive intensity of intra- and inter-specific associations of these two species. An intra-stem analysis was used to investigate differential competitive stress on opposite sides of individual trees.

Study Relevance

Competition studies are particularly important to agronomists and foresters concerned with the quantity and quality of crop and tree production. Understanding the mechanisms and processes involved will undoubtedly lead to even greater advances in crop control, specifically fertilization schedules, thinning and harvesting directives and plant spacing designs. Monocultures, which represent our prevailing methodology to maximize productivity, may be supplanted with mixed-species systems, given that species interactions may be

found to ameliorate present day drawbacks and increase production levels.

Forest models have provided a significant adjunct to field and laboratory research in evaluating the short and long term dynamics of forests, which otherwise might require decades to observe directly (Shugart and West 1977). These models serve as an ecological construct to test our understanding of tree growth and forest development. Most include some expression to account for inter-tree competitive effects. However, there is little uniformity in model design or in the competition submodels they employ. Model type and purpose has as much to do with this as does the lack of data support and an accepted measure of the competition-growth relationship. Improved experimental and modeling designs to quantify competition may further our ability to forecast growth and to simulate possible consequences of grave environmental importance (West et al. 1980).

One study area of much concern today centers about the regional and long-term impact of air pollution and acidic deposition on forest productivity. It is not known to what degree competition may compound growth loss or sensitivity of individuals and species, or whether it may simply confound any effort to determine the effect and extent of chronic air pollution exposure. It is felt that resolving a field approach and analytical techniques to isolate the competition factor among individuals and species will not only prove

a contribution to forest research, but also to further understanding of an ecological concept of which relatively little is known.

CHAPTER II

STUDY DESIGN AND PROCEDURES

This section outlines the design and procedures used to investigate the effect of competition on the growth of white oak and tulip-poplar in a mixed-aged, mixed-species forest community in East Tennessee. Sampling involved tree-ring coring of study trees and surrounding neighbors in conjunction with a detailed stem-mapping and measurement effort. Tree-ring width data provide a long-term growth and historical record of both individual and site. This growth record represents an imprint of past climatic activity as well as of age- and disturbance-related events (i.e., fire, cutting, tree replacement, air pollution) relevant to competition.

Site Selection and Sampling

Study plots were established within Walker Branch Watershed of the National Environmental Research Park (NERP) on the Department of Energy's Reservation near Oak Ridge, Tennessee (Harris 1977). Individual plots were selected on the basis of species complement, absence of apparent artificial disturbance and homogeneity of site conditions (i.e., site quality, slope, aspect, soil type and drainage). Each plot represented a circular 1/12 hectare area centered about a subject tree pair. The subject tree pair consisted of nearest neighbors of approximately equal size and crown class of white oak and tulip-poplar species in either pure or mixed

combinations (i.e., WO-WO, TP-WO, TP-TP). Plots were chosen to obtain relatively equal representation of species pairings. A total of 21 plots and 400 cored trees were measured in this study. Table 1 shows each plot and its corresponding site characteristics and species complement.

Plot sampling was conducted in the spring and summer of 1982. Field procedures involved tree measurement, stem-mapping and core extraction. Tree measurement data included plot number, tree number, species code, diameter at breast height (dbh), azimuth and distance from plot center, crown position (dominant, co-dominant, intermediate and suppressed), and viability status (0-live, 1-dead less than 1 year, 2-dead in recent years, 3-dead within last decade, 4-death date indeterminable). Plot center was set midway between the subject tree pair, from which a polar coordinate sampling approach was employed to stem-map each tree. Azimuth and distance (cm) from plot center was obtained for all trees greater than 2.54 cm dbh, whether cored or not, to determine each tree's location. The azimuth reading represents the horizontal angle (i.e., 0-360) clockwise from magnetic north to the basal intercept of the sampled tree.

Core Collection, Preparation and Measurement

All corable trees, whether live or dead, within 10m radius of plot center were tagged and cored along with any additional trees in direct crown contact with either of the subject trees. At least two

TABLE 1. Plot description, species complement and historical characteristics.

Plot Code	Species Pair	Pair-Age (Years)	Basal Area (M^2/ha)	Density (#/.08ha)	MDBH[1] (cm)	Cohort Class	Fire History[3]	Cut Event[3]
A	WO-WO	160-160	35.7	53	22.1	M	N	Y
B	WO-WO	80-80	25.9	110	10.3	M	Y	Y
C	WO-WO	78-78	28.1	101	12.4	B	Y	N
D	WO-WO	35-35	11.1	117	7.4	E	Y	N
E	WO-WO	113-113	21.5	91	11.2	M	N	Y
F	TP-WO	67-67	25.6	91	13.4	B	N	Y
G	TP-WO	41-41	21.4	138	8.4	E	Y	N
H	TP-WO	41-41	15.8	171	6.3	E	Y	N
I	TP-TP	41-41	19.8	131	8.1	E	Y	N
J	WO-WO	136-164	28.1	89	11.7	M	N	Y
K	TP-TP	67-67	29.5	81	13.3	E	Y	Y
L	WO-WO	64-64	27.9	28	29.9	E	Y	N
M	WO-WO	64-64	17.7	32	21.9	M	Y	Y
N	TP-WO	64-64	24.4	26	28.4	B	Y	Y
O	TP-WO	57-73	25.8	59	18.1	M	Y	Y
P	TP-WO	67-91	20.9	28	24.3	M	N	Y
Q	TP-WO	69-69	30.4	60	19.2	B	Y	N
R	TP-TP	66-66	25.9	79	15.0	E	N	N
S	TP-TP	51-51	25.3	64	16.1	M	Y	Y
T	TP-WO	58-52	26.8	75	16.3	E	Y	N
U	TP-TP	34-34	29.9	74	17.5	E	N	N

[1]Mean stand diameter for all trees above 2.54cm.

[2]Denotes the number of common age classes where E = even-aged, B = bievenly-aged and M = multi-aged.

[3]Signifies whether there is evidence in the tree-ring record of past disturbance events from fire and/or thinning, Y = Yes and N = No.

cores were extracted from opposite sides of eligible trees at or about breast height (1.4m). Core A was removed from the tree side closest to the nearest neighbor of near equal or greater dbh or in the direction of the subject tree pair, wherever competition was deemed most prevalent. While core B was generally taken opposite of core A, in many cases a third or fourth core was taken when the prevailing competitive direction was in question.

Standard cores, 4mm in diameter, were extracted with a Swedish increment borer. Numbered plastic soda straws were used to code and transport study cores in and from the field to the laboratory. This was done to protect the core as well as assure proper core identification and orientation. A core identification code was used to identify each extracted core by plot, tree, straw and core. In addition, each core was assigned an azimuth reading which described the direction from magnetic north of core orientation from tree center outward.

Cores were allowed to air dry for 24 hours before being glued into grooved wooden mounts following procedures by Stokes and Smiley (1968). Mounted cores were first trimmed with a modified jointer and then belt sanded to a high gloss finish using 340 grit sandpaper, and, if necessary, hand sanded with 600 grit paper. Sanded cores were then crossdated to verify yearly growth rings with key years of wide or narrow ring width before measurement and aging. Dated cores were measured for growth years 1930-1981 on a Bannister incremental measuring device to the nearest hundredth of a millimeter.

Data transfer was aided by a microcomputer link with the core reading device by directly storing ring-width data on magnetic tapes.

Cores were also used to establish pith date and age of each tree, to determine pre-1930 trunk radius and to estimate the heartwood-sapwood transition zone and years for calculating sapwood area. Sapwood basal area represents a newly introduced and potentially improved measure of competition based on its strong relationship to foliar biomass and leaf area (Grier and Waring 1974). Leaf area in turn is thought to be closely linked to an individual tree's functional environment determined by its competitors (Zedaker 1982). Fire scars and dates along with stand-wide ring releases and cohort regeneration dates were also identified (see Table 1).

Model Design and Data

A FORTRAN computer program was written to reconstruct each plot's tree and stand development back in time from the present, and to compute competition and growth for each year. Each field plot was recreated as determined by each tree's location and adjusted measurement. The model reset the initial stand conditions and tree sizes for each year, though without those individuals that may have existed, but whose presence was not evident at the time of sampling. This was accomplished by decrementing the observed growth performance (i.e., mean ring width by year) from the previous year's adjusted dbh. The measurements of non-cored trees were readjusted by calculating average growth from age estimates determined from

supplemental coring efforts or plot and species-specific age-dbh regressions.

Since 1982 represented an incomplete growth year, model data were generated for years 1981 to 1930, or for the life of the tree if established between these dates. An evaluation of the true competitive or stand conditions becomes less reliable with each passing year, though it was consistent in that it can only be underestimated. In the event a dead tree was cored and dating and measurement were possible, it was reinstated into the stand profile the year of its death. Each year the model outputs year, plot number, tree number, species code, adjusted tree data (dbh, age, crown class, viability status, sapwood basal area, etc.), and a host of competition and growth measures to be discussed in detail. Figure 1 illustrates the flow of the model, and describes the order and function of each subroutine.

The model calculated four different kinds of competition-related variables: (1) competition indices, (2) competition-density values, (3) light distribution-use estimates and (4) tree parameters. Competition indices are expressions which describe an individual's competitive status as a function of the number, size and proximity of neighbors. Competitor-density values represent the number of competitors used in calculating a competition index. Light distribution-use estimates consider the position and photosynthetic activity of foliar biomass as determined by crown class. Tree parameters include direct measures of tree age, anatomy and physical stature.

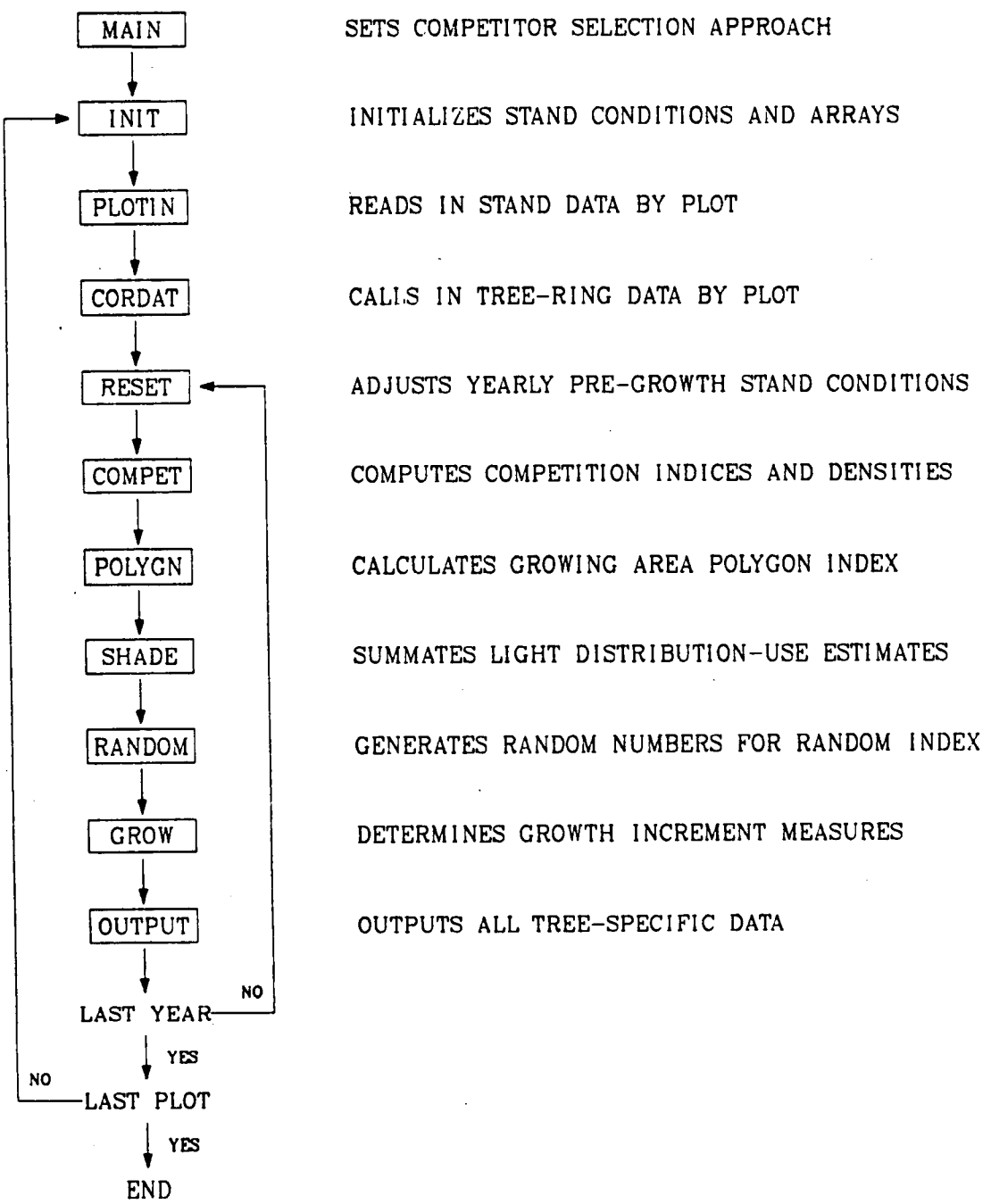


FIGURE 1. Model flow diagram of subroutines and their function.

Table 2 lists, by category, alphanumeric code and description a total of 36 variables generated from the model. Following is a detailed discussion of each variable by category along with competitor selection options used in each of four model runs.

Competition Indices and Density Calculations

Each competition index may be classified according to groups of indices which share some communality with respect to data input and/or descriptive design. They are often categorized by the required data and mathematical manner employed in their computation (i.e., stand density, influence-zone overlap, distance-weighted size ratios, and growing-space polygons). Successful and adaptable measures of these various types were chosen for this study. Table 3 outlines the type, mathematical expression, comments and authorship of the competition measures used in the model; a more comprehensive discussion of each follows.

Each competition index upon its inception was generally designed with particular competitor selection criteria or routines. For example, area overlap indices define competing neighbors as those whose influence-zone intersects with that of the subject tree. In this study, and when amenable, indices were generated for each of four different competitor selection methods. These encompassed two basic designs already mentioned, variable radius and fixed radius. The variable radius approach included all surrounding trees whose influence-zone overlapped with the subject tree.

TABLE 2. Symbols and descriptions of variables measured and calculated for this study.

Code	Description
	Competition Indices
C1	Relative stand basal area index
C2	Relative tree basal area index
C3	Prism count basal area estimate by plot
C4	Prism count basal area estimate by tree
C5	Gerrard's (1969) competition quotient
C6	Bella's (1971) C10 model
C7	Hegyi's (1974) size ratio
C8	Modified-Hegyi size ratio (Daniels 1976)
C9	Monserud and Ek (1977) overlap ratio
C10	Species-weighted index
C11	Crown-area polygon index
C12	Random effect index
	Competitor-Density Values
N1	Tree density by plot
N2	Competitor number by tree
N3	Prism count by plot
N4	Prism count by tree
N5	Tree number defining crown-area polygon
	Light Distribution-Use Estimates
L1	Leaf area above tree
L2	Light intensity index
L3	Species photosynthetic potential
L4	Average biomass by canopy group
	Tree Parameters
DBH	Diameter at breast height
AGE	Tree age
CC	Crown class of tree
BA	Basal area
SAP	Basal area of sapwood
ELA	Sapwood/basal area ratio
XDI	Mean annual increment for dbh
	Growth Measures
G1	Observed radial increment
G2	Observed radial growth trend
G3	Observed basal area increment
G4	Observed basal area growth trend
R1	Relative radial increment
R2	Relative radial growth trend
R3	Relative basal area increment
R4	Relative basal area growth trend

TABLE 3. Type, code, mathematical expression, and authorship of competition indices used in this study.

Index Type	Code	Expression[1]	Authorship
Stand Density	C1	1.0 - SBIO/SOILQ	Botkin et al. (1972)
Relative Tree Size	C2	1.0 - XBIO/CBIO	This study
Stand Prism Count	C3	$\sum_{j=1}^{n} BA_j$ from plot center	Anonymous
Tree Prism Count	C4	$\sum_{j=1}^{n} BA_j$ from subject tree	Anonymous
Area Overlap	C5	$1/A_i * \sum_{j=1}^{n} O_{ij}$	Gerrard (1969)
Area Overlap	C6	$\sum_{j=1}^{n} O_{ij}/A_i*(D_j/D_i)^{EX}$	Bella (1971)
Size Ratio	C7	$\sum_{j=1}^{n} D_j/D_i* 1/DST_{ij}$	Hegyi (1974)
Size Ratio	C8	$\sum_{j=1}^{n} (D_j/D_i)^2* 1/DST_{ij}$	Daniels (1976)
Size Ratio	C9	$\sum_{j=1}^{n} D_j/D_1 * e^{-¢*DST_{ij}/(CR_i+CR_j)}$	Monserud and Ek (1977)
Species-weighted	C10	1.0 - (CBIO-SPBIO)/(CBIO-XBIO)	This study
Area Polygon Model	C11	$\sum_{j=1}^{n} \frac{\theta ij}{360.} * (\frac{Di}{Di + Dj}*DST_{ij}, CR_i)^2$	This study
Random Effect	C12	Uniform distribution (0.0-1.0)	This study

[1]Where SBIO=stand basal area total, SOILQ=maximum recorded forest basal area, ($61m^2$/ha), XBIO=biomass of subject tree, CBIO=total biomass of subject tree and competitors, BA=basal area, j=competitor, i=subject tree, A=influence-zone area, O=overlap area, D=dbh, EX=exponential factor, (=2), DST=distance between trees, ¢=parameter estimate for competitive rate, (=2), CR=open-grown crown radius, SPBIO=biomass total of competitors of same species as subject tree, θ=subtended angle of crown influence of competitors on subject tree.

Influence-zone was determined from a mixed-species, dbh-crown width relationship (i.e., CW(ft.) = 1.829*DBH(in.) + 3.12) for open-grown oak-hickory trees taken from Krajicek et al. (1961). In contrast, the fixed radius method deemed any neighbors within 8 meters of the subject tree as competitors. In the situations outlined above, competitors were selected from neighboring trees regardless of size or crown position. Two more selection groups were established on the basis of crown class restrictions. This was accomplished by further distinguishing eligible competitors as those of near equal crown height or position with that of the subject tree.

Stand Density Measures

In closed forest stands, the stand density effect assumes that the greater the living biomass, the more intense the competition (Bella 1971). A relative biomass measure of stand density (C1) has been adopted from Botkin et al. (1972) forest stand simulation model, wherein the competitive effect is modeled as a function of total stand basal area and the maximum known basal area recorded for the same forest. This function supposes a linear relationship between growth and competition. And because it is calculated for the plot as a whole, it assumes that the competitive effect is the same for all trees regardless of size, species, vigor and/or distribution. The total number of trees greater than 2.54cm dbh used in the computation of the C1 index is recorded as the competitor-density value, N1. To account for differences in tree size and spatial distribution, a similarly derived index for individual trees (C2) is

generated by considering each tree's biomass relative to the summed biomass of its immediate competing neighbors. The number and selection of competitors (N2) contributing to the C2 index varies depending on the competitor search method employed.

Variable plot-radius sampling is another means of surveying a forest to obtain an estimate of stand density. The point sampling technique (Grosenbaugh 1958) was used to derive a stand density estimate (C3), also known as point density (Spurr 1962), angle or prism count. The technique involves the selection of a subgroup of trees based on diameter screening through an optical prism or angle gauge. This method identifies potential competitors that are either sufficiently close or large to subtend a minimum angle size from the point of the study tree. It was determined from previous studies (Daniels 1976) that a 2.3 m^2/ha (i.e., 10 ft2/acre) prism or angle gauge provides the best results. As before, separate measures were taken for the plot (C3) as a whole and at each tree (C4), and the competitor density, N3 and N4 respectively, selected for each sample. Competitor number (N4) for the prism count biomass estimate (C4) equaled the number of trees included in a prism count from eligible competitors preselected by the various competitor searches.

Influence-zone Overlap Models

The influence-zone concept is based on the assumption that there exists about every tree a circular zone, roughly equivalent to the crown area of an open-grown tree, wherein direct competition occurs (Staebler 1951). This zone is thought to be related to the

expected growing space given full crown and root development (Opie 1968). The extent to which this area is shared with the influence zones of neighboring trees (i.e., overlap) represents a measure of encroachment and crowding of the subject tree's optimum functional environment. Overlap indices vary with the type of overlap expression (i.e., linear, angular, areal) and input of tree size relationships. This study includes the area overlap measures of Gerrard (1969) and Bella (1971) (see Table 3).

Gerrard (1969) developed his "Competition Quotient," an index based on the sum of area overlap with adjacent trees as related to the influence zone area of the subject tree. A criticism of Gerrard's approach and a group of similar overlap models (Newnham 1964, Opie 1968, Stabler 1951), is the lack of any weighting factor for competitor size. These methods assume the competitive effect equal for and from all trees regardless of size. Bella (1971) recognized this shortcoming and devised his "CIO" model which he defined as a function of relative area overlap and size between each competitor and the subject tree weighted by an exponent (C6, see Table 3). Competitor density (N2) is the same for all tree-specific measures, and dependent on the particular model run and selection routine in effect.

Distance-weighted Size Ratios

This class of competition indices specifies the competitive effect to be the sum of size ratios multiplied by weighted-distance measures of selected competitors in relation to the subject tree. Problems with this approach include its empirical design and the

numerous techniques employed to identify eligible competitors (i.e., fixed radius, nth nearest neighbor, point density among others). For comparison purposes, the same criteria and competitors for each study tree were used here as for the area overlap models and other tree-specific competition measures.

Hegyi's (1974) index (C7), the first and most noted index of this design, is calculated as a function of the sum of the competitor-subject tree size-ratios and the inverse distance between them. A modified Hegyi index (C8) previously tested by Daniels (1976) and also included here, differs from the above only in that the size measures are squared. Monserud and Ek (1977) introduced an index (C9) which is a hybrid of Hegyi's empirical model and the influence-zone overlap concept by adding an exponential term onto the distance measure that accounts for linear overlap of maximum crown widths of subject tree and competitor.

Species-weighted Index

An additional index was generated to consider a weighting adjustment based not only on size, but also on the species of surrounding competitors. The species-weighted index (C10) is a percentage of competing basal area of trees of the same species as the subject tree relative to the basal area for all competitors. Given that trees of the same species utilize the same resources, conceptually one would expect them to compete more intensely with each other than trees of other species. However, species are distinguished by different growth characteristics and requirements

suggesting that they not only use different resources, but also exploit them with more or less efficiency. This further implies that some species may present a greater or lesser competitive effect than other species depending on overlap of resource demands and use-efficiency. It seems plausible to say that inter-specific competition is most intense between species which need and share similar resources, especially when those resources become limiting. Inter-tree competition on the species level, whether within or between species, may be expressed most when competing trees use more of the same resources and use any or all common resources more efficiently.

Growing-space Polygon

Also considered in this study is a measure (C11) representative of a class of competition models which approximate growing space using elaborate geometrical constructions, appropriately termed polygons. Though detailed in design and computation, the polygon method is not new and has been tried and tested by several researchers (Brown 1965, Moore et al. 1973, Adlard 1974, Alemdag 1978, Pelz 1978). Because of the nature of the study design herein (i.e., reevaluating competitive situations back through time) it was deemed necessary to devise a new methodology to overcome the practical limitations and theoretical implications involved with adopting any previous approach.

Subroutine POLYGN constructs a geometrical outline of the realized crown area (i.e., growing space) for each subject tree formed by the summed area of sections with its competitors. It assumes that only one competitor is eligible to affect the limits on

crown dimensions in any one direction. This prevents the error of cumulative competition influence from competitors that are intersected with the subject tree with other eligible competitors of the same crown class. This assures that there is only one competitor for each point of shared space and that all competitors be of approximately the same crown class and height.

Since POLYGN represents a measure of crown area, only competitors with a crown classification equal to or greater than that of the subject tree are included in the sample. The degree to which any one competitor confines crown radius is determined by the dbh ratio of subject tree and competitor. If the size ratio is greater than 2.5 times that of the potential competitor, though of the same crown class, it is excluded from having any likely influence on crown development of the subject tree. The restriction any one competitor may exert on subject tree crown size is limited to the angle of possible influence determined by the maximum crown diameter and distance of the competitor from the subject tree. The number of angles used to dimensionalize crown size is equal to 360 degrees, coinciding with the arc of a circle. This relationship was based on a ratio of mean diameter of sample trees in canopy and subcanopy positions. If a large enough crown section is unaffected by neighboring trees (i.e., greater than 85 degrees), the entire section of crown radius is assumed to be at full development (i.e., open-crown) for a tree of its dbh. This figure was chosen rather arbitrarily and not on any known biological basis. However, if there

exists uninfluenced sections less than 85 degrees, the section radius is limited to the same degree as adjacent sectors though proportional according to the relative size of the adjacent competitors. After determining the crown radius in each sector for all 360 degrees, total crown area (C11) is computed by summing all sector areas. A schematic example of the crown area polygon design is shown in Figure 2.

Random Number Index

As a means of evaluating the success of each competition measure previously described, a random number index (C12) was generated to determine the contribution and significance of each index from randomness. For each subject tree each year, a random number routine randomly extracted a unique value from a uniform distribution between 0 and 1, such that 0 represents no competition and 1 signifies extreme competition. For analysis purposes, this random index is treated as any other competition measure, though expected to mimic a random effect.

Light Distribution-use Estimates

Taking into account the stand structural profile, the SHADE subroutine calculates the vertical distribution of leaf area by crown class (i.e., dominant, co-dominant, intermediate, suppressed). Leaf area is determined from a linear leaf-area diameter relationship (Sollins et al. 1973) derived from tree species data taken from the study area. The leaf area index (L1) assigned to each tree

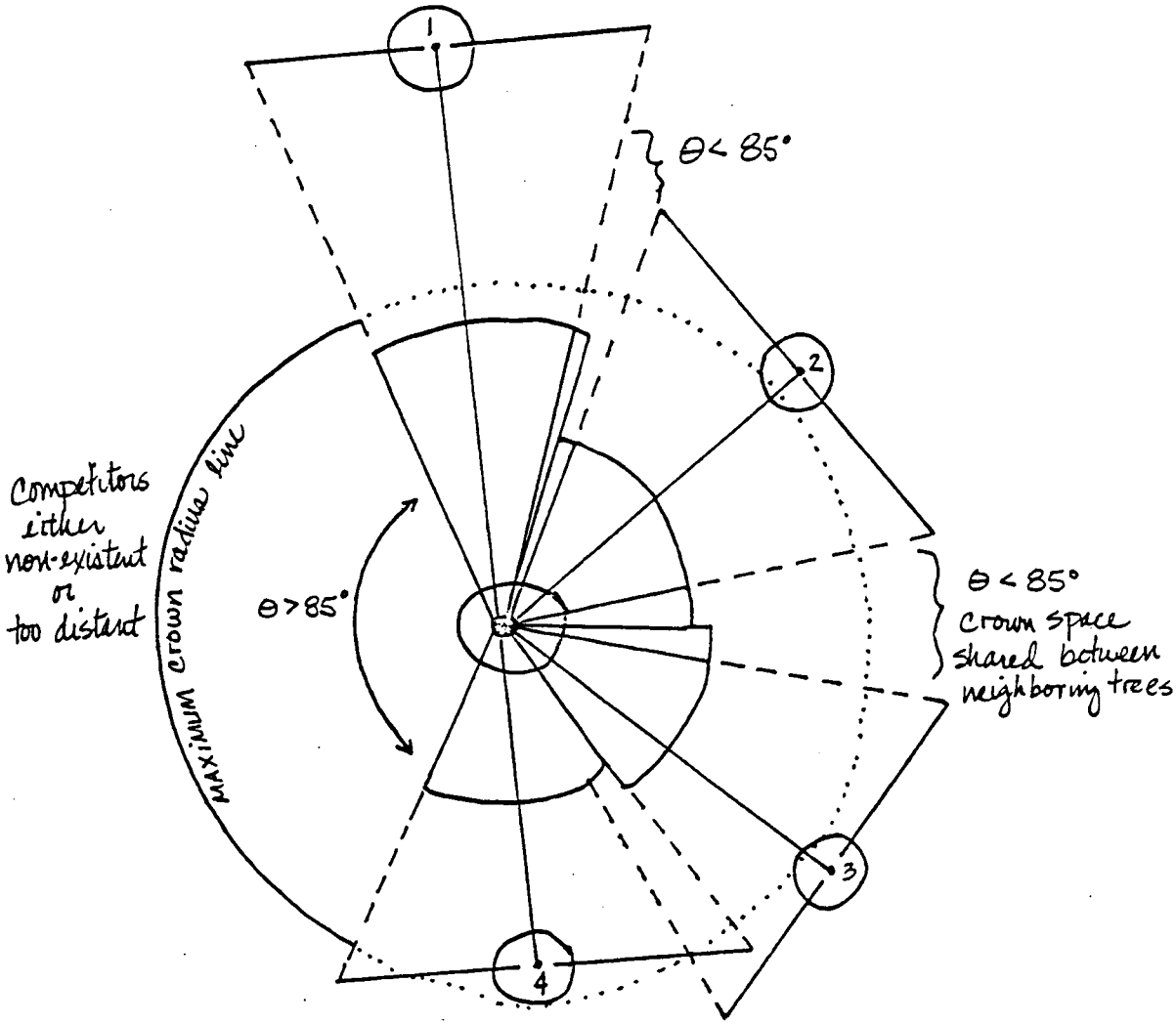


FIGURE 2. Illustration of crown-area polygon design.

represents the summed leaf area of all taller trees in higher crown classes. This index is then used to estimate the amount of available light (L2) to each tree as determined from a non-linear light extinction equation following Beer's Law (Kasanga and Monsi 1954, Loomis et al. 1967, Perry et al. 1969). After determining the amount of light available to each tree, scaled to 1.0 at maximum exposure, the model computes a tolerance coefficient (L3) associated with decreased photosynthetic efficiency under shaded conditions based on species shade tolerance (Fowells 1965) and equations (Kramer and Decker 1944). Another measure (L4) is introduced which assumes that overstory growth is related to the biomass in the understory component and vice versa, though involving different resource demands and abundance.

Growth Measures

Eight growth increments of six different types were generated from the model: (1) observed, (2) relative, (3) actual, (4) averaged, (5) radial and (6) basal area. The observed annual increments include mean ring width (G1), radial growth trend (G2), mean basal area (G3), and basal area growth trend (G4). Growth trend measures are the result of using a spline function to interpolate running mean growth for each tree by averaging the year to year variation mostly due to climate. Figure 3 illustrates an actual ring-width series and its corresponding radial growth trend for a typical overstory and understory tree.

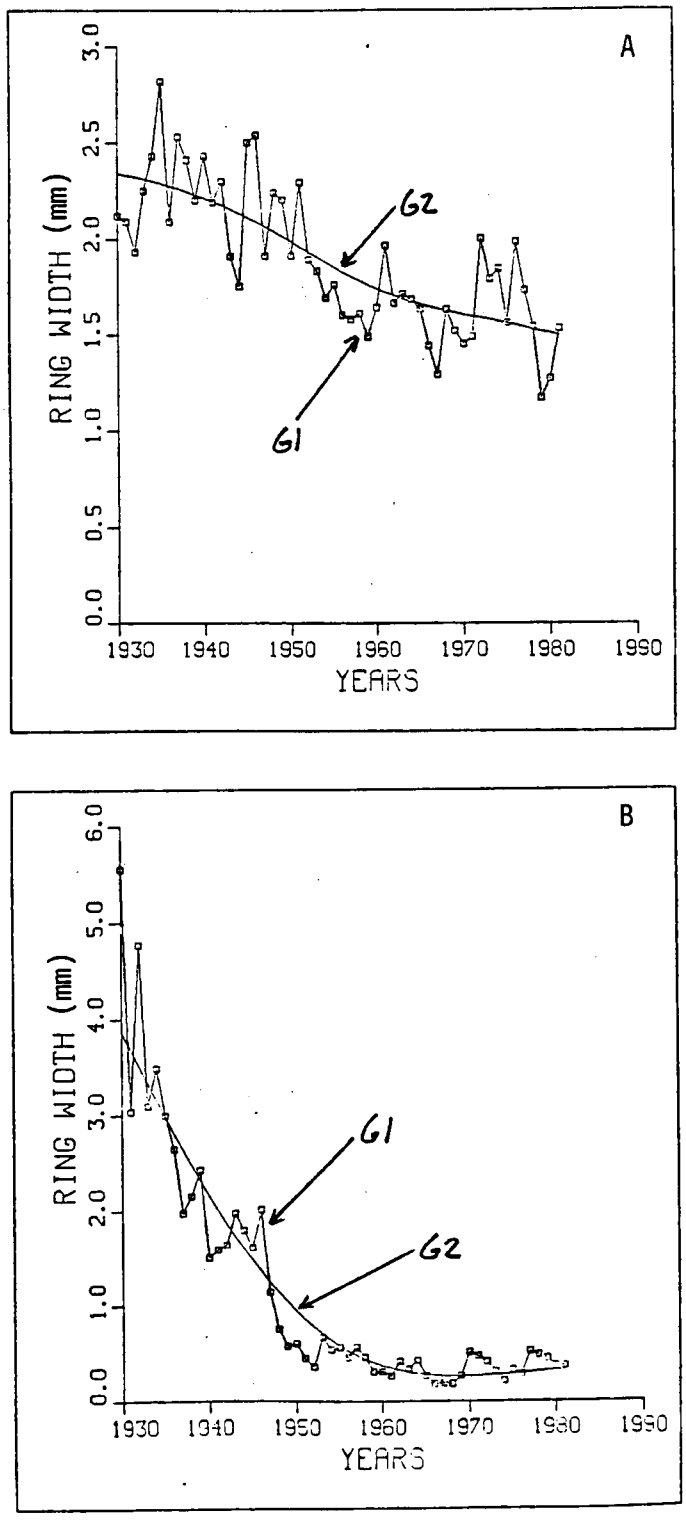


FIGURE 3. Actual ring width series (G1) and splined growth trends (G2) for a typical overstory (a) and understory (b) tree.

Relative growth is defined as a ratio of the observed annual increment to a maximum known potential for trees of the same species on similar sites. Since this study was designed primarily to investigate the growth of white oak and tulip-poplar, relative measures were generated for trees of these two species only. Maximum potential growth was determined by considering the maximum annual growth increment (MAG) for ring width and basal area accomplished by any tree in this study of its species and age. Figure 4 shows the actual maximum growth increments and a smoothing spline line for the range of tree ages represented by each species.

The MAG increment is believed to represent site and climate adjusted growth potential, while expressing the least possible competitive influence. This allowed a further comparison of competition measures with not only the realized growth situation, but also, and perhaps more importantly, the measure or extent to which trees failed to grow relative to their potential. Relative growth should be more indicative of competitive stress since it represents the degree to which growth is inhibited rather than expressed. Relative growth performance included measures of each of the afore-mentioned observed growth increments, G1-G4, expressed as percentages of the corresponding MAG increment, coded R1-R4, respectively.

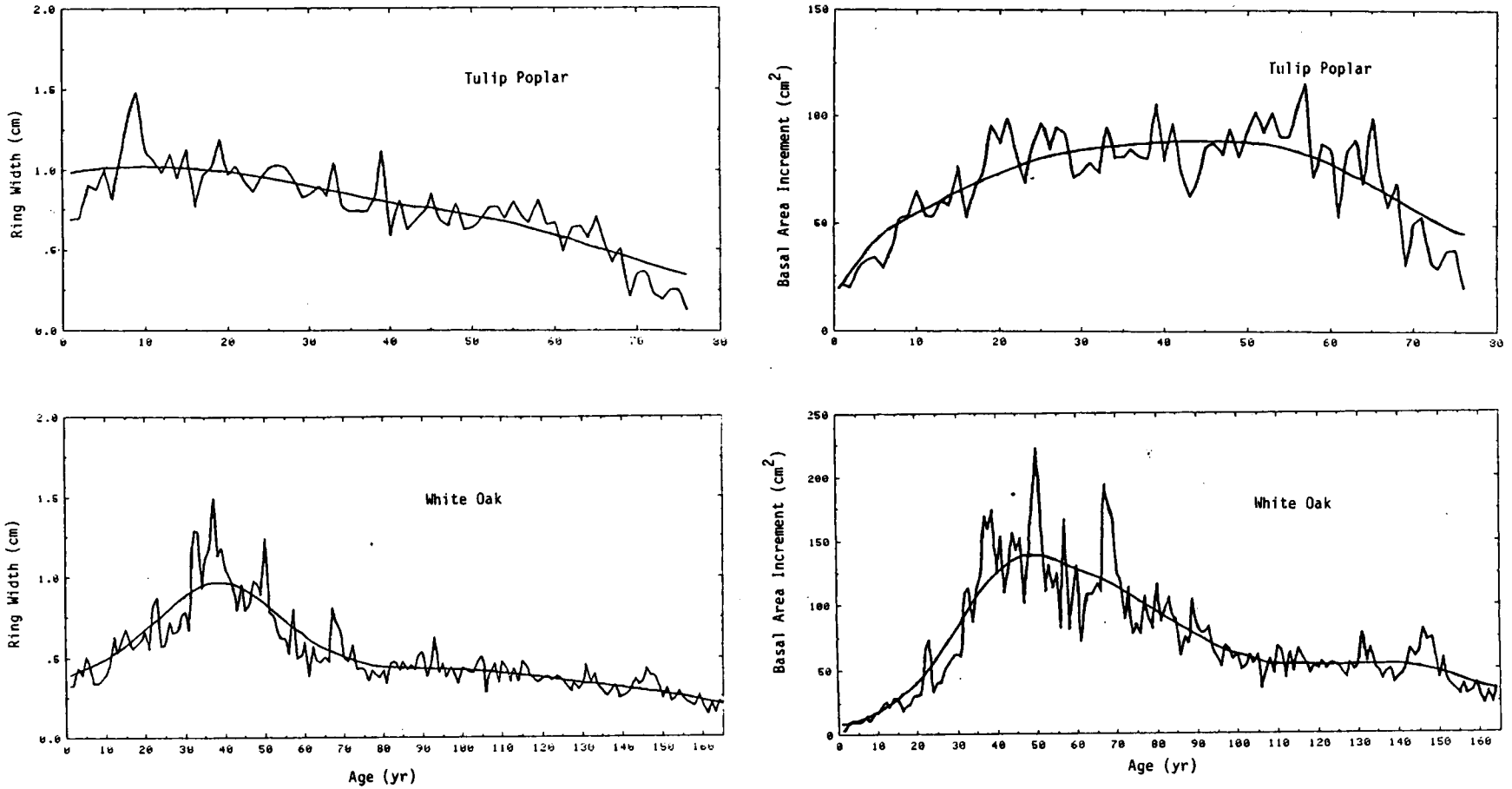


FIGURE 4. Actual and splined, maximum annual growth composites of ring width (cm) and basal area (cm^2) for tulip-poplar and white oak.

CHAPTER III

COMMUNITY STRUCTURE AND DEVELOPMENT

With the multilevel field design incorporated in this study, analysis was likewise partitioned to examine competitive-growth relationships acting on the individual, species and community levels of organization and function. Because of the time series element of tree-ring data, data treatment includes both spatial and temporal considerations. This chapter investigates the competition process that exists among individuals and species as related spatially to forest structure and temporally to forest succession.

While this community level evaluation considers both spatial and temporal aspects of competition and growth, only the most recent years (1977-81) growth and stand data were included. It was assumed that the latter growth years provide the most reliable assessment of true stand and competitive conditions. Although it is possible to re-estimate stand conditions of the past, the further one recedes from the present, the greater likelihood there is that competition-induced mortality and release is not taken into account.

Each species group, white oak and tulip-poplar, was analyzed separately to eliminate species-specific bias and to contrast species response. In order to prevent error from plot boundary constraints, only interior trees contributed data for testing. Correlation analysis was used to evaluate the degree of linear association, or lack thereof, between each competition measure and

individual tree growth. Pearson product-moment correlation coefficients were calculated for every variable combination. This was done to test for collinearity among variables and to determine the possible origins of these effects.

Spatial Aspect of Forest Structure and Competition

Each competition variable is categorized, coded and discussed by type: (1) competition indices, (2) competitor densities, (3) light distribution-use estimates and (4) tree parameters (see Table 2, page 18). Some of these measures are further characterized in the text on the basis of measurement level, whether by plot or stand, crown class, species, or tree-specific assessments. It is thought that tree growth might possibly be affected on any or all these levels of community organization. This represents an effort not to be too restrictive in the interpretation of how and on what level, competition should be measured and/or is acting upon individual tree growth. It is hypothesized that the newly introduced crown-area polygon model, light distribution-use estimates, and sapwood basal area may prove more comprehensive than already established competition indices.

Competition Indices

One objective of this study was to establish whether there existed any strong relationship between derived competition indices and growth among individuals in a mixed-aged, mixed-species forest community. In general, both the white oak and tulip-poplar data indicated some significant association between nearly all competition

measures and at least one or more growth variables, excluding the random number index (C12). The fact that the random effect index (C12) demonstrated extremely weak association on every account verified its true randomness and/or the presence of at least some pattern in every other variable.

To evaluate the success of the various indices, a rank order table was constructed in order from best to worse by absolute correlation (Table 4). Among the best and most significant indices, for either species, were those including some relative measure of subject-competitor size ratio. These included the relative size measure (C2), Bella's CIO index (C6), each of the distance-weighted size ratios (C7, C8, C9) and the crown-area polygon model (C11).

The success of these indices appears to be attributed to strong colinearity with tree size and crown position. Table 5 outlines the best correlation and rank order of competition indices with tree diameter and crown class. Given that the competition indices in comparison with other tree-specific or tree-environment measures do not significantly improve the statistical fit for explaining growth, one might then conclude that the effort in collecting the needed data and computing each index would be unwarranted in lieu of simpler, easily obtained tree measures such as dbh.

Table 6 capsulates the best measures and correlations for every type of independent or competition variable with each dependent or growth variable for 1981. As a group, competition indices (CI) not only proved highly correlated ($p < .0001$), but also superior

TABLE 4. Rank order of absolute correlation with 1981 growth measures from best to worst for tulip-poplar and white oak.

1981 Growth Rank	Tulip-Poplar (n=58)								White Oak (n=46)							
	G1	G2	G3	G4	R1	R2	R3	R4	G1	G2	G3	G4	R1	R2	R3	R4
1	C6	C2	C2	C2	C6	C11	C2	C2	C2	C2	C2	C2	C11	C11	C11	C11
2	C9	C6	C6	C11	C9	C2	C6	C11	C9	C9	C9	C11	C2	C2	C2	C2
3	C5	C9	C9	C6	C2	C6	C9	C6	C4	C6	C6	C9	C9	C9	C9	C9
4	C2	C8	C11	C9	C7	C9	C11	C9	C6	C4	C11	C6	C6	C6	C6	C6
5	C8	C5	C8	C7	C11	C7	C7	C7	C1	C7	C4	C8	C8	C8	C8	C4
6	C10	C7	C7	C8	C8	C8	C8	C8	C8	C8	C8	C7	C7	C7	C4	C8
7	C7	C11	C5	C5	C5	C5	C5	C5	C7	C11	C7	C5	C4	C4	C7	C7
8	C11	C10*	C4*	C4*	C4*	C4*	C4*	C4*	C11	C1	C5	C4	C5	C5	C5	C5
9	C1*	C4*	C10*	C10*	C12*	C10*	C10*	C12*	C3	C5	C1*	C10*	C10*	C10*	C10	C10
10	C4*	C12*	C1*	C12*	C10*	C1*	C1*	C1*	C5*	C10*	C3*	C1*	C3*	C3*	C3*	C3*
11	C12*	C1*	C12*	C3*	C1*	C12*	C12*	C10*	C12*	C3*	C12*	C12*	C1*	C1*	C1*	C1*
12	C3*	C3*	C3*	C1*	C3*	C3*	C3*	C3*	C10*	C12*	C10*	C3*	C12*	C12*	C12*	C12*

*Denotes non-significance at the .05 level.

TABLE 5. Absolute correlation values of competition indices with tree diameter and crown class in rank order for tulip-poplar and white oak data from 1981.

Rank of 1981 Data	Tulip Poplar (n=58)				White Oak (n=46)			
	Diameter		Crown Class		Diameter		Crown Class	
	CI[1]	r^2	CI	r_s[2]	CI	r	CI	r_s
1	C6	.79	C2	.80	C11	.88	C11	.85
2	C9	.79	C8	.80	C2	.84	C2	.84
3	C2	.75	C11	.79	C9	.78	C9	.84
4	C11	.68	C9	.78	C6	.75	C8	.81
5	C7	.68	C7	.76	C4	.64	C7	.80
6	C8	.68	C6	.72	C7	.63	C6	.72
7	C5	.51	C5	.61	C8	.61	C5	.47
8	C4	.40	C4	.28	C5	.61	C4	.37
9	C1	.16	C3	.25	C3	.39	C1	.17
10	C10	.08	C10	.13	C1	.35	C3	.16
11	C12	.05	C1	.10	C10	.19	C10	.12
12	C3	.02	C12	.07	C12	.11	C12	.04

[1]Refers to competition indices, see Table 2, page 18, for variable descriptions.

[2]Represents the absolute value for the Pearson product-moment (4) and Spearman rank (r_s) correlation coefficient.

TABLE 6. Best correlations for the different types of competition measures and competitor selection methods tested with all growth variables (1981) for tulip-poplar and white oak.

Annual Growth Measure (1981)	Competition Index			Competitor Density			Crown Position		Tree Parameter	
	CI[1]	CSM[2]	r[3]	CD[1]	CSM	r	CC[1]	r	TP[1]	r
				Tulip-poplar (n=58)						
G1	C6	IZ	.44	N2	RFC	.40	L2	.55	XDI	.78
G2	C2	IZ	.51	N2	RFC	.44	L4	.55	SAP	.70
G3	C2	IZ	.60	N2	RFC	.49	L2	.66	SAP	.86
G4	C2	IZ	.65	N2	RFC	.49	L2	.59	SAP	.78
R1	C6	RF	.61	N2	RFC	.51	L2	.60	SAP	.77
R2	C11	PM	.62	N2	RFC	.51	L4	.58	SAP	.68
R3	C2	IZ	.65	N2	RFC	.51	L2	.67	SAP	.85
R4	C2	IZ	.66	N2	RFC	.50	CC	.60	SAP	.76
				White Oak (n=46)						
G1	C2	IZ	.68	N4	RFC	.43	L4	.64	XDI	.75
G2	C2	IZ	.62	N4	RFC	.46	L3	.63	XDI	.61
G3	C2	IZ	.79	N2	IZ	.57	L3	.74	SAP	.73
G4	C2	RF	.72	N2	IZ	.65	L2	.74	DBH	.76
R1	C11	PM	.80	N2	IZ	.62	L1	.74	DBH	.77
R2	C11	PM	.80	N2	IZ	.66	L2	.74	DBH	.80
R3	C11	PM	.84	N2	IZ	.66	L2	.62	BA	.79
R4	C11	PM	.84	N2	IZ	.67	L2	.64	BA	.83

[1]See Table 2, page 18, for corresponding variable description.

[2]Refers to Competitor Selection Method: Influence-zone (IZ), Radius-fixed (RF), Influence-zone competitors of same canopy class (IZC), Radius-fixed competitors of same canopy class (RFC) and the Polygon Model (PM).

[3]Absolute value of the Pearson correlation coefficient (r).

to all other measures in relation to radial growth trend (G2), observed basal area increment (G3) and all relative growth measures for white oak. The crown-area polygon index (C11) produced the highest correlations, while the relative size measure (C2) demonstrated the most consistent association.

Several previous studies (Moore et al. 1973, Alemdag 1978, Daniels 1981) reported superior results from calculating growing space with elaborate geometrical assumptions and configurations. Since most of this work focused on even-aged plantations, a modified approach was employed to compensate for differences in dealing with mixed-aged, mixed-species, multi-strata forests. The crown-area model (C11) presented here assures that no trees in the same crown class share the same space. Space on any one vertical or crown class plane is considered a mutually exclusive resource that is either unoccupied or occupied by one tree only. It was also assumed that there exists only one competitor to define each boundary point in space, and that all competitors be of similar crown position. In this context, crown area specifies implicitly the tree's position to light and explicitly its horizontal crown expanse and ability to intercept light as determined from the size, crown class and distance of competing neighbors. These features seem to quantify more accurately a tree's competitive advantage relative to competition. One additional note on its performance was its consistency and generally stronger association with relative growth than with observed growth, affirming its relation to competition.

Because distance-dependent measures require detailed inter-tree distance data, it follows that they signify a more comprehensive, and therefore better measure of competition than distance-independent types. The findings in this study suggest that such a generalized assumption cannot be supported. Aside from the crown-area index, the relative size measure (C2), deemed distant-independent, tested best and most consistent of all indices in correlation to growth (see Table 6). This result is contrary to what Daniels (1981) found in loblolly plantations. The difference in findings probably originates with relating the index to a mean stand condition (Daniels 1981), rather than that of the immediate competing neighbors as in this study. Bella's (1971) CIO model (C6) proved third most significant ahead of the distance-weighted size ratios (C7, C8, C9). Alemdag's (1978) evaluation of competition indices for planted white spruce stands showed the same relative success of these latter indices. Bella's use of area overlap instead of a linear measure, as in the other indices, may have accounted for its slightly improved performance.

Other tree-specific measures not already mentioned demonstrated significant, but modest association with growth. These included the prism count biomass estimate (C4) and Gerrard's Competition Quotient (C5). The prism count biomass estimate (C4) probably does not deserve its ranking since its correlations were often nonsensical and opposite of other measures. The reduced fit of Gerrard's index (C5) with respect to Bella's index (C6) affirms the shortcoming of not

incorporating subject-competitor size differences in area overlap indices.

In part, it has been shown that those indices uniquely calculated for each tree served much better as single determinants of individual tree growth than the more general plot and species-level estimates. Because every tree within each plot is assigned the same stand density measure (C1 and C3), it is suspected that the poor performance of these indices is due to expecting a single plot variable to explain incremental growth for individual trees without respect to age, size, crown class and/or species of subject tree and competitors. As for the species-weighted index (C10), it may be stated that knowing the percentage basal area of same or other species about the subject tree does not appreciably account for growth variation in and of itself. Like the stand density indices, the species-weighted index was only expected to complement other more comprehensive measures within the framework of a multivariate growth model.

Competitor Search Methods

If understanding the processes of tree growth is as important or more so than solely forecasting growth, then a closer look at the success of the various types of indices under different competitor selection methods and directional stress assumptions might prove useful. Two competitor selection approaches were employed and contrasted. The first chooses competitors from adjacent neighbors whose projected influence zone (i.e., open-grown crown radius) overlaps with the subject tree. The second differs from the variable radius

design in that it outlines a subplot of fixed radius wherein all surrounding trees within 8 meters of the subject tree are considered competitors.

The effect of either selection method varies with the size of the subject tree. For large trees, the influence-zone search selects more competitors of greater distance and spacing, and adds more competitive weight to their presence than for smaller, subcanopy trees. Conversely, the fixed radius design attracts approximately the same number of potential competitors whether large or small subject trees. However, from the reference point of a suppressed understory tree, a fixed radius is more likely to encounter more larger neighbors than that for a canopy tree due to spatial patterning of forest trees.

Only tree-specific indices can be compared for degree of fit among competitor search methods, excluding the growing space polygon model which was designed with its own selection rules. The relative size measure (C2) was the best overall competition measure, and the only index which demonstrated any advantage from employing an influence-zone competitor search. Except for the species-weighted index, the remaining indices showed at least some if not considerable improvement with the fixed radius approach. This result is also contrary to Daniels' (1976) study where selection by angular displacement proved more satisfactory.

Area overlap indices by Gerrard (C5) and Bella (C6) indicated a reduced fit with the influence-zone method for which they were designed. This result suggests that the influence-zone approach

includes too many competitors on the edge of the subject tree zone that are too far away and/or whose influence is too heavily weighted to have any direct competitive effect. In addition, the projected open-grown crown radius may be overestimated for these trees and the site quality represented. It may also support the notion that there exists a more or less fixed distance about each tree wherein competitors are found and competition is defined. The same basic result and explanation holds for the distance-weighted size ratios (C7, C8, C9), which also show an improved fit with the fixed radius approach.

Competitor Discrimination by Crown Class

Competitors may be further distinguished on the basis of what direction or resource they apply competitive stress on the subject tree. For instance, light is an essential resource necessary for growth that is vertically distributed. Crown space, on the other hand, is primarily limited by other trees of similar crown height in the horizontal dimension. Crown spread may then represent the ability or degree to which light can be intercepted from the vertical plane. These distinctions are implemented by considering all competitors regardless of crown position in one case, and in the other limiting eligible competitors to those of near equal crown class.

Findings of this study indicate that definite patterns are generated from choosing competitors by a particular search technique, as well as on the basis of crown class distinctions. The relative size measure (C2) exhibited about equal propensity with either the influence-zone selection without class discrimination and the fixed

radius design including only competitors of similar crown class. These two alternatives are quite similar to one another, except that the influence-zone method tends to include more distant competitors. Because this index represents a comparative measure, it is relatively unaffected when the reference measure, the sum biomass of competing neighbors, is consistently greater or lesser between selection methods.

Both the prism count biomass estimate (C4) and Gerrard's Competition Quotient (C5) demonstrated their best fits with a fixed radius search of competitors of near equal crown height. This may explain the success of these and similar measures when used in studies of even-aged monocultures where only one crown class generally exists.

Bella's CIO index (C6) and the distance-weighted size ratios (C7, C8, C9) behaved similarly, but with distinct differences in species response. Their best measures for tulip-poplar revealed slightly improved fits using the fixed radius method with no crown class restrictions. However, white oak gave consistently higher correlations with all growth variables, again involving the fixed radius approach, though among competitors of similar crown status. This could represent a species related phenomenon, but more likely an indirect effect of spatial patterning of trees in stands of varying maturity. The even-aged tulip-poplar stands are characterized by more uniform spacing across all classes than was found for white oak plots. By imposing crown class restrictions on competitor

selection, the mixed-aged white oak stands appear more regularly spaced and comparable with the tulip-poplar group. The variability of calculated growing space is then reduced among white oaks where the understory component is eliminated.

Competitor-density Values

Competitor-density values represent integer approximations of circum-tree competition by summing the number of competitors selected under some competitor search criteria. These values are discrete variables as compared to the more continuous estimations derived with competition indices. They therefore would not be expected to demonstrate as strong an association with growth as other measures, but if near so or better, they would provide an easier, less costly field effort.

Competitor density proved to be weakly correlated with individual tree growth, except in a few cases depending on the measure and search technique employed. This result is not surprising since competitor number fails to reflect the differential size and proximity of competing neighbors. Furthermore, these density estimates of competing trees assume that each competitor is of equal stature or influence, or that the total count specifies an average which is more or less maintained across forest stands of varying age and development.

Plot estimates of tree density (N1 and N3) revealed no significant association with any growth variables. Like the stand biomass measures (C1 and C3), a single count for all trees on the

same plot is inadequate to explain the within-stand growth variation, due to its being greater than the between-stand variation in tree growth.

The improved, but modest performance of competitor density determined from the growing-space polygon method suggests that the relationship between growth, crown area and the number of trees defining its boundary (N5) appears stronger for young, even-aged stands than for mature, disturbed and/or mixed-aged stands. This is probably due in part to the more regular spatial distribution of trees in early stand development than in mature stages.

The most successful of the competitor density counts included those used in tree-specific competition measures (N2 and N4), though subject to the particular competitor search technique employed. Only competitors selected from either the influence zone approach without crown class distinctions or the fixed radius search of trees of near or equal canopy status demonstrated any significant correlations. These methods, unlike their counterparts, increase the differentiation of competitor numbers by size or crown class, but having directly opposite effects. With the influence-zone criteria, large canopy trees overlap with a larger number of eligible competitors, while small, suppressed trees intersect fewer trees. In the case of the fixed radius search, large dominant trees have fewer neighbors of similar crown class within the same fixed radius as do smaller subcanopy individuals. Despite the best of these density values exhibiting highly significant correlations with tree growth, they show

the weakest association among the class of competition measures tested, most probably demonstrating the problem or loss of discretely approximating inter-tree competition. However, this should not reflect the contribution of density measures in company with other competition and tree parameters in predicting growth or competitive status.

Light Distribution-use Estimates

Trees in closed forests naturally segregate into fairly well defined crown classes. The competitive effect of light reduction by canopy shading is no doubt the most important factor limiting tree growth on mesic sites, and subsequently determining stem size and crown position. It is therefore believed that competition for light and its effect on tree growth can be summarized for each tree relative to its position and the vertical distribution of leaf biomass by crown class.

All of the light distribution estimates (L1-L4) proved highly significant, despite being assigned by crown class (see Table 6, page 37). Very little difference in fit existed between them, suggesting no appreciable gain from projecting light extinction (L2) or species photosynthetic efficiency (L3) over the average leaf biomass above each crown class (L1). This may be due in part to the lack of any true intermediates, thus allowing a favorable linear fit between the two major groupings, shaded and unshaded.

Following the assumption that canopy strata represent distinct groupings in response to particular resource limitations, biomass

estimates by crown class were examined for their effect on growth by trees in other class designations. In developing a hypothesis, it is suggested that the overstory element is a function of the understory and vice versa, though involving different resource demands and abundance. First, understory growth can be related to the average biomass in the overstory as a measure of canopy cover or average leaf area related to light availability as has already been shown. Secondly, the growth of overstory trees can be associated with the understory component brought about by residual light penetrating through an incomplete canopy closure. The presence of understory trees and shrubs might then indirectly reflect a source of additional moisture stress on the larger, exposed individuals. They may also reflect a measure of inefficient spacing and crown geometry of canopy dominants and codominants and their ability to intercept light. The results support the proposed hypothesis in revealing a generally strong relationship where each component, canopy and subcanopy, is expressed as functions of one another's average biomass (L4). This relationship may have been even stronger if smaller trees and forest floor cover species below the 2.54 cm dbh size limit were included in this test.

Tree Parameters

Most inter-tree competition studies fail to treat tree-specific data like dbh and basal area as competition measures. They are inherently related to growth, and therefore not entirely independent of it. Nonetheless, tree measurement variables constitute the sum

result of years of competitive influence and growth response from other extrinsic factors, mainly climate and site conditions. Throughout stand development individual tree growth is determined by the confines of the functional or competitive environment (i.e., position, size and number of competing neighbors), which, in turn, dictates tree stature and dominance.

Sapwood basal area was included in this study because of its easy determination from extracted tree cores and its close relationship to leaf area (Grier and Waring 1974). Zedaker (1982) proposed and justified the use of leaf area as a competitive index due to its correlary response to the immediate environment set by surrounding competitors. Therefore, it is hypothesized that sapwood basal area may represent a more comprehensive measure of competition with its relationship to leaf area and the active conducting tissue of the stem. A related index, ELA, is also introduced as an index of effective leaf area; it assumes a relationship between sapwood basal area and tree size based on potential productivity and the cost of structural maintenance.

Of the tree-specific parameters listed in Table 6, page 37 (i.e., DBH, AGE, CLASS, SAP, BA, ELA, XDI), sapwood basal area correlated best and most consistently with all growth measures. Though highly correlated with tree size and crown position, sapwood basal area may also reflect the quality or vigor of the photosynthetic surface area of the crown, thus including another dimension possibly responsible for the improved fit. In the same manner, it may

represent an indicator variable of water availability or stress, as dictated by the most recent year's climate and species response. This is supported by its generally better fit with the observed growth increments than with the growth trend measures or relative growth. Sapwood basal area may not have been as prominent a competition measure in the white oak group because of the disjunctness of stand development represented. Stands from which white oak samples were taken often revealed three or more age classes (see Table 1, page 12). It may also constitute a species-specific anomaly of sapwood-heartwood formation in oaks (Rogers and Hinckley 1970).

For white oak, the best-fit variables included a mix of tree size and average growth measures. These correlate well with growth since they themselves are the result of a cumulative competitive effect and the success of the individual over its life history (Bella 1971). Dbh, for instance, equals the sum of diameter increments for all years of growth. As with basal area and mean diameter increment, past growth performance is a good estimate of how much a tree is likely to grow. However, it should be noted that tree size measures, dbh and basal area, exhibited higher correlations with relative growth than with actual growth increment, while mean diameter increment displayed the opposite relationship--strong association with observed growth and not with relative growth.

Age and effective leaf area (ELA) exhibited extremely weak association with observed growth though strong association with

relative growth. Correlations were extremely high between tree age and relative growth (R1-R4), mostly due to the age adjusted nature of growth potential. At first, it was not obvious why a measure of sapwood basal area per unit tree basal area (ELA) did not perform up to expectations. It would seem that the effective leaf area estimate would be as good or better than other measures since it not only takes into account sapwood basal area, but also the maintenance requirement for supporting the existing tree biomass and structure. From all indications, the strong correlation between sapwood basal area and tree basal area only negated the variation and growth association of either alone when expressed as a ratio. The significant fit of ELA with relative growth and not observed growth, suggests a true relationship with competitive stress.

Multi-component Nature of Competition Measures

The goal of most competition-growth studies is to develop a new index of competition and compare its performance against established indices. Where attempts are made to improve growth prediction, competition studies often go beyond single variable models to multivariate analyses. Some authors have recognized the pitfalls of multicollinearity when using two or more variables, particularly competition indices, in a multiple regression effort (Waller 1981, Liu 1981). While the result may indeed improve the statistical fit or R-squared, the amount of added variation explained is often a procedural anomaly of no biological significance. The

intent of the user is paramount to the validity of the results. If the sole purpose is to forecast growth, then factor loading will always produce better results. Because other studies fail to recognize the multi-dimensional qualities of many competition indices, trial variable loading of competition indices and tree parameters is the common practice. For example, dbh is usually treated as a parameter disjunct of competition and indicative of potential growth. It may also represent a tree's relative success with respect to its neighbors, and thus an effective competition measure. As noted earlier, diameter reflects the cumulative response over the tree's life history to competition, climate, and other factors. In effect, competition indices are attempts to redefine tree size and position in rank order of its ability to exploit its surrounding environment and to increment growth. Depending on the index, a competitive evaluation incorporates to one degree or another several tree and stand parameters (i.e., age, size, crown class, density) into a single relative measure. Their effectiveness in the company of tree and stand variables is often limited due to the multi-component nature of these indices and the collinearity that exists.

A fair yet complete multivariate treatment of all the measures and competition selection modes included in this study would certainly be prohibitive both in time and expense. A preliminary evaluation demonstrated that the best two and three variable models for tulip-poplar and white oak explained little more than 5 percent more variation than that explained by the best single variables,

sapwood basal area and polygon crown-area, respectively. Any variable, including the random number index, in combination with either of the above-mentioned variables contributed to a more significant relationship, though not appreciably more than what might be expected from randomness.

Forest structure determines the primary competitive influence in mixed-aged, mixed-species stands. While the horizontal spacing of trees has been emphasized in the design of competition indices, vertical stratification and differential resource partitioning of light is of the utmost importance. As expected, light distribution-use estimates demonstrated significant relationships between vertical distributions of foliar biomass and projected light levels with growth.

The amount of light available to the individual in turn dictates the degree to which energy can be put into grown structure if space is not limiting. Horizontal spacing, in this respect, is more of a problem for the crown-restricted overstory than the light-starved understory. Timing of crown development and distance between neighboring trees determines crown area or the size of the structural receptor devoted to light interception. This may explain the success of tree-specific competition indices which reduce both the vertical positioning and horizontal crowding into a single relative size measure. Likewise, tree diameter and basal area work well given that larger trees are generally in the more favorable vertical and horizontal positions, while small trees in closed stands are light suppressed.

Chance establishment and incidental spacing contribute to the inability of dominant and codominant trees to efficiently subdivide the canopy plane and intercept light. Residual light passing through the canopy is then available to stimulate growth of suppressed individuals with enough resource and tolerance to meet their maintenance demand. These and their overstory counterparts compete for below-ground resources (i.e., nutrients, water) not already tied up in the standing and nondecomposed biomass. Stand density measures fail to adequately describe how and on what basis trees apportion these resources. Root competition appears to be much more diffuse than crown competition (Stiell 1970). It is difficult to assess or separate increased stand density from its imposition on above-ground spacing and below-ground processes. Nonetheless, its role appears secondary to above-ground structural development and possibly species differences on sites where environmental conditions are not limiting.

Competition indices account for one or more of the following means of exploiting resources and/or allocating growth: vertical position and light availability; horizontal space and acquired ability to dominate light and plot resources; cost of maintaining existing structure; and stand density and shared apportionment of below-ground resources. Other factors not explicitly but implicitly incorporated into competition measures (i.e., species, age, site quality) no doubt affect goodness of fit depending on the species complement, developmental phase, site history and quality and data treatment. However, these competition-growth principles just

discussed capsulate what are believed to be the major mechanisms and influences by which trees affect each other's environment and growth.

Different growth models may also be warranted for overstory and understory trees and species wherein the demand, abundance and use of certain resources vary. While the common approach usually involves linear equations and assumptions, competition and growth are almost certainly non-linear. Because of the complex and pervasive interactions involved in tree and forest growth and development, competition remains a difficult plant growth process to reduce to simple terms or even to evaluate using multiple expressions.

Temporal Aspects of Forest Succession and Competition

Forests are dynamic in nature and constantly changing, as are the competitive relationships which direct those changes. Theory suggests that competition increases with increasing forest development with respect to age, density and biomass. However, the degree of competitive intensity varies with individuals in space and time depending on the structural positioning of the individual tree already discussed, and whether the localized stand condition is in a building or breaking up phase.

Mortality represents the extreme of the competitive effect wherein the individual is stressed beyond its inherent ability to compensate or survive the changing forest environment (Yoda et al. 1963, Ford 1975, Keister and Tidwell 1975). There are other direct causes of natural tree death related to or apart from competition,

including insect attack and disease, senescence and fortuitous disturbance events (i.e., fire, flood, wind, other treefalls). Where trees succumb to mortality, whether due to competition or other cause, the environment changes in ways that allow surrounding trees to benefit from the relinquished space and the elements it contains. A tree's response in this manner is called a growth release. While competition-induced mortality is difficult to anticipate and thus observe, forests are nonetheless composed of trees in different stages of suppression and release. Likewise, individuals and species are expected to respond more positively or negatively to competitive stress imposed yearly with fluctuating climatic conditions. This section considers the temporal aspect of the competition-growth response as related to climate and stand development.

Because of the dendroecological design of this study, both the growth response and competitive status of eligible trees can be determined on a yearly basis from 1930 through 1981. However, the accountability for trees which may have existed in the past but not at the time of sampling cannot be ascertained. Therefore, analysis was restricted to the last five growth years (1977-81) to avoid this uncertainty. Fortunately, enough climatic variability has occurred during this time to consider whether competitive intensity and predictability changes in good and bad years of climate.

It is hypothesized that years where climatic conditions are most limiting to observed growth (i.e., drought years) represent the

best approximation of an individual's position to exploit the available resources, and therefore its true competitive status. Table 7 displays the best competition index and correlation with each year from 1977 through 1981 with each growth measure. In almost every case, and regardless of the index, correlations with annual growth measures (G1, G3, R1, R3) for either species were strongest in 1980, the severest drought year for the decade between 1971 and 1981.

Since the growth trends (G2, G4, R2, R4) represent running growth averages, it is expected that correlations with competition would be highest in latter years where spatial and positional variation in stand structure through time is likely to be greatest. While the results seem to support this generalization, there is a consistent interruption in a perfect pattern in the extreme drought year, 1980. This may be the result of stand restructuring in a year where many tree deaths can be attributed to the added stress of a severe drought. It may also be an artifact of the manner in which the spline function uses endweights to compensate for the lack of data points beyond year 1981.

One additional note on temporal aspects of forest growth involves the response of understory and overstory trees with respect to additive stress effects. Mere observation of ring width series of these two competitive classes (see Figure 3, page 29) indicates that suppressed individuals are so light-starved that there is little or no yearly growth variation with respect to climate. Instead, growth declines exponentially, not in proportion to light or

TABLE 7. Best correlations among competition indices and annual growth increments for years 1977 through 1981 for tulip-poplar and white oak.

Growth Measure	1977		1978		1979		1980		1981	
	CI[1]	r^2[2]	CI	r	CI	r	CI	r	CI	r
			Tulip-poplar (n=58)							
G1	C2	.67	C2	.58	C6	.56	C2	.68	C6	.44
G2	C2	.49	C2	.51	C2	.52	C2	.49	C2	.51
G3	C2	.75	C2	.70	C2	.66	C2	.80	C2	.60
G4	C2	.64	C2	.65	C2	.66	C2	.64	C2	.65
R1	C2	.69	C2	.68	C6	.66	C2	.78	C6	.61
R2	C11	.58	C11	.59	C11	.66	C11	.61	C11	.62
R3	C2	.75	C11	.70	C2	.68	C2	.79	C2	.65
R4	C2	.62	C2	.64	C2	.65	C11	.65	C2	.66
			White Oak (n=46)							
G1	C2	.65	C2	.65	C2	.66	C2	.73	C2	.68
G2	C9	.55	C9	.58	Cp	.58	C2	.61	C2	.62
G3	C2	.77	C2	.73	C2	.77	C2	.79	C2	.79
G4	C2	.72	C2	.72	C2	.72	C2	.72	C2	.72
R1	C11	.79	C2	.76	C11	.74	C11	.80	C11	.80
R2	C11	.79	C11	.79	C11	.80	C11	.80	C11	.80
R3	C11	.81	C2	.77	C11	.78	C11	.82	C11	.84
R4	C11	.84	C11	.84	C11	.84	C11	.84	C11	.84

[1]See Table 2, page 18, for corresponding variable description.

[2]Absolute value of the Pearson correlation coefficient (r).

microclimatic stress, but with the inability to meet the cumulative demands and/or its carbohydrate deficit needed to maintain its existence. A similar pattern appears to be prevalent in overstory trees as well but to a lesser degree. Both increasing age and competitive condition with time contribute to the decline in year to year growth variation. Competitive release reestablishes greater yearly variation until a time when growing space becomes limiting again. This indicates that the degree of competitive influence seemingly affects the individual's ability or response to climatic variation. It might also suggest that there is a threshold of competitive stress, particularly as demonstrated in suppressed trees with reference to light availability, wherein competition is the result of a single limiting factor or the capacity to meet the demand or deficit brought on by a limiting resource. The ability to meet resource demands may be altered or influenced by other intrinsic or synergistic factors affecting tree function. Consequently, competition indices only account for the present competitive situation based on tree structure, and not what may have been in years past which may also be indirectly affecting tree growth at present.

Growth Measures

Most competition-growth studies correlate index values with observed or actual growth averaged over a measurement period. This may be an adequate approach where sample trees are all of the same age. However, this study includes trees having a range of age, and

thus introduces the basis and comparison of observed and relative growth. Relative growth is specified as the lack of observed growth in relation to potential growth in the absence of competition. This growth measure should be more indicative of competitive stress given that competition represents the degree to which growth is inhibited rather than expressed. Potential growth is based on site-adjusted, maximum growth increments for white oak and tulip-poplar as outlined in the methods section. Table 7 demonstrates that, in all but a few cases relative growth does prove superior to observed growth as expected. While observed growth may well produce respectable results, competition is more aptly described by the lack of actual growth relative to potential growth.

Because forest remeasurement studies are often the source of competition-growth data, growth is expressed as an average annual increment for the growth period. The study design herein permitted a test of averaged and actual yearly increments. Averaged growth in this study is unlike that of other studies wherein a running mean is established from a flexible spline function designed to interpret a smooth continuous growth trend. This technique, in effect, reduces the year to year variation attributed to climate, and abrupt growth release or suppression. Each year has a unique average, whereas remeasurement studies can only calculate a single average for all years between measurements. It is hypothesized that averaged growth is likely to masque the year to year response that should correspond strongly with the true competitive condition, particularly in years

of extreme climate as already shown. In observing Table 7, it appears that actual annual increments generally provide better results than splined or averaged growth, though there are some exceptions. This relationship seems to hold more for earlier years, perhaps suggesting that the greater number of years used in the average, the less reliable the estimate of competition by comparison. Reduction of the yearly variation in growth probably contributes to the loss of fit from averaged figures.

Tree-ring data are generally referenced in ring widths or radial increments rather than basal area measures. Because of the modeling approach used in this study, it was possible to estimate basal area increments given tree size and reversing the growth process back with time. The emphasis was to establish whether there was any difference or benefit in using linear (radial) or areal (basal area) growth measures. It is assumed that areal measures, which inherently incorporate the growth effort relative to tree size, should generate greater growth variation indicative of the competitive effect than is expected from linear measures. By all comparisons (see Table 7), basal area increment proved consistently superior to radial growth regardless of the year or other type of measure. This result suggests that volumetric growth, if readily obtainable, might produce even higher correlations.

CHAPTER IV

SPECIES INTERACTION

Competition studies designed to examine species interaction usually contrast the yield of individuals of the same species grown in pure and mixed associations (Harper 1977). The objective of these studies was to determine whether individuals of a certain species tend to grow more or less in the company of individuals of the same species or of other species. A comparative analysis of radial growth increments of matched tree pairs for years 1930 through 1981 was conducted to elucidate temporal trends that may be attributed to intra- and inter-specific competition.

Subject tree pairs (see Table 1, page 12) were employed in the initial analysis to relate the growth patterns of nearest neighbors on the same site. It was assumed that these represent trees most likely to be exerting more competitive influence on each other than any other single individual. Additional tree pairs and comparisons consisted of subject trees matched individually with non-neighboring trees of near equal age, size and competitive condition from other plots, but whose competitors were composed of either the same or other species.

Tree pairs were assigned and grouped into pure and mixed species associations. Each species combination was further sub-divided into groups which included those trees designated the first or second tree in the pair. In pure species comparisons, the larger

tree was always placed in the first group to expose growth differences attributed to size. In the mixed species associations tulip-poplar was always in the first group and white oak in the second. Analysis was accomplished by comparing the combined radial increment for the same years for all trees in each group of each association to obtain a mean ring width ratio. This ratio indicates the degree of greater radial growth of one group over its counterpart. A ring width ratio of 1.0 represents equal mean radial increment among all trees in each group.

It was expected that subject tree pairs of the same species are more likely to behave similarly growthwise than mixed species pairs (i.e., TP-WO). Figure 5 shows the mean ring width ratio for all group and species combinations. Results indicate little difference in the mean ring width of neighboring pairs of the same species, Figures 5a and 5b, respectively. However, the mixed species pairs exhibit both yearly and long-term trends that may be attributed to species tolerances and intra-stand synamics (see Figure 5c).

White oak demonstrates greater tolerance to moisture stress than tulip-poplar, noted by the significant peaks in drought years (i.e., 33, 36, 44, 48) and dry years following extremely hot, dry years (i.e., 55, 58, 81). This result corresponds with the xeric to mesic classification of white oak and tulip-poplar, respectively (Fowells 1965), especially on poor xeric sites (Doolittle 1958), as in this study. It further suggests that competitive ability may

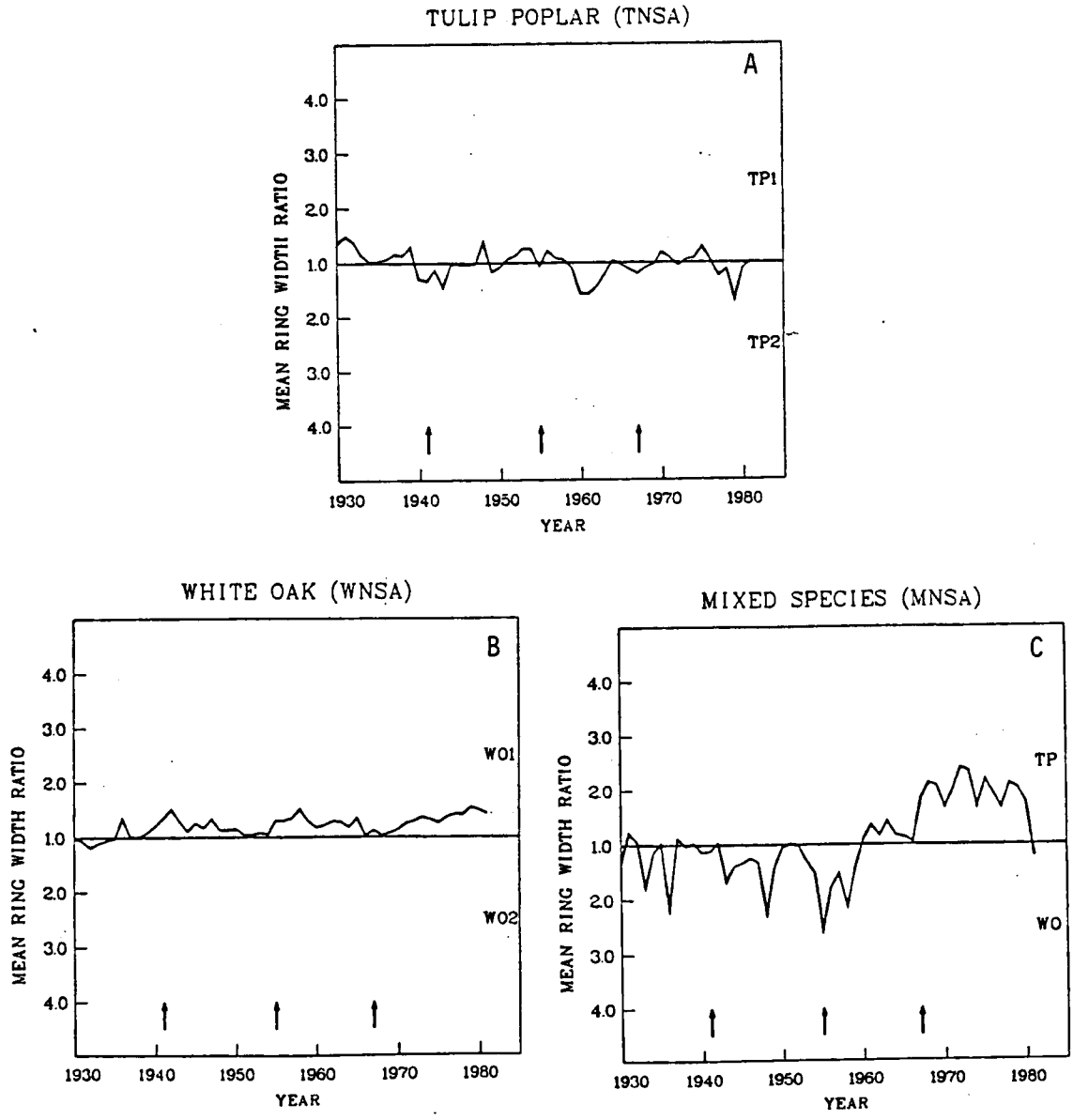


FIGURE 5. Mean ring width ratios of combined nearest neighbor, subject tree pairs in pure (PTP, PWO) and mixed (MTP, MWO) species associations.

diminish proportionally to species adaptedness for any site relative to its optimum site environment.

Early white oak dominance between 1930 and 1960 suggests its presence prior to tulip-poplar establishment, though tulip-poplar appears to overtake neighboring white oaks after this period. Based on growth potential, tulip poplar would be expected to outgrow neighboring white oaks of the same age. However, several factors appear to favor white oak, namely site adaptability and conditions, timing of establishment, and frequent drought occurrences during the study period. Ross and Harper (1972) found that early establishment sets the stage for eventual plant or species predominance. Cultural practices, in this case, may have indirectly contributed to white oak's development prior to tulip-poplar invasion either as sprouts of cut trees or released understory. Early establishment in this manner may have helped white oak to compete and grow more equitably with tulip-poplar than what might otherwise be expected.

Tulip-poplar, however, responded more favorably following the late fifties and the 1967 fire disturbance. What seems to be a dominance reversal in the early sixties may represent tulip-poplar's release response upon breaking into the canopy or to wetter climatic conditions following the frequent drought in the fifties. Another remote possibility exists considering differential species response to air pollution from the onset of area fossil fuel facilities during this period. Nonetheless, tulip-poplar exhibits greater growth release from competition following disturbance.

To determine whether these growth differences are accentuated due to interspecific competitive effects, these mixed species subject trees were compared with non-neighboring trees of the same species of similar age, size and competitive status, but whose competitors were predominantly of the same species. If there is no significant difference in growth of trees in pure and mixed associations we can conclude that the differences shown in Figure 5c may be obtained solely on the basis of differential tolerances and growth rate potential.

Figure 6 presents differences attributed to growth response of individuals competing within and between white oaks and tulip-poplar. Individuals in pure stands of tulip-poplar appear to compete less intensely with one another than do tulip-poplar contending with neighboring white oak (see Figure 6a). As a result, tulip-poplar in mixed associations demonstrates its inability to compete with white oak in years when moisture stress is greatest by displaying a similar sensitivity to drought, as in Figure 5c. This finding seems to confirm the intensity of interspecific competition where species exploit certain limiting resources more efficiently or with less demand than other species.

The same trend of early dominance by white oak and then eventual dominance reversal suggests a lag effect of canopy dominance of white oak in early years and a mild release as tulip-poplar finally achieved full canopy status in the latter years. This result re-emphasizes the importance of forest structure and particularly canopy development where individuals or, in this case species, have

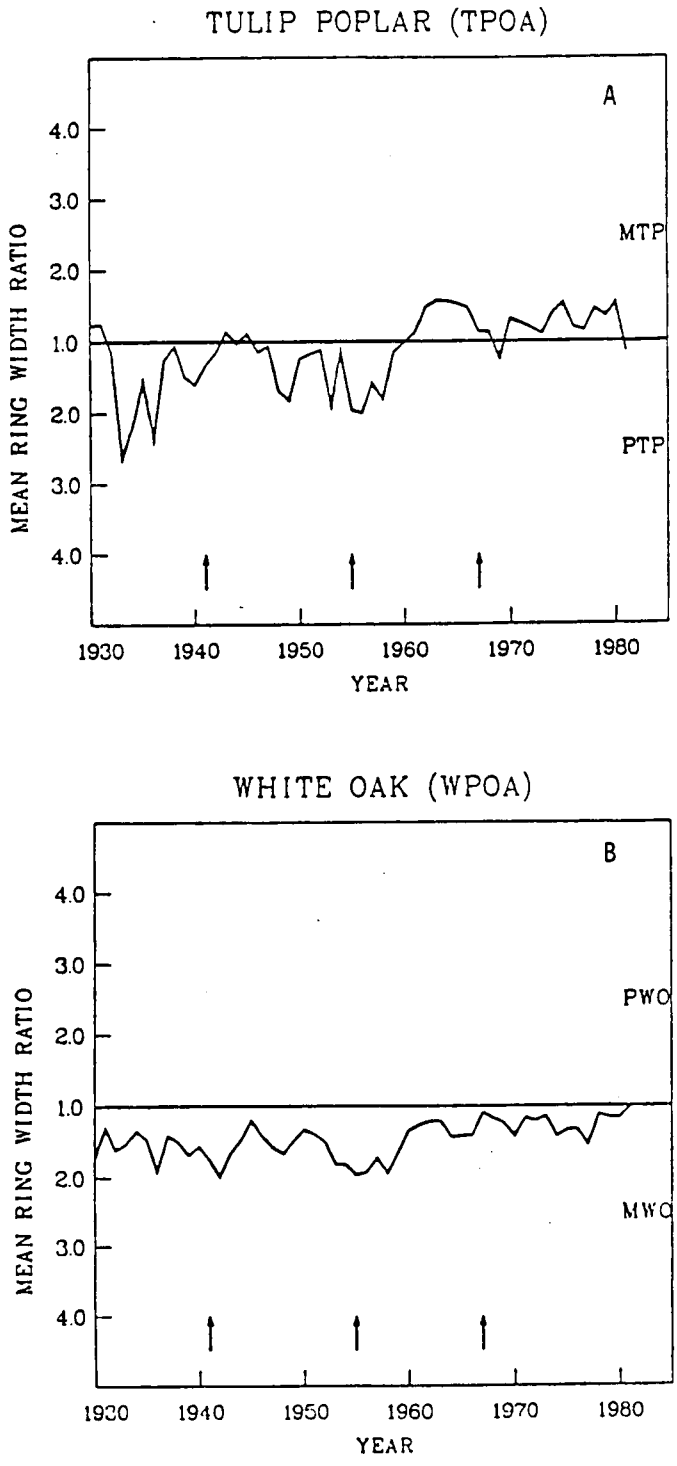


FIGURE 6. Mean ring width ratios of grouped non-neighboring tree pairs of the same species, but competing with trees of the same (pure--PTP, PWO) or other (mixed--MTP, MWO) species.

an improved crown position with respect to light. Likewise, the competitive effect to respond under light stress to varying climatic conditions may also play a part. It is also possible that this trend represents a response to nutrient stress where tulip-poplar has the ability to capitalize in a nutrient limiting system.

Figure 6b indicates that white oak grows more and therefore encounters less competition when surrounded by tulip-poplar than individuals of its kind. It also shows a decreasing dominance in latter years that corresponds with the increasing dominance of tulip-poplar in mixed associations over the same period. This indicates greater competitive intensity of an intraspecific nature within white oak and from an interspecific relationship for tulip-poplar in company with white oak.

To investigate the implications of this result further, subject trees in mixed associations were compared with other individuals of similar age and competitive status, though of the same species as the competing individual and in pure associations. Figure 7a compares the response of tulip-poplar and white oak though of mixed and pure associations, respectively. The results are similar to that of Figure 5c (MNSA) except that tulip-poplar tends to show consistently greater growth as might be expected based on growth potential. Years where white oak outgrows tulip-poplar as a group are years of climatic (moisture) stress.

Figure 7b illustrates the growth response of tulip poplar in pure associations and white oak in mixed associations. Tulip-poplar

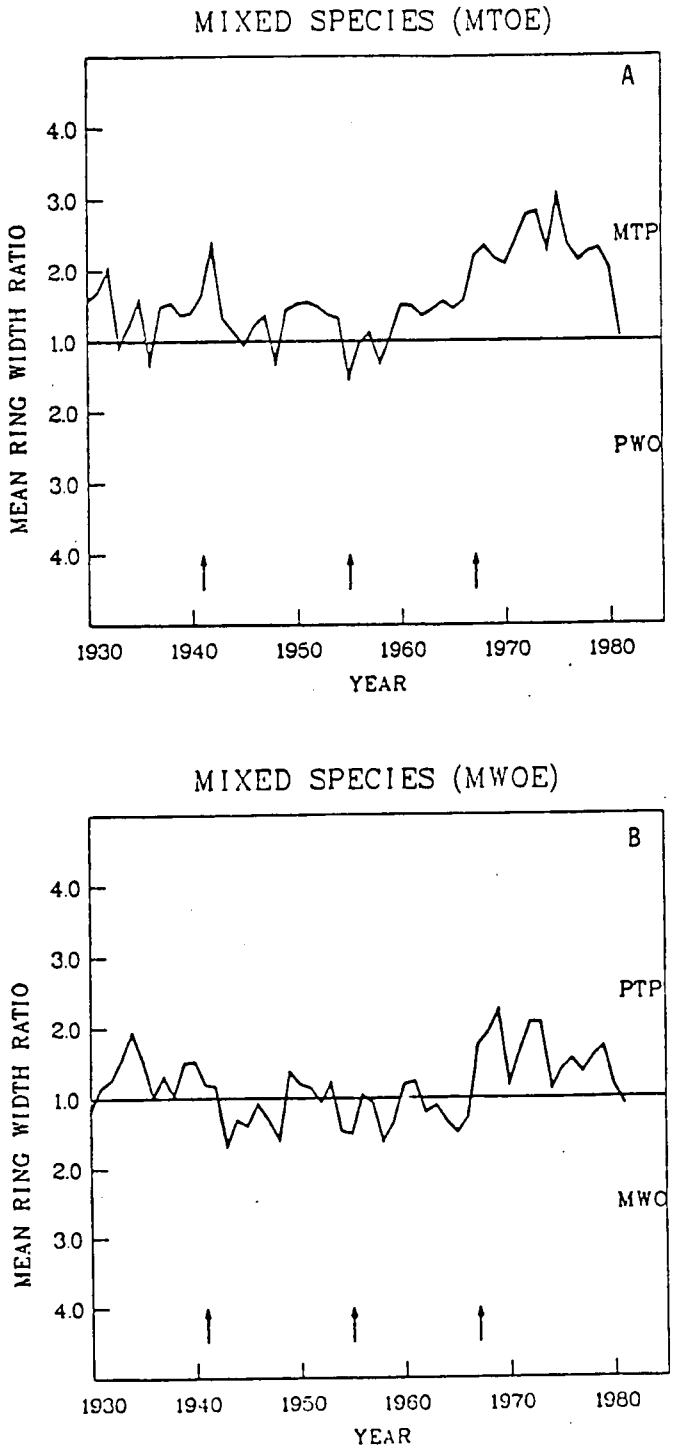


FIGURE 7. Mean ring width ratios of grouped non-neighboring trees of mixed species contrast, tulip-poplar and white oak, in pure (PTP, PWO) and mixed (MTP, MWO) associations.

dominates in the early years between 1930 and 1940 before growth appears to even through the remaining years excluding those following the 1967 fire. White oak continues to maintain a competitive advantage in drought years, while tulip-poplar responds more readily and to a greater degree to disturbance as expected. There is not, however, the dominance reversal in the early sixties suggesting that white oak was unaffected by the change and that it represents a localized stand response by tulip-poplar.

To account for differences that might be attributed to site quality, or tree response apart from any species interaction, an absolute ring width ratio was derived. This index represents an average of the absolute ring width ratio across all paired tree comparisons regardless of which tree or species in the pair that dominates. In every case, results from these tests, though not included, confirm both the homogeneity among sites as well as the predominance of species interactions rather than individual tree differences.

CHAPTER V

INTRA-STEM ASSESSMENT

Competition studies generally calculate the influence of neighboring trees as an average of a full circular (i.e., 360 degrees) condition and as more or less evenly distributed on all sides. This chapter focuses on an intra-tree growth analysis to evaluate whether ring width differences in oppositely oriented core radii are related to differential competitive stress on the respective sides of an individual tree. This involves determining whether differences actually exist in intra-tree growth apportionment, and whether competitive conditions on opposite sides (i.e., 180 degree semicircular evaluation) can account for them. By contrast, open grown trees on level sites are known to reflect ring complacency and fairly uniform growth on all sides (Fritts 1976). The following tests are designed to establish whether trees in closed stands distribute stem-wood equitably and to what degree competition may influence its production and deposition.

All cored trees with core radii oppositely oriented by 135 degrees or more were compared by noting the difference in ring width for all common years. The data are dichotomized by determining whether the ring width on one side was greater or less than the counter side. When the ring widths for both radii were equal the sign was made opposite that of the previous year so as not to bias the sample pattern toward a significant effect. Given that there is

no competition or that it is evenly distributed on all sides, it is expected that ring widths from opposite core radii be near equal in size and should, more or less, dominate (i.e., greater size) from year to year due to chance. The laws of probability hold that chance events of this type should generate a change of ring width dominance about every year and a half.

A runs test for trend data (Sokal and Rohlf 1969) was used to evaluate whether the sequence of sign changes for any tree departed significantly from randomness, the expected pattern for an open grown tree. The test is based on the number of runs or sets of consecutive years with like signs preceded or followed by sets of unlike signs. Results of this test indicated that over 90 percent of the trees sampled show significant deviations from a random response toward more systematic trends.

Differentially restricted crown and/or root development may prove responsible for this apparent disparity of growth in opposite radii of individual trees. This assumes that stem-wood distribution is somewhat related to tree structure, which in turn is directly influenced by competitive conditions. To test this hypothesis, subject tree pairs were singled out for specific study because of their selection as nearest neighbors of near or equal size and crown class. It is assumed that the sides toward the neighbor represent the more competitive, while the opposite side might be considered less so. A "t-test" (Snedecor and Cochran 1967) was used to determine whether ring width was greater more times on the outer radii than inner radii

between the paired trees. Table 8 shows the number of greater ring widths in each subject pair series on the competitive (C) and non-competitive (NC) sides. Results of the means across all plot pairs showed no significant difference and only a slight tendency for greater growth on the open side as opposed to the closed side. However, 6 of the 21 study pairs demonstrated a strong inclination of a competitive effect. The remaining study pairs exhibited a directional response, perhaps related to solar exposure, site drainage, or even stand disturbance and density.

Enhanced crown development and photosynthetic activity related to a southerly exposure might account for the apparent unidirectional response of ring width growth among subject tree pairs. In order to test this idea, core radii comparisons for all canopy trees were assigned to one of the four compass directions (i.e., North (315-45), East (45-135), South (135-225) and West (225-315)) to determine whether there was any association with core azimuth and/or crown orientation.

The total number of ring widths greater than counterparts in opposite radii was tallied for all trees by principal compass axes. Results showed no significant difference with core orientation either with site, species, or the entire sample as a whole (see Table 9). Though crown exposure to sunlight may nevertheless be important, it is superseded by other more influential factors or a combination of effects.

Although slope and site drainage represent possible contributing factors to one-sided ring width dominance (Fritts 1976),

TABLE 8. Ring counts and response descriptions of greater growth under different circum-tree influences by subject tree pair and total across all plots.

Plot	Species	NC[1]	C[1]	A[1]	B[1]	Response
A	WO	82	22	40	64	Competition
B	WO	61	43	31	73	Directional
C	WO	59	14	26	47	Competition
D	WO	29	28	3	54	Directional
E	WO	65	39	15	89	Directional
F	Mix	75	29	37	67	Competition
G	Mix	51	18	19	50	Competition
H	Mix	32	34	12	54	Directional
I	TP	37	36	18	55	Directional
J	WO	70	34	38	66	Competition
K	TP	58	46	32	72	Directional
L	WO	38	66	34	70	Directional
M	WO	85	18	44	59	Competition
N	Mix	47	57	22	82	Directional
O	Mix	53	51	19	85	Directional
P	Mix	44	60	22	82	Directional
Q	Mix	44	60	14	90	Directional
R	TP	23	81	51	53	Mechanical
S	TP	48	37	22	63	Directional
T	Mix	45	52	24	73	Directional
U	TP	11	44	17	38	Mechanical
Totals		1064	862	590	1336	

[1]Refers to core position or azimuth relative to the side of the subject tree or direction from plot center: (NC)--non-competitive side or direction away from competitor or plot center; (C)--opposite of NC, sides closest to competitor or plot center; (A)--direction of fewest ring counts; (B)--direction of greatest ring counts.

TABLE 9. Mean number of years of greater ring width growth contrasted between cores oppositely oriented and categorized by principal compass direction.

Number of Cores Sampled	Mean Number of Greater Ring Widths	Compass Orientation of Core
127	25.3	W
90	24.5	S
99	23.7	E
120	22.7	N

plot selection criteria limited any decisive basis on which to test this notion. However, root expanse and development into unoccupied and/or disturbed zones seems more probable. One of the study plots was chosen not only for its species complement but also for the presence of an adjacent clearing to consider the influence of an edge effect. Indeed, the dominant trees of this particular plot showed an overwhelming response of consistently greater radial growth on the side toward the opening, and despite being within the forest interior. Other plots demonstrated similar associations though in the direction of younger cohort patches of trees, perhaps related to an earlier disturbance or forest opening.

The production of tension wood due to mechanical stress may also explain uneven radial growth apportionment (Zimmermann and Brown 1971), though few if any of the sampled trees exhibited irregular stem form. Exceptions included two pure stands of tulip-poplar where stem eccentricity seemed to be prevalent. This effect may well be the result of extremely tight spacing and disproportional branching of the crown.

Even though cores displaying obvious fire injury were replaced with unaffected recores, scar tissue formation in fire-damaged stems presents yet another potential explanation for directional radial growth. Any one or combination of the factors discussed, including chance, could act as driving forces of disparate ring width growth about the stem. Certainly more study should be given this topic as a means of investigating competitive effects.

CHAPTER VI

CONCLUSION

During forest development, the effect of competition on individuals varies with both time and space. Differences in forest structure account for most of the growth variability attributed to competition. Structural positioning with respect to light appears to be the dominant factor determining the growth of an individual. Vertical stratification more often than horizontal spacing of stems and crowns dictates the individual's ability to exploit space and the resources it contains.

Newly introduced indices of competition, sapwood area and polygon crown-area each explained more than 70 percent of the growth variation in tulip-poplar and white oak, respectively. Their success is attributed to their close association to foliar leaf area or the tree's position and ability to intercept a greater portion of the available light resource. Results also show that a distance-independent measure of relative size proved more effective than other more frequently used distance-dependent indices.

None of the competitor selection methods displayed any significant advantage over each other in overall success or with index type. Competitor selection by crown class generally failed to meet expectations due to its ameliorating effect on the variation in competition indices by comparing subject trees and competitors of similar size.

The forest environment is rarely static either seasonally or from year to year. Individuals and species responded differently to yearly climatic fluctuations depending on their competitive position and/or inherent attributes. The relationship between competition and annual growth is strengthened in years of climatic extremes, such as drought years. Results in this study also demonstrated that competition intensifies with greater structural variation and stand development through time.

The manner in which growth variation is expressed affects the strength of its relationship with competition measures. Relative growth, the degree to which growth is inhibited rather than expressed in relation to potential growth, demonstrated a better fit than observed growth. Annual increments generally performed better than averaged growth increments. Areal growth measures, such as basal area increment, proved more sensitive to competitive change or status than linear, radial growth.

Differences in species attributes and tolerances may play a greater role in forest growth and development than what is presently indicated in the literature. The discussion on species interaction indicates drought tolerance in white oak and an inability for tulip-poplar to compete in hot, dry years or years following such years. Tulip-poplar showed opportunistic qualities by responding more readily and to a greater degree than white oak following disturbance. Contrary to conventional thought inter-specific interactions may be more prominent than intra-specific competition. White oak appears to

suffer less competition in the company of tulip-poplar than with white oak. In contrast, tulip-poplar seems to do better in the presence of other tulip-poplar than with white oak. These results suggest that greater competitive intensity can arise from both intra- and inter-specific interactions, though this relationship might not hold under different stand or site conditions.

Efforts to test whether competition is collectively and equally distributed on all sides of a tree proved inconclusive. There seems no doubt that patterns in ring width on opposite sides of a tree reflect systematic trends. Results indicated a unidirectional response in most cases, possibly related to root competition and microsite variations. Scar tissue formation from injury due to fire may also have contributed to this apparent disparity of radial growth. Crown development with respect to solar exposure showed little, if any, tendency to direct this response. Tension wood production from mechanical stress also failed to demonstrate any effect. Stemwood distribution may certainly be less random than expected, and the end result may involve all the factors mentioned acting in accord, though predominating at different times in the growth history of the individual and stand.

The dendroecological approach and stem-mapping design employed in this study proved extremely effective in investigating competition-growth relationships in a mixed-aged, mixed-species forest community. It allows a basis from which to conduct field sampling in managed and unmanaged forests alike for which little

or no substantial data may exist. The information this study provides renders a multiplicity of uses for competition study. Its most promising application involves an improved understanding of the complex interactions influencing the spatial and temporal dynamics of forests on the individual, species and community levels of organization and function.

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