COMPETITION QUOTIENT: AN INDEX OF THE COMPETITIVE STRESS AFFECTING INDIVIDUAL FOREST TREES

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ABSTRACT

COMPETITION QUOTIENT: AN INDEX OF THE COMPETITIVE STRESS AFFECTING INDIVIDUAL FOREST TREES

By Douglas James Gerrard

A new index of the competition exerted upon individual forest-grown trees by their neighbours was evaluated according to two criteria: (1) its capacity, relative to three other indices, to account for periodic basal area growth, and (2) its sensitivity to the release from competition which accompanies partial cutting.

The method rests upon the concept of circular zones of competition surrounding individual trees, with competition circle radii proportional to d.b.h. Competition is assumed to occur only when circles of adjacent trees overlap. The measure of competitive stress, termed *competition quotient*, is simply the sum of overlap areas within the competition circle of a subject tree, divided by its own total area.

Since there were no *a priori* grounds for choosing the appropriate constant of proportionality (termed *competition radius factor*), which related circle radius, in feet, to tree d.b.h., in inches, a series of eleven different radius factors was explored, ranging from 0.25 to 2.75 inclusive. Those producing the best-fitting regression models corresponding to different species and indices of competition were selected for detailed analysis.

The particular regression model, which was used to represent the basal area growth of individual trees, comprised fourteen terms among which were: a measure of relative site, d.b.h., one of the four competition indices, and *release* as expressed by the change in the value of competition quotient accompanying partial cutting.

Lansing Woods, a previously undisturbed oak-hickory stand in central Michigan provided the data for the investigation. Of five different species groups distinguished in the analysis, only maple (predominantly *Acer rubrum*) displayed a pronounced response to release, and even this represented the removal by the model of merely ten per cent of the total variation in growth.

Although all effects were small, several turned out to be significant because of the extremely large sample sizes characterizing the analyses.

Competition quotient proved consistently to be superior to the other prospective measures of competition, although only to a slight degree. The failure of any measure to account for appreciable amounts of variation seemed to suggest that the individual tree approach to growth prediction may have little practical potential in natural stands containing a diversity of species and age classes.

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CHAPTER I

INTRODUCTION

A fundamental principle in silviculture is that partial cuttings regulate the subsequent growth and development of trees left standing. It is because of this that *normal* yield tables, based as they are, upon data from undisturbed stands, are inappropriate for managed forests. Accordingly, over the years forestry literature has dealt repeatedly with the response in growth of stands to various silvicultural manipulations.

One aim of modern thinning experiments is to discover functions which relate expressions of stand growth to independent variables susceptible to measurement at the beginning of the growth period (Buckman, 1962). Typical stand variables are average age, d.b.h., height, site index, stand density and cutting intensity. In the case of mixed forests, different species are generally treated separately.

A restrictive aspect of all such studies has been their perpetual adherance to sample plots as primary experimental units. The strong appeal of plots has sprung from their close analogy to agricultural field plots with which experimental design had its beginnings. Since replication is a necessary ingredient of every respectable experiment, the research forester faces the often impossible task of finding mutually comparable plots within scattered natural stands. Frequently his only recourse is to severely limit the size of his study, and thus its precision, in order to adapt it to available forest conditions.

A further disadvantage of sample plots is their failure to permit an adequate measure of competition. The variables usually considered to reflect its influence are the various expressions of stand density, such as stems per acre, basal area per acre, and more recently, *crown competition factor* (Krajicek *et al.*, 1961). None of these accounts for variation in the spatial distribution of stems, yet this could be an important component of competition.

Buckman (1962) attempted to quantify the positional pattern of stems within plots by means of the standard deviation of tree diameters. His premise was that trees in clusters are likely to exhibit more variable diameters than those uniformly spaced. For his red pine sample plots the partial correlation between growth and standard deviation of d.b.h. proved nonsignificant. This, of course, might have implied simply that standard deviation is not an appropriate measure of stem pattern.

The current trend toward computer simulation of forests and forestry enterprises (Newnham and Smith, 1964; Newham, 1966; Clutter *et al.*, 1965) has stimulated a modicum of interest in the performance of individual trees. When the tree, and not the plot, is the primary object of study, a number of previous concepts need re-examination. Certainly one of these is stand density.

An expression of stand density is effective as a predictor of growth only to the extent that it reflects the competitive status of individual trees. Trees in mutual competition do not, in general, react alike. The relative size, tolerance and vigor of each determines individual tree performance under stress. Accordingly, any attempt to quantify competition should somehow account for its relative effect on different subject trees.

The main objective of this study has been to evaluate, on an individual tree basis, a newly proposed measure of competition, and to assess its utility in predicting the basal area growth of trees in the residual stand after partial cutting.

CHAPTER II

PREVIOUS MEASURES OF COMPETITION

Brown's Point Density

Stem count per acre clearly supplies a measure of stand density over definite forest areas, but what meaning does it convey in reference to a single tree? Brown (1965) attempted to settle this question by considering the inverse of stems per acre, viz. *area potentially available* (APA) per stem.

To measure APA he advocated partitioning the forest into a closed network of interlocking polygons, each encompassing a single tree. Operating on the premise that a tree has potentially available to it half the distance to each of its neighbours, he defined the boundary of available space between trees by a line normal to and bisecting the line connecting their centers. If such lines are drawn between all pairs of neighbouring trees, as shown in Figure 1, a distinct pattern of closed, non-overlapping polygons emerges, each of which represents the APA or potential growing space of the enclosed tree.[1]

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[1] This procedure is identical to the well-known "Thiessen method" of averaging precipitation gauge readings, in hydrologic studies (Thiessen, 1911).

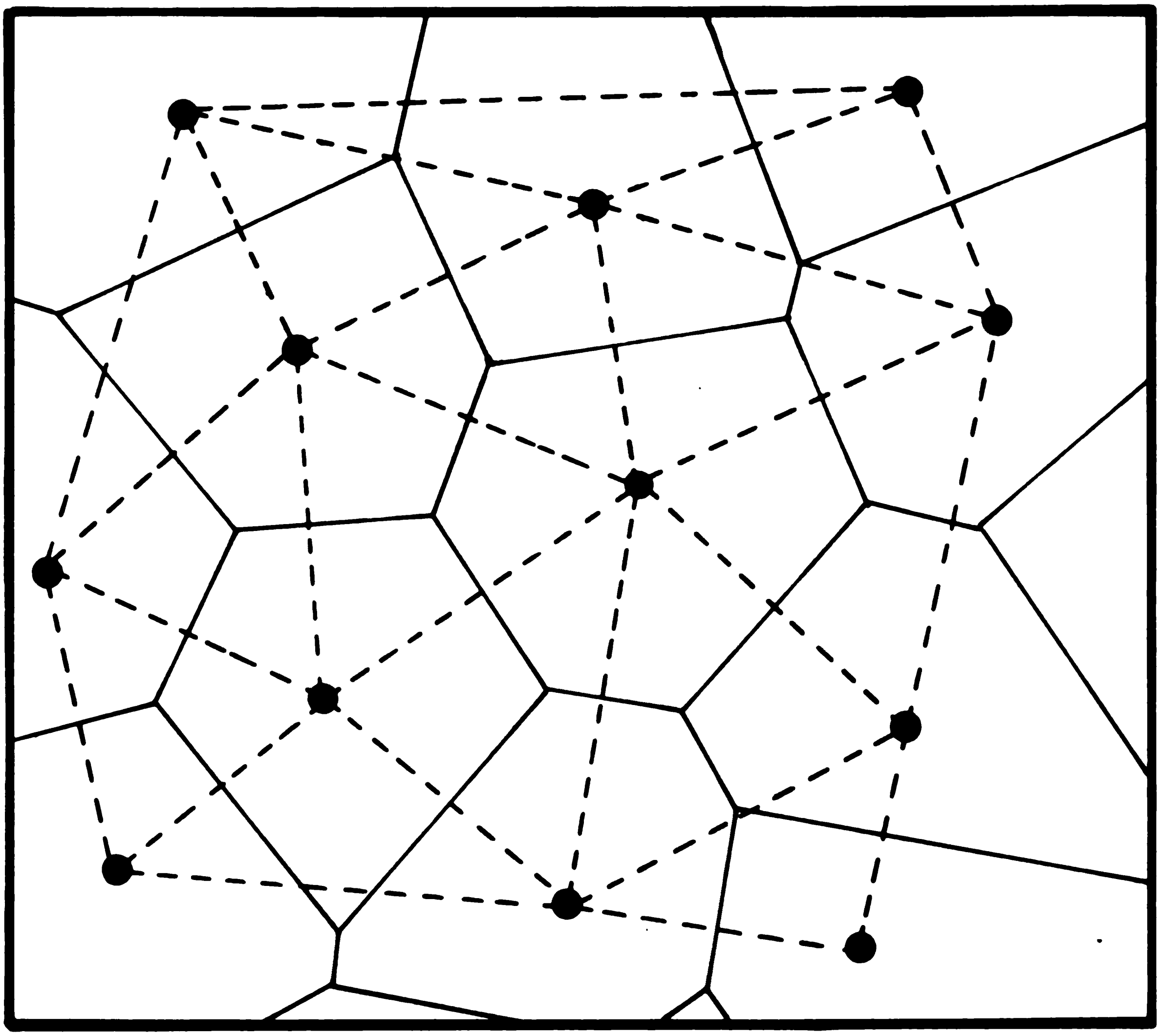

Figure 1. A random arrangement of trees enclosed by polygons according to the method proposed by Brown (1965). The sides of polygons are right-bisectors of the sides of triangles.

Inasmuch as competition is inversely related to growing space, the reciprocal of APA, is in some sense a measure of competition at a point. Since the dimensions of this quantity are stems per unit area, it constitutes an expression of point density as well.

Brown's technique for finding the APA of a given tree fails to account for variation in the competitive ability of different trees, since it rests upon the premise that the available growing space of any tree extends exactly half the distance to its competitors. This might be remidied by dividing the distances between neighbouring trees in relation to their relative sizes, or according to some other characteristic believed to reflect their ability to compete. Unfortunately, any such modification poses difficult geometrical problems.

As a measure of competition, the method does possess some desirable features. One of these is objectivity. Unlike other approaches, this one automatically determines which trees qualify as neighbours, thereby eliminating the necessity for guesswork (Figure 1).

Although Brown determined APA's by graphical methods, using measured distances and bearings, there seems no reason why the technique could not be computerized to work from individual tree coordinates. The location of APA boundaries would be analagous to the solution of a linear programming problem, whereby the sides of polygons would correspond to linear constraints.

The concept of point density based upon APA holds promise as a useful growth predictor for simulation models, but it needs further study.

Spurr's Point Density

Just as the variable, stems per acre, requires special interpretation when referenced to single trees, so does basal area per acre. Spurr considered this problem in 1962. Possibly motivated by the term *point sampling*, he proposed a measure of point density somewhat similar in concept to the well-known sampling method of Bitterlich. However, Spurr was careful to emphasize in his article that the proposed measure is not a method of forest sampling, and should not, therefore, be judged on such grounds.

Whereas Bitterlich sampling employs a fixed angle to define clusters of sample trees in the vicinity of a point, Spurr's proposal involves the varying sequence of actual angles subtended at a point by the stems of surrounding trees. An unsatisfactory feature of his measure is its failure to specify precisely which of the neighbouring trees qualify as competitors. In each new situation a decision is necessary as to the size of angle a tree must subtend to be included.

Nevertheless, Spurr's point density has the appealing characteristic of being expressed in the familiar units of basal area per acre. As in the case of Brown's measure, it pertains only to the point position for which it is computed. Such expressions cannot be applied to definite areas.

The formula for Spurr's measure is

$$B_n = \frac{76.625}{n} \sum_{k=1}^{n} (k - 1/2)(D_k^2/L_k^2) \qquad \text{(Equation 1)}$$

where

B_n = Point density based upon n competitors,

D_k = The d.b.h. of the k^{th} competitor,

and

L_k = The distance to the k^{th} competitor.

In the study upon which the present report is based, Spurr's point density was one of the measures of competition investigated. Because of its inherent vagueness in respect to which trees qualify as competitors, a special criterion was used to facilitate computer selection. The details are discussed later.

Staebler's Competition Index

An approach conceptually different from those just described was suggested by Staebler in 1951. So far as I can determine, this was the first attempt to measure individual tree competition on the basis of its relative size and position in a stand. Basic to his method is the assumption that the growing space occupied by an individual tree is a circular area whose radius is related to d.b.h. by the linear function: $r = a + b(\text{d.b.h.})$. Although not specifically stated by Staebler, it would seem that this circle expresses, in some sense, the effective area of rooting development. The existence of an exact physical counterpart, however, is not essential to the utility of the measure.

If the rooting systems of neighbouring trees did not overlap, it is reasonable to suppose that there would be little, if any, mutual influence upon growth. It is only when their roots interlace within the soil that trees are likely to experience appreciable competition and inhibit each other's growth rates--especially diameter increment. The area surrounding a tree in which the sharing of nutritional requirements can occur is appropriately termed its *competition circle*. Staebler hypothesized that the competition exerted upon a tree is directly proportional to the overlap of its competition circle with those of its neighbours. The reader may better visualize this by reference to Figure 2 where competition circles are indicated for a typical group of neighbouring trees.

He reasoned that the actual area of overlap supplied the most direct measure of competition. The mathematical formula which expresses this area is too complex for repeated manual computation, so he settled for *linear overlap*--the radial width of the overlap region.

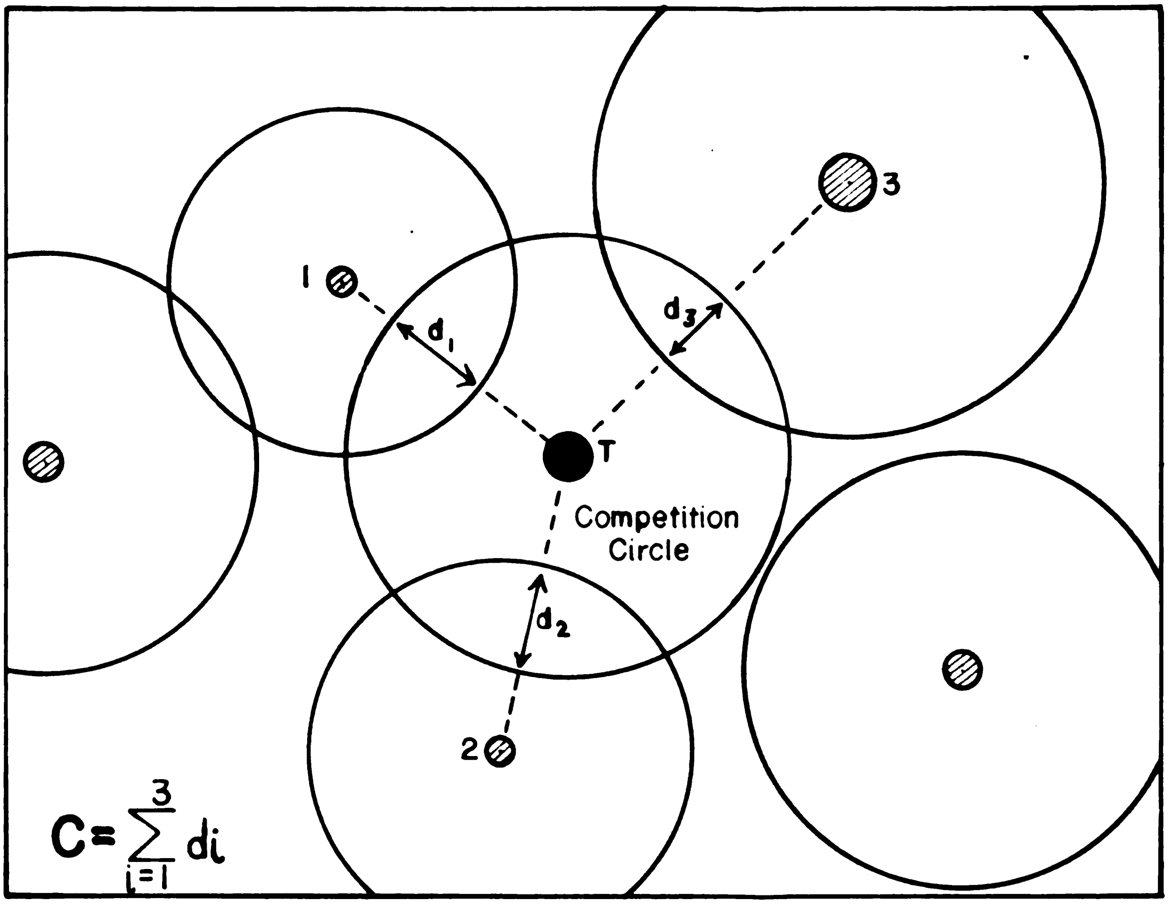

Figure 2. Staebler's competition index. The competition exerted on tree T is expressed by the sum of the linear overlap within its competition circle.

The competitive ability of trees depends, to some extent, upon their relative size or *dominance*. To compensate for this effect, Staebler developed a series of adjustment factors which he applied to his regression model. A somewhat simpler device, which he apparently overlooked, is presented in the next chapter.

Lacking electronic computer facilities, he used a combination of graphics and least squares in an effort to partially account for 12-year diameter increment of Douglas fir. Because his study was confined to a sample of just 32 survivor trees, it led to inconclusive results.

Newnham's Competition Index

Recently, Newnham (1966) investigated the competition exerted upon individual forest trees. Working with red pine near Chalk River, Ontario, he studied the correlation of growth with several measures of competition including Staebler's index. Like Staebler, he used competition circles to determine which trees qualified as competitors, although his circle radii were specified somewhat differently.

Assuming the crown radius of open-grown trees to be correlated with d.b.h., he estimated the average relationship between these two variables for a representative sample, using a second degree curve. Values from this curve were then used as estimates of competition radii, on the premise that the crowns of open-grown trees roughly define their rooting areas.

Another device which he used to specify competition circles was simply a constant expansion factor applied to individual stem diameters. This method of defining competitors is analagous to Bitterlich point sampling, where sample trees are selected according to the angle they subtend at the observation point. The d.b.h. expansion factors or *competition radius factors* investigated by Newnham were 1.375 and 0.972, corresponding respectively to the basal area factors 40 and 80.

It should be emphasized that all three of these criteria were merely means of identifying competitors. There remained the problem of measuring the competition they exerted.

The index proposed by Newnham is the proportion of a subject tree's competition circle circumference enclosed by those of adjacent trees. An equivalent expression is $1/(2\Pi)$ times the sum of angles (in radians) subtended at the circle center by the common chords of overlapping circles (Figure 3).

This and five other measures were simultaneously tested by Newnham, using multiple regression techniques to determine their relative effectiveness in predicting 5-year diameter growth, basal area growth, total height, height to base of live crown, and crown width. Among the other independent variables included in his 24-term regression model were d.b.h., age, and two indices of juvenile micro-site.

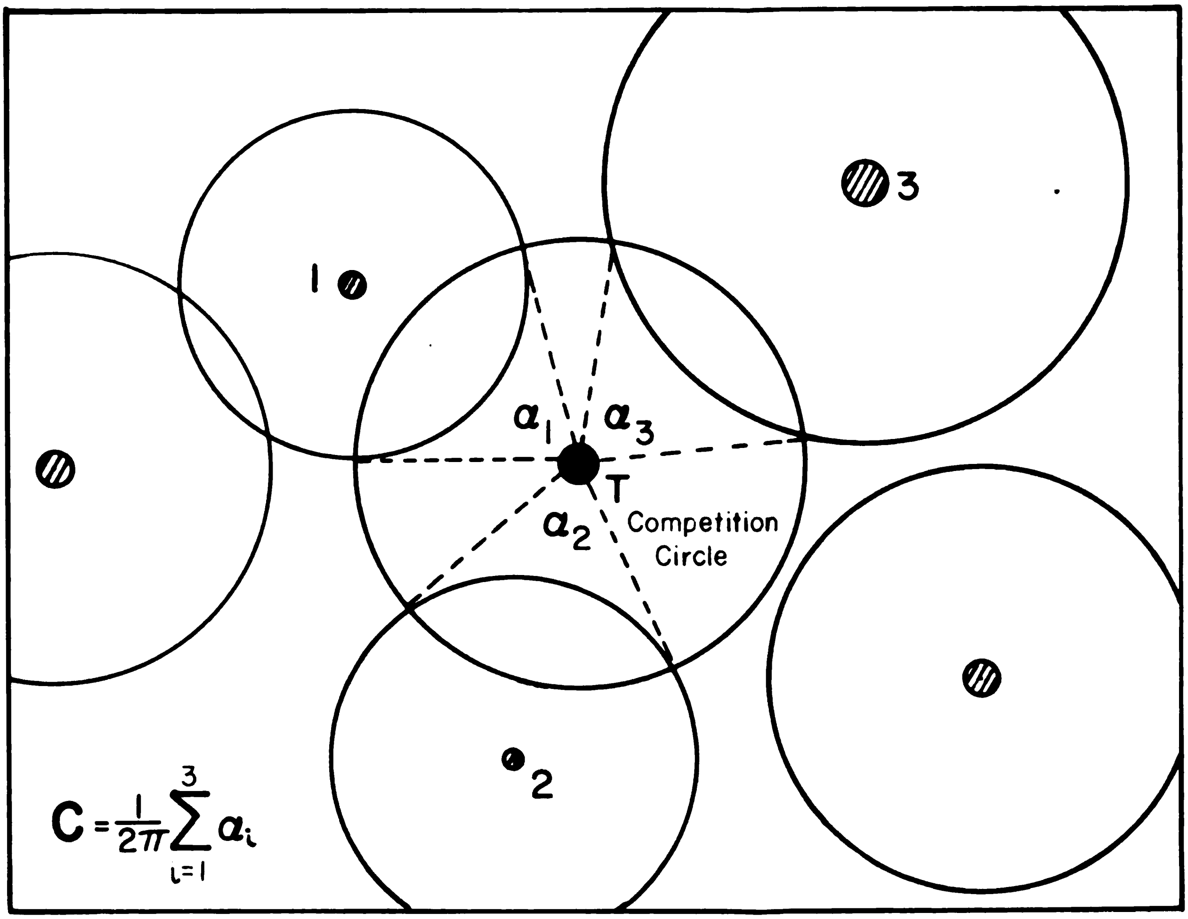

Figure 3. Newnham's competition index. The competition exerted on tree T is expressed by the proportion of its' competition circle circumference enclosed by adjacent circles.

His competition index made no significant contribution to the regression analysis of basal area growth, yet it was significant at the 0.001 level in the case of diameter growth. Such a paradoxical result is typical of regressions involving large numbers of correlated terms. If the different expressions of competition had been included one at a time in his analyses, comparatively clearer results might have emerged.

CHAPTER III

A NEW INDEX OF COMPETITION: COMPETITION QUOTIENT

By enlarging slightly upon Staebler's original hypothesis, stated previously, I developed an index of competition which accommodates differences in relative dominance associated with variations in tree size. The revised hypothesis may be stated as follows: The competitive stress sustained by a tree is directly proportional to the overlap of its competition circle with those of its neighbours and inversely proportional to the area of its own competition circle. Thus, it is assumed that the larger the tree, the more intense the competition it should be able to endure. The competitive stress index suggested by the hypothesis was termed *competition quotient*, defined by

$$\text{Competition quotient} = \frac{1}{A} \sum_{i=1}^{n} a_i \qquad \text{(Equation 2)}$$

where

n is the number of competitors,

a_i is the area of overlap with the i^{th} competitor, and

A is the competition circle area of the subject tree.

Figure 4 depicts these quantities for a typical group of competing trees.

The formula which may be used to compute a_i on the basis of the radii of two intersecting circles and the distance between their centers is derived in Appendix I. Inspection of the formula clearly indicates the desirability of electronic computer processing.

To calculate the competition quotients of trees, it is necessary first to estimate the radii of their competition circles. It appears reasonable, for a first approximation, to assume that competition radius, in feet, is some constant multiple (called the competition radius factor) of d.b.h., in inches. As mentioned before, this was one of the possibilities considered by Newnham. (Recall that he employed the radius factors 1.375 and 0.972). If, in fact, the assumption of proportionality holds, then some criterion is needed to determine the actual radius factor or factors characterizing a particular forest aggregation. One such criterion, which I employed in this investigation, was to select as optimum radius factor that which produced the largest coefficient of determination for the fitted growth model. More will be said about this in the chapters to follow.

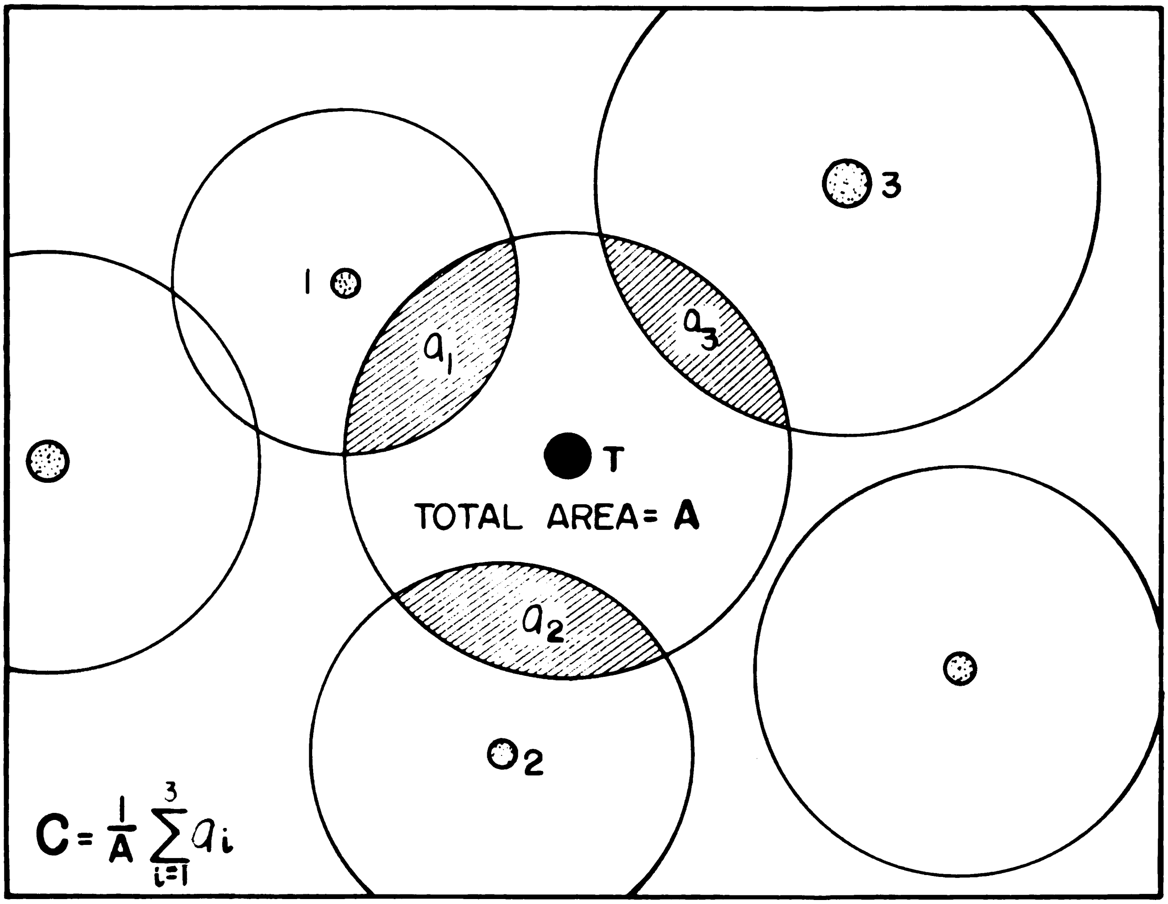

Figure 4. Competition quotient. The competitive stress exerted on tree T is expressed by the proportion of its' competition circle area overlapped by adjacent circles.

CHAPTER IV

THE STUDY AREA

A 40-acre oak-hickory stand known as Lansing Woods was chosen for the investigation. It is situated near Maple Rapids, in Clinton County, Michigan, approximately thirty miles north of Lansing (Figure 5).

The former Lansing Company, which owned the tract since the time of World War I, initiated a 10-year cooperative agreement with the former Lake States Forest Experiment Station on April 19, 1952, making the property available for research and demonstration.

An outstanding feature of Lansing Woods at that time was its freedom from cultural disturbances since presettlement times. By 1952, it was one of the few remaining uncut stands in Southern Michigan.

White oak and red oak together with their hardwood associates are the principal tree species found on the property (Table 1). The white oak component, which is approximately 300 years old, forms the main overstory. The scant age information which was taken indicates that the other oaks range in age from 80 to nearly 120 years, not having established themselves until the original stand of white

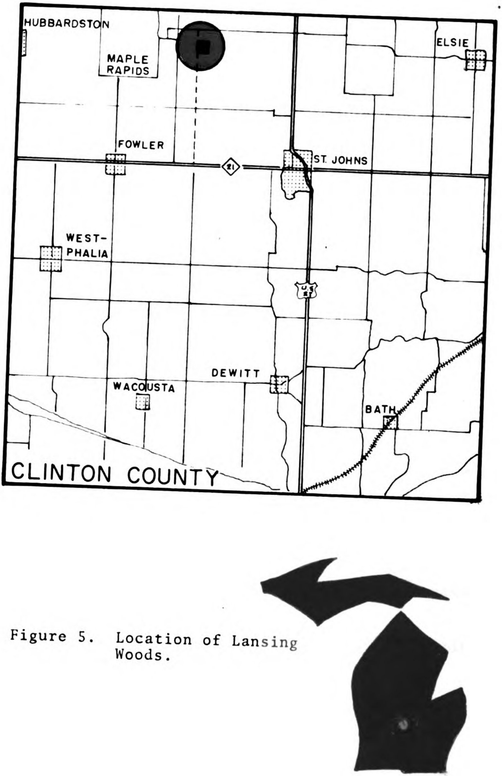

Figure 5. Location of Lansing Woods.

TABLE 1.--Species composition of Lansing Woods in 1952.

Species	No. trees per acre	Board-feet[a] per acre
White oak	28.2	4,345
Red oak	19.0	1,556
Black oak	9.6	697
Hickories[b]	44.7	696
Red maple	24.4	236
American elm	2.3	200
White ash	2.8	77
Sugar maple	1.0	9
Black cherry	2.5	7
Largetooth aspen	0.3	3
Cottonwood	0.1	3
TOTAL	134.9	7,829

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[a] Net volumes by International 1/4" Rule for trees with d.b.h. greater than 11 inches.

[b] Bitternut, pignut and shagbark hickories combined, in about equal proportion.

oak had attained maturity. It is estimated that the ages of the remaining species range up to about 100 years.

Mean stand density over the property in 1952 was about 110 square feet per acre. The net merchantable volume of growing stock, which averaged 7,829 board feet per acre, was increasing about 2 per cent per year during the study period.

Soils in the area are generally fine-textured (Blount and Morley silt loams) characterized by approximately 12 inches of silty clay loam overlaying glacial tills of the Saginaw lobe. Elevations range from 733 to 768 feet above sea level. Because of gently undulating topography and fine-textured subsoils, site conditions tend to be mesophytic and well-suited to the production of high quality oak sawtimber. A miniature sample of dominant red oaks (eight trees) averaged 97 feet in total height at 90 years of age, indicating a site index in the neighbourhood of 70. This is representative of some of the best oak sites in the Lake States (Gevorkianz, 1957).

CHAPTER V

ASSEMBLING THE DATA

Data Collection

Complete inventories of Lansing Woods were taken on three successive occasions, commencing in April, 1952. Remeasurement occurred during the spring of 1956, and again in 1962. The 6-year interval between these last two inventories furnished the growth period for this study.

During the initial survey a grid system was installed to simplify the relocation of individual trees. Every square chain within the forty acres became a separate plot with respect to which separate records were maintained for all trees at least five inches in diameter.

The data recorded for each tree included plot number, tree number, species, d.b.h. (o.b.), and status (merchantability-class, mortality, logging damage, or harvested). In the case of stems twelve inches and larger in d.b.h. additional information included merchantable height, per cent soundness, and vigor class. Unfortunately total height and age were not among these extra measurements. Because the study was to deal with all trees above four inches, the only recorded items which could be used were species, d.b.h., and status.

Concurrent with the initial inventory, a light improvement cutting took place within a six-chain-wide strip along the south end of the woods (Figure 6). The twelve acres affected by this particular operation were judged unsuitable for inclusion in the investigation.

During the spring of the following year, a few oak stems were removed from a narrow swath extending across the center of the woods. Considering the small number involved, these trees were treated in the study as though they had remained standing until 1956 when a major white oak improvement cutting took place.

The operation in the spring of 1956 occurred during the second inventory. As will be shown in the chapters to follow, one of the chief aims of this study was to assess the effect of this particular cut on the basal area growth rates of trees released.

The last inventory, which marked the conclusion of the second growth period, took place early in 1962, again during a major felling operation. This cut influenced the study only to the extent that the felled trees were difficult to remeasure. In fact, about one hundred overmature white oaks, which had been standing until 1962, could *not* be used as response trees because their final measurements were unobtainable.

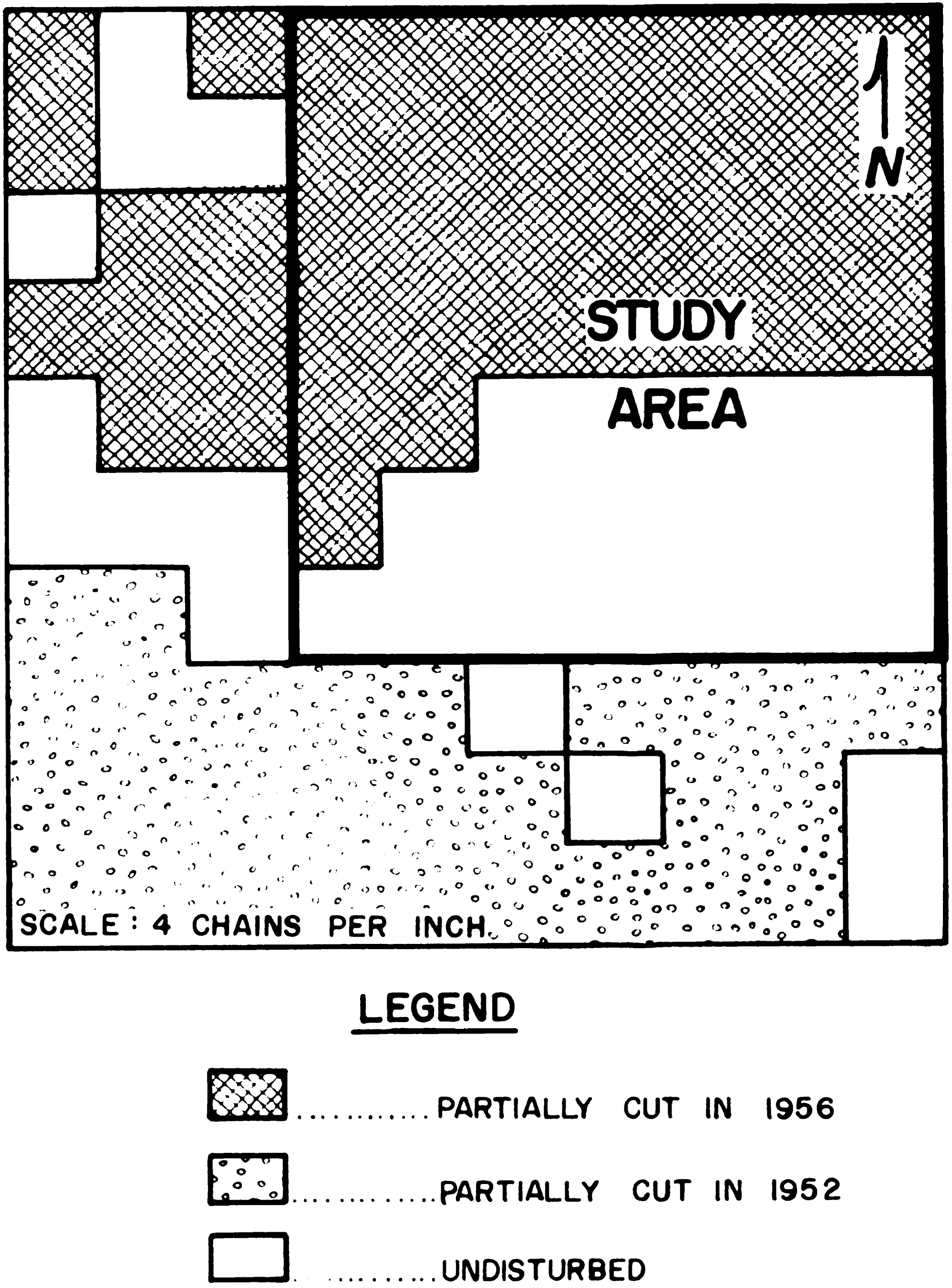

Figure 6. Location of study area in relation to the distribution of partial cuttings in Lansing Woods.

By the time I decided to use the successive records from Lansing Woods for a study of tree competition, the original grid, which had been installed in 1952, was essentially obliterated. Since the investigation required individual rectangular coordinates for all measured trees, it was necessary to restake the grid system throughout the woods.

Following this, coordinates of all trees were measured to the nearest foot in relation to the northwest corners of their individual plots. Harvested trees were identified on the basis of their stump diameters and species.

Once the coordinates had all been recorded, they were assigned to IBM punched cards and then collated with existing tree data. Finally, the entire 5,414 tree records were transferred to magnetic tape for storage and subsequent computer processing.

Data Preparation

All phases of data preparation and analysis were performed on the CDC 3600 digital computer at Michigan State University.

Phase one of the study entailed a series of consistency checks, whereby faulty tree records were identified and then corrected or, in some cases, deleted from the data tape. Among those requiring correction were the formerly mentioned white oaks lacking 1962 d.b.h. values. The remedy for the white oaks was to assign each of them zero growth for the period. The regression analysis, described in the chapters to follow, ignored such trees. Less than one per cent of all records were deleted from the study because of gross errors.

Not all of Lansing Woods was suitable for inclusion in the study. In fact, the only trees chosen for actual analysis were those in a 19.6-acre block occupying the northeast corner of the woods (Figure 6). Other parts of the woodlot were disqualified because they had sustained partial cuttings *prior* to the beginning of the chosen growth period. Another reason for selecting the northeast corner was the wide range of cutting intensities it incurred right at the start of the period. Thus, it provided an excellent situation in which to observe, during a common growth interval, tree performance following varying degrees of release.

The second phase of the investigation was concerned with bringing the tree data into a more convenient form for sorting and computation purposes. Although there were thirteen different species altogether, several of these occurred in very small numbers. A certain amount of combining seemed appropriate. Thus, while the three oaks were kept separate, the three hickories (bitternut, pignut, and shagbark) were grouped together, and so were red and sugar maples. Those remaining, I designated collectively as miscellaneous species. There were therefore six different groups of species recognized in the study, although only the first five were used as response trees.

To further simplify the data, I eliminated certain differences in tree status. All trees were assigned to one of three categories: *survivors*, *ingrowth*, or *removed in 1956*. Survivor trees included all those which were alive on the two occasions straddling the growth period. Ingrowth comprised trees which entered the 5-inch class during the period and had not suffered previous logging damage. The rest of the measured trees were classed as removed in 1956. Included among these were a few trees which died naturally both before and after that date.

The actual numbers of trees falling into each of the revised species-status classes for the 19.6 acres are displayed in Table 2.

TABLE 2.--Distribution of numbers of trees by status and species groups within the 19.6-acre study block.

Status	Species Groups						Total
	Red Oak	White Oak	Black Oak	Hickory	Maple	Misc.	
Survived	346	298	134	695	507	103	2,083
Removed '56	44	279	33	50	63	14	483
Ingrowth '62	7	10	2	51	55	10	135
TOTAL	397	587	169	796	625	127	2,701

CHAPTER VI

THE REGRESSION MODEL

Functional relationships among biological variables are generally too complicated to be described in simple mathematical terms. Just a few of the countless factors governing the growth of trees are even susceptible to measurement. Thus, in formulating regression models which relate growth to other measurable parameters, we seek merely to approximate whatever underlying laws exist.

The proportion of observed variation in growth which is accounted for by a particular model depends upon the importance of the included variables and their manner of inclusion. For example, if a pair of intensely interacting variables were inserted into the equation in linear combination instead of in product form, they might fail to make any significant contribution to the regression. Care is evidently called for in the development of effective growth models.

To adequately perceive the influences of competition and release from competition upon individual tree growth presumeably requires a fairly elaborate regression model. In an ideal study, the independent variables would include age, d.b.h., total height, crown volume, relative crown position, micro-site quality, and (in the case of mixed stands) an index of species tolerance. The pure effects of competition and release could then be separated from these extraneous sources of variation by multiple regression analysis.

Unfortunately, the particular model developed for this study contained only d.b.h. and site quality as concomitant variables. It was anticipated, therefore, that there would be a relatively large amount of variation unexplained by the regression.

The actual equation studied was

$$G = b_1 + b_2 D + b_3 D^2 + b_4 S + b_5 C + b_6 C^2 + b_7 \rho + b_8 \rho^2$$
$$+ b_9 DS + b_{10} DC + b_{11} DS + b_{12} SC + b_{13} S\rho + b_{14} C\rho$$

(Equation 3)

where:

G is estimated 10-year basal area growth (based on 6 years' actual growth),

D is d.b.h. at the beginning of the growth period,

S is a measure of site quality (to be explained later),

C is an index of competition (to be explained later),

and ρ is an index of release from competition (to be explained later).

A Possible Index of Relative Site Quality

Differences in basal area growth among individual trees are attributable partially to variations in local site quality. Although this investigation was aimed principally at the influences of competition, and release, I thought it desirable to include some expression of site merely to eliminate its effect from the analysis.

A study of oak sites in Southern Michigan by Gysel and Arend (1953) indicated that the species composition of undisturbed mixed oak stands is closely related to site quality. The stand tables included in their publication showed a distinct relationship between the relative occurrence of red oak and the productive capacity of the site. The percentage of red oak basal area ranged from zero on the poorest sites to thirty on the very best.

Working with these stand tables, I investigated three different candidates for an index of relative site quality. The one which seemed to be the most sensitive to site variation was the ratio of red oak basal area per acre to the combined basal areas per acre of red oak and white oak (Table 3). For reference purposes, I designated this quantity *red oak ratio*. No special claim is intended here for its validity as an index of oak relative site quality. I included it in the analysis merely on the remote chance that it might account for some of the unexplained variation in basal area growth, thereby permitting a clearer look at

TABLE 3.--Comparison of three possible indices of oak relative site quality in Michigan

Site Quality[b]	Basal Area Ratios[a]		
	R/(R + B + W)	R/(R + B)	R/(R + W)
Very poor	0.000	0.000	0.000
Poor	0.018	0.027	0.054
Medium	0.150	0.187	0.430
Good	0.418	0.465	0.807
Very good	0.424	0.460	0.843

[a] Tabular entries are ratios among the basal areas per acre of red oak (R), black oak (B), and white oak (W), computed as shown at the head of each column. Values are based upon stand tables reported by Gysel and Arend (1952).

[b] Sites were rated according to soil and topographic characteristics.

the effect of competition. To compute red oak ratios for Lansing Woods, I first partitioned the tract into square 0.4 acre plots. All trees within the same plot were then assigned the same red oak ratio.

Inspection of Figure 7 reveals a weak but discernable pattern to the distribution of these values. The highest ratios are concentrated in the northwest corner, just outside the actual area selected for study. Both the northeast and southeast corners display groups of low values. Otherwise, the distribution is more or less random.

Despite the questionable validity of red oak ratio as an index of site, it did turn out to be significant in the main analysis of basal area growth.

Prospective Measures of Competition

Four different expressions of competition were selected for investigation as possible alternative predictors of basal area growth. These were:

1. Competition quotient: $$C_1 = \frac{1}{A}\sum_{k=1}^{n} a_k \qquad \text{(Equation 4)}$$

2. Newnham's competition index:[2] $$C_2 = \frac{1}{\Pi}\sum_{k=1}^{n} \theta_k \qquad \text{(Equation 5)}$$

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[2] I inadvertantly omitted the factor 2 from the divisor of C_2.

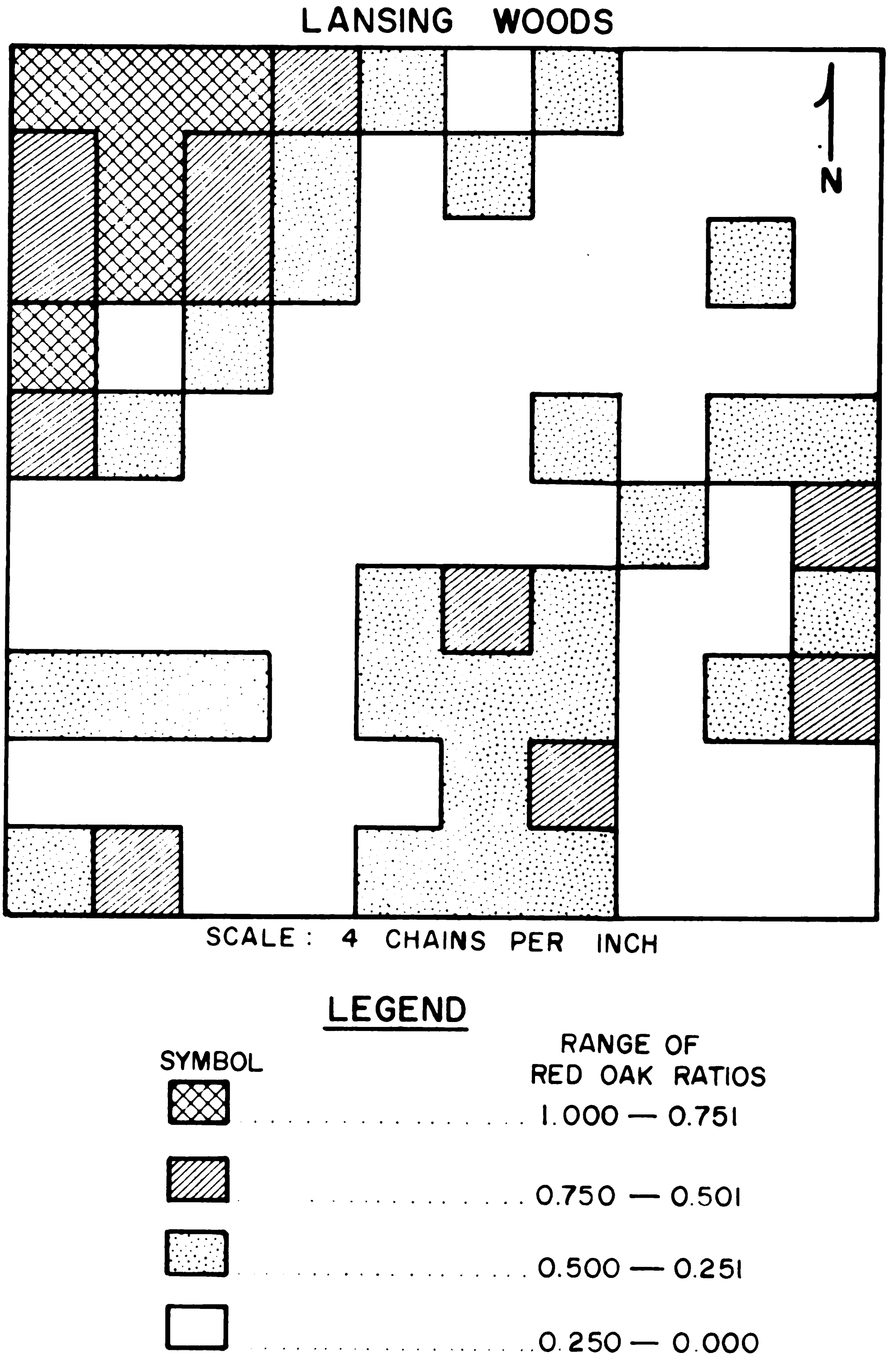

Figure 7. Distribution pattern of red oak ratios throughout Lansing Woods.

3. A modified version of Spurr's point density: $C_3 = \sum_{k=1}^{n} (D_k/L_k)^2$ (Equation 6)

4. Spurr's point density:[3] $C_4 = \frac{1}{n}\sum_{k=1}^{n} (k - 1/2)(D_k/L_k)^2$ (Equation 7)

where:

n is the number of competitors,

a_k is the area of overlap with the k^{th} competitor,

A is the competition circle area of the subject tree,

θ_k is the angle (in radians) subtended at the subject tree by the common chords of adjacent competition circles,

D_k is the d.b.h. of the k^{th} competitor,

and L_k is the distance to the k^{th} competitor.

To evaluate the relative merits of these four alternative measures, I performed successive regression analyses on the same data, each time using a different expression as the variable C in the model. The resulting regression statistics supplied me with the appropriate criteria for comparison.

Competing trees were selected according to whether or not their competition circles overlapped that of the subject tree, with the result that the same competitors

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[3] For simplicity, I dropped the factor 76.625 from C_4 since it would have had no effect on the tests of significance.

entered into the calculation of all four expressions of competition. Spurr's point density was thus freed from its usual vagueness in this respect.

As remarked in Chapter III, an empirical procedure was needed to establish the competition radius factor (radius in feet/d.b.h. in inches) which best characterized a particular class of trees. There could very well have been a different optimum radius factor corresponding to each of the different expressions of competition. In anticipation of this possibility, I employed a series of different radius factors, repeating essentially the entire analysis for each.

A Measure of Release

As stated previously, a relatively heavy improvement cutting took place in the study area at the start of the six-year growth period. Trees which had succumbed naturally or sustained logging damage at about this time raised the total of trees which were effectively removed from the stand to about 480. This corresponded to a 40 per cent reduction in the basal area over the 19.6-acre block, most of which comprised overmature white oaks.

One aim of the study was to measure the effect of this disturbance on the basal area growth of trees left standing. The extent to which any tree responds to the removal of competition depends, among other things, upon its proximity to trees removed. Different trees within the same block sustained vastly different degrees of release. One prospective measure of this effect was provided by

$$\rho = C_1 - C_1' \qquad \text{(Equation 8)}$$

where C_1 and C_1', respectively, are the competition quotients of a tree before and after release. This was the expression I used in all regression models. Its effectiveness was presumed to reflect the adequacy of C_1 as an indicator of competition.

CHAPTER VII

THE ANALYSIS

The analytical procedure was designed to resolve three interrelated questions:

1. What competition radius factors best characterized the major species in Lansing Woods?
2. Which of the four expressions of competition produced the most effective regression models?
3. Did the different species groups vary significantly in their susceptability to competition or in their response to release?

Procedure

The regression analysis was performed for a succession of different radius factors which were increased by steps of 0.25, from 0.25 up to 2.75. This whole series was repeated within every species group for the three competition indices C_1, C_2, and C_3. In the interest of computer economy, the analysis based upon C_4 was restricted to radius factor 1.00 because of the similarity of results to those for C_3. Testing of the others was terminated at radius factor 2.75, because competition beyond this limit was considered implausible. For example, trees 10 inches in d.b.h. separated by 55 feet or more would be expected to have negligible influence on each other's growth rates.

A sizeable array of statistics was generated by each repetition of the full regression analysis. Only a selected few of these were susceptible to meaningful interpretation. They may be enumerated in the order in which they were considered, as follows:

1. The F-statistic and the corresponding change in R^2 reflecting the contribution of site over and above the effect of d.b.h.
2. The F-statistic and the corresponding change in R^2 reflecting the joint contribution of the last 10 terms of the model after the effects of d.b.h. and site were removed.
3. The series of F-statistics and the changes in R^2 reflecting the consecutive *improvements* in the regression model as each of the last ten terms was introduced.

Significance Levels

Theoretical Considerations

The effectiveness of a significance test in discriminating real from random effects is contingent upon the size of its critical region, or the probability of the test contradicting a true null hypothesis. For the simple hypothesis, $H_o:\mu = \mu_o$, there exist two complimentary interpretations of significance level. One view holds that the specified level of significance a is the expected relative rate of type-one errors in repeated testing (for cases in which H_o is true). The other interpretation regards α to be the conditional probability of falsely rejecting H_o in a particular experiment. In the case of a single null hypothesis, the two points of view are equivalent (Miller, 1966).

In simultaneous statistical inference, where several hypotheses are considered collectively, the level of significance assumes new meaning. The probability of wrongly discarding at least one hypothesis depends upon the number true. In the worst possible case, where all in a set are true, the chances of error are considerably greater than α, the selected rejection level. The actual value of the probability will depend upon the kind of dependence which exists among the several test criteria. If they are truly independent (e.g. t-statistics with independent error terms), then the *probability error rate* α' for the family of tests may be determined exactly by the relation:

$$\alpha' = 1 - (1 - \alpha)^k, \text{ for k true hypotheses.} \qquad \text{(Equation 9)}$$

For example, if k is 2 and the significance level per test is set at 5 per cent, then the actual probability of at least one false rejection will be 9.75 per cent which is nearly twice that for a single test.

True independence rarely occurs among tests pertaining to the same experiment. The typical experimental situation features test-statistics containing mutually orthogonal contrasts, but the same error term. In multiple regression analysis, the interdependence of tests is accentuated by non-orthogonal data, and consequently, mutually correlated regression coefficients.

An experimenter who might wish to control the maximum probability error rate of a family of interdependent tests is unable to make use of the above simple calculation. He can, however, call upon an extremely useful relation, called the *Bonferroni inequality*, which furnishes a crude protection level for the collective null hypothesis. It states simply that

$$\alpha' \leq k\alpha \qquad \text{(Equation 10)}$$

where α is the significance level per test. This is true for any degree or kind of interdependence whatsoever.

If α is small (say .05) and k is not excessively large (say 10 or less), the upper bound supplied by the inequality shows surprising agreement with the result pertaining to independent tests. For example, in the case considered above where $k = 2$, the Bonferroni estimate of α' is 10 per cent, which is not much larger than the exact value.

Application to the Study

The study reported in this paper embraces large numbers of simultaneous tests which fall into certain natural groupings or families. To treat each test in the customary fashion on an individual basis, without regard to the overall probability error rate per family, would be a serious oversight. Suppose, for example, that the one per cent significance level were applied across the board to all 150 individual tests forming the main body of the analysis. Then the chances of wrongly proclaiming significance at least once somewhere among the results would be virtually certain (according to the Bonferroni inequality). Such a situation would render untrustworthy whatever conclusions were drawn from the study.

To avoid this unsatisfactory circumstance, protective measures were built into the test procedure, based upon the concept of controlled probability error rates for families of logically related tests. The particular rejection criteria appropriate to specific hypotheses were then estimated either by inverting Equation 9 to give

$$\alpha = 1 - (1 - \alpha')^{1/k}, \text{ for k independent tests,} \qquad \text{(Equation 11)}$$

or by inverting the Bonferroni inequality to give

$$\alpha = \frac{\alpha'}{k}, \text{ for k interdependent tests.} \qquad \text{(Equation 12)}$$

Maximum protection of the collective null hypothesis was ensured by setting k (the maximum number of null hypotheses assumed true) equal to the family size.

The first distinct family to be considered was the set of five independent tests of the variable S (red oak ratio) in the abbreviated regression model:

$$G = b_0 + b_1 D + b_2 D^2 + b_3 S \qquad \text{(Equation 13)}$$

fitted to each different species group. Both methods of estimating α specified essentially the same rejection level of 1 per cent per test.

The main body of the analysis concerned the last ten terms of the complete model, which contained the various effects of competition and release. By performing the entire regression analysis repeatedly for the three successive competition indices (at each of 11 consecutive radius factors), within each of the five species groups, I generated an enormous array of separate null hypotheses, 1,650 to be exact. This number was immediately reduced to 150 by restricting tests to the set of 15 optimum radius factors (corresponding to different species and competition indices). Separate regressions supplied natural subfamilies of ten-term sets. These are schematically depicted in Figure 8.

Tables of critical F-values which are presently available extend down to the 0.1 per cent significance level. Levels below this would be unsatisfactory because of increased

	Red Oak	White Oak	Black Oak	Hickory	Maple	Competition Index Totals
C_1	f_{11}	f_{12}	f_{13}	f_{14}	f_{15}	$f_{1.}$
C_2	f_{21}	f_{22}	f_{23}	f_{24}	f_{25}	$f_{2.}$
C_3	f_{31}	f_{32}	f_{33}	f_{34}	f_{35}	$f_{3.}$
Species Totals	$f_{.1}$	$f_{.2}$	$f_{.3}$	$f_{.4}$	$f_{.5}$	$f_{..}$

FIGURE 8.--Array of ten-term subfamilies used in the specification of probability error rates.

sensitivity to the assumed form of the *tails* of the distribution. By applying the 0.1 per cent rejection criterion to each individual term within each subfamily we produced (by the Bonferroni inequality) upper bounds for the family and subfamily probability error rates as displayed in Table 4. The overall probability error rate of 15 per cent (i.e. 85 per cent *protection level*), was considered quite acceptable in view of the extraordinarily large number of tests involved.

For additional protection in cases in which all ten hypotheses per model were collectively true, a two-stage testing procedure was adopted. Stage one tested the variation removed jointly by each ten-term subset (using the 1 per cent F-value for the improvement in the complete model over the abbreviated version). Stage two permitted testing of individual terms only if the first-stage test was significant. The effect of this extra safeguard was to diminish (by an unknown amount) all the subfamily and family probability error rates.

Statistical Results

Concomitant Variables

Earlier the statement was made that the concomitant sources of variation, d.b.h. and red oak ratio, were included in the model for the single purpose of exposing the effects of competition and release. The percentages of

TABLE 4.--Array of upper bounds for subfamily and family probability error rates (in per cent) for the 0.1 per cent significance level per test.

	Red Oak	White Oak	Black Oak	Hickory	Maple	Competition Index Totals
C_1	1	1	1	1	1	5
C_2	1	1	1	1	1	5
C_3	1	1	1	1	1	5
Species Totals	3	3	3	3	3	15

variation removed by these first two variables are displayed, for the five major species groups, in Table 5. Tabular values listed opposite d.b.h. are coefficients of multiple determination (in per cent) for the model

$$G = b_0 + b_1 D + b_2 D^2. \qquad \text{(Equation 14)}$$

Diameter is apparently an important predictor of basal area growth in all five groups of species. Entries in row two of the table are the further percentages removed by the inclusion of red oak ratio in the regression. The minuteness of these improvements may be due in part to the existence of hidden correlations between d.b.h. and site. By including d.b.h. in the model first, I may have already accounted for much of the variation due to site. Additional percentages removed by red oak ratio would have to be reflections of environmental conditions unrelated to d.b.h.

One puzzling aspect of these results in the relatively minor response to red oak ratio manifested by red oak. Since the frequency of occurrence of this species furnished the index of site, I had expected it to exhibit the maximum effect.

Owing to the advanced age of white oak, I was not surprised at its failure to show response. Black oak and hickory were apparently both susceptible to the influences of site, since they proved to be highly significant. I can offer no substantial explanation for the lack of

TABLE 5.--Percentages of variation[a] removed by the regression on d.b.h. and on red oak ratio after d.b.h.

Sources	Species Groups				
	Red Oak	White Oak	Black Oak	Hickory	Maple
D.b.h.	52.7*	46.7*	45.3*	34.1*	47.6*
Additional for red oak ratio	0.9*	0.1	4.9*	3.7*	0.1

[a] Significance at the 1 per cent level is indicated by an asterisk.

correlation in maple, except for the obvious possibility that red maple (the main component) may be insensitive to minor site variations.

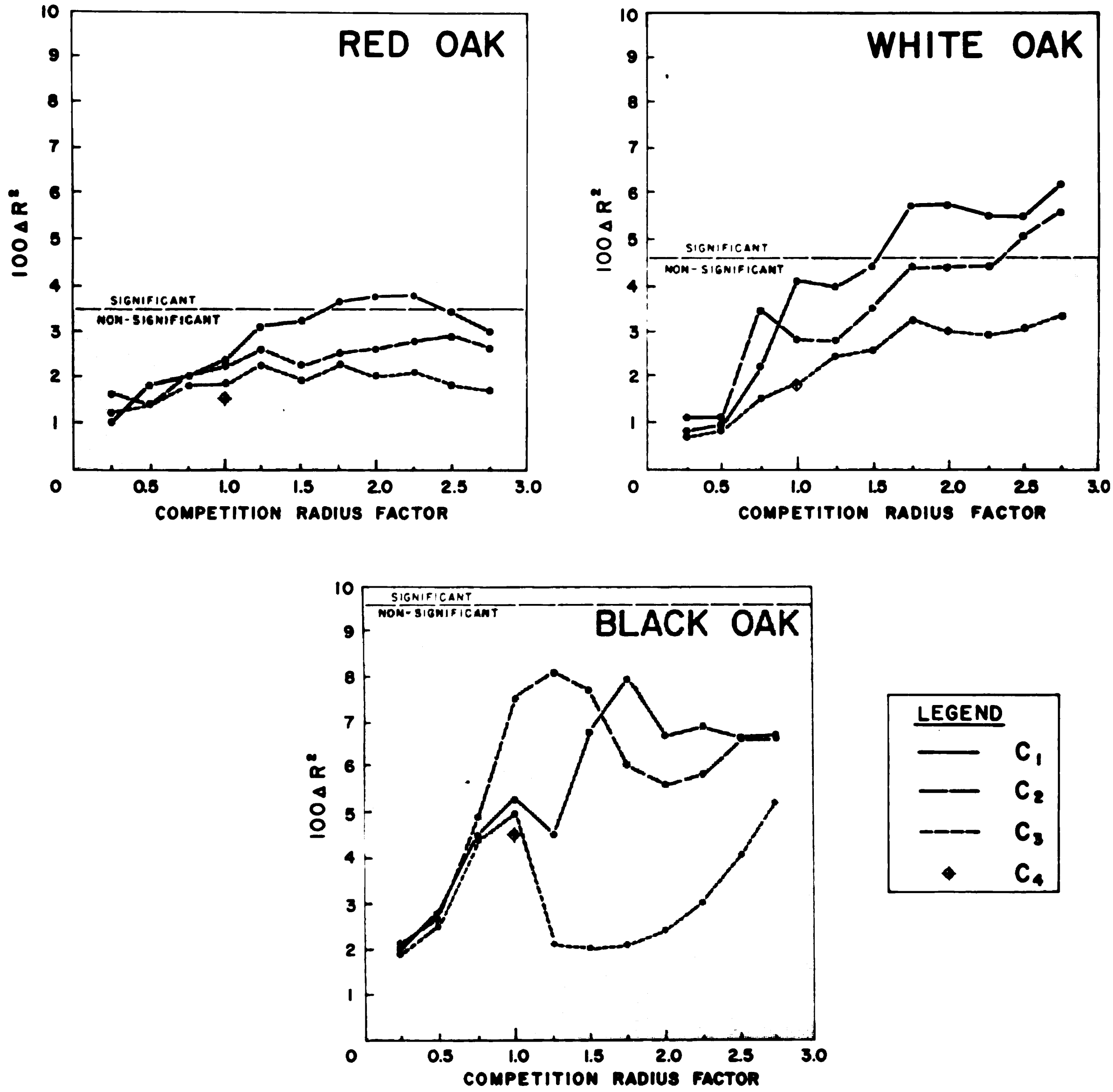
Despite the distinct absence of effect in two of the five groups of species studied, the apparent contribution of red oak ratio to the other three justified its retention in the model. Subsequent analyses dealt with residuals from the basic four-term expression (Equation 13).

Comparison of Competition Indices

The relative effectiveness of the four competition indices is portrayed in Figure 9, where the percentage variation accounted for by the final ten-term subset of the model is plotted against radius factor, separately by species groups. Evidently different optimum radius factors characterize different measures of competition within each species group. For comparisons among indices and among species groups to be valid, they should, therefore, pertain only to the specific radius factors evoking the strongest correlations.

According to this criterion, competition quotient stands out consistently as the most effective measure, while C_2 and C_3 exhibit successively weaker correlations. The one exception to this pattern occurs in black oak wherein C_2 appears to give a slightly better result than C_1. However, this is somewhat discredited by the fact that both responses are non-significant.

LANSING WOODS STUDY



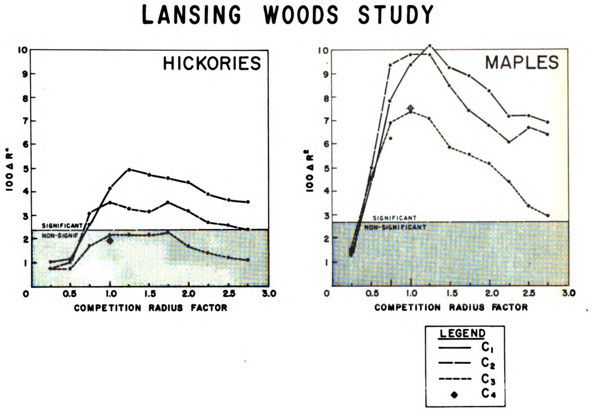


Figure 9. Percentage variation accounted for by the final ten-term subset of the complete regression model as a function of competition radius factor, for each of the four competition indices studied. C_4 is represented only at radius factor 1.00.

Although C_4 was tested just at radius factor 1.00, the resemblance of its response to that of C_3 is quite apparent. It would be difficult to identify the weaker of the two. Considering their similarity of definition (Ch. VI), such close agreement comes as no surprise.

Species Comparisons

Comparisons among species should be tempered with caution, for the percentage improvement in R^2 which is necessary to produce significance depends upon both sample size and percentage variation already removed by Equation 13. Specifically:

$$\Delta R^2_\alpha = \frac{F_\alpha(1 - R^2)}{F_\alpha + (f_e/f_r)} \qquad \text{(Equation 15)}$$

where

F_α is the critical variance ratio for the last ten terms of the complete model,

R^2 is the coefficient of multiple determination for Equation 13,

f_e represents degrees of freedom for residual variation,

and f_r represents degrees of freedom for the ten terms added to Equation 13.

Thus, we observe in black oak that while the variation accounted for by the model containing C_2 seems favourable, it fails to exceed the specified level of significance. Yet hickory, which displays only half this response, features statistically significant results nearly everywhere.

White oak differs distinctly from the other four species in failing to attain its optimum radius factors over the range of values studied. Two possible explanations suggest themselves. Previously it was remarked that about 100 of the survivor white oaks had to be ignored in the regression analysis because of unobtainable measurements at the end of the growth period. This being the case, the results for white oak may simply be nonsense. On the other hand, if it is assumed that those trees included were reasonably representative of trees ignored, then we might suspect that white oak competes over very extensive areas. Considering its very advanced age, 300 years, this seems a likely explanation.

In the case of red oak, all competition indices gave a feeble performance. Competition quotient is the only measure which produced a significant response and even this is unimpressive. About the only interesting feature of red oak is its optimum radius factor of 2.00. A recent study of this species in West Virginia by Trimble and Tryon (1966), disclosed a crown radius/d.b.h. ratio of approximately one foot per inch just prior to partial cutting. If this value is at all typical of red oak crowns in an undisturbed stand, then the optimum competition radius factor observed in Lansing Woods may actually reflect average rooting area per tree.

The only really pronounced effect is that occurring in maple. In this case, at least, we can observe a distinctive response to release from competition (as tests of individual terms reveal). This can be readily explained by the higher tolerance, relative to the other species, of both red and sugar maples. It is also noteworthy that maple is the only species group studied whose optimum radius factor is fairly consistent among different competition indices. Inspection of the plotted values suggests an optimum value in the neighbourhood of 1.15.

Interpretation of Individual Terms

The final regression model (Equation 3) was built up from the initial four-term expression (Equation 13) by the successive addition of single terms. At each consecutive stage in the process, the increase in R^2 was computed and tested at the 0.1 per cent significance level. All individual terms were retained in the cumulative regression whether or not they were judged significant, so that direct comparisons would be possible among different species groups and measures of competition at their optimum radius factors.

Successive percentage changes in R^2 accompanying each addition per model are presented in Table 6. The sums of entries per column are the total percentages removed by

TABLE 6.--Percentage changes[a] in R^2 accompanying successive additions per model.[b]

Term	Red Oak			White Oak			Black Oak			Hickories			Maples		
	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3	C_1	C_2	C_3
C	.55	.91	.45	.11	.21	.07	2.90	2.79	.09	1.31*	.64	.41	.51	.59	.10
C^2	.17	.17	.05	1.51	1.77	.02	.00	.02	.01	.24	.01	.09	.43	.17	.50
ρ	1.86*	1.24	.76	.37	.26	.73	.52	1.01	.35	2.54*	2.17*	1.17	3.87*	3.50*	1.83*
ρ^2	.09	.31	.24	1.42	1.42	.74	.22	.17	.05	.19	.12	.28	.11	.01	.02
DS	.02	.01	.06	.52	.68	.41	.12	.05	.06	.05	.05	.06	.03	.00	.00
DC	.04	.05	.05	.35	.12	.14	.99	.55	.05	.27	.10	.17	.04	.55	.00
$D\rho$	.04	.00	.02	1.15	.39	.47	.71	.79	2.86	.05	.00	.01	4.71*	4.75*	4.83*
SC	.19	.03	.44	.45	.37	.00	2.25	2.14	.01	.18	.26	.00	.00	.00	.03
$S\rho$	.35	.02	.15	.32	.34	.71	.01	.46	.66	.00	.06	.13	.07	.03	.06
$C\rho$	.43	.23	.03	.01	.08	.01	.02	.12	.83	.16	.19	.01	.43	.13	.01
Total	3.74*	2.97	2.25	6.21*	5.64*	3.30	7.74	8.10	4.96	4.99*	3.60*	2.33	10.20*	9.73*	7.38*

[a] Significance at the 0.1 per cent level is indicated by an asterisk. This particular choice of significance levels assures a protection level of at least 85 per cent for the entire family of 150 null hypotheses.

[b] Column headings, C_1, C_2 and C_3, indicate which index of competition was used as the variable C in the regression.

the last ten terms of each model. Several inferences may be drawn from inspection of the table.

Although none of the contributions is sufficiently large to be of much practical importance, all statistically significant results have theoretical implications. For the most part, significant effects are maximum in models containing C_1 (competition quotient), and minimum for those containing C_3. This is consistent with the pattern observed previously in comparisons among collective effects.

Of the ten terms subjected to tests, only ρ, the measure of release, proved significant with any degree of consistency. Red oak, hickory, and maple evidently all reacted, in some degree, to release from competition, whereas white and black oak were not perceptibly affected. White oak's failure to respond is readily explained on the basis of its age. The apparent insensitivity of black oak may be due partially to its smaller sample size; that is, the test and not the species may have been insensitive to release.

Competition quotient was the only index whose insertion in the model caused a directly significant effect in the variable C, and even this was confined to the single instance, hickory.

One especially interesting outcome was the highly significant response of maple to the interaction term DR. Apparently the influence of release upon basal area growth was, in this case at least, dependent upon the size of the subject tree.

CHAPTER VIII

SUMMARY AND CONCLUSIONS

This study has been an attempt to evaluate a new index of the competition exerted upon individual forest-grown trees by their neighbours. The merits of the measure were judged on the basis of two criteria: (1) its capacity, relative to three other indices, to express the influence of competition upon periodic basal area growth, and (2) its sensitivity to the change which occurs in individual tree competitive status following release by partial cutting.

An index of the competitive stress sustained by a tree should reflect the relative size and spatial arrangement of its neighbours--specifically those with which it competes for vital requirements. One approach which leads to a variety of such measures assumes that the growing space of every tree may be represented by a circular area, termed its *competition circle*, whose radius is a function of its d.b.h. On this assumption, it was postulated that the competitive stress in a tree is directly proportional to the overlap of its competition circle with those of its neighbours, and inversely proportional to the area of its own circle. The index suggested by this hypothesis, termed *competition quotient*, was simply the sum of overlap areas within the competition circle of the subject tree, divided by its own total area.

Competition circles provide not only the measure of competitive stress, but also the means of defining competitors, since competition occurs only between trees whose circles meet. Applied to this study, the radii of circles, in feet, were assumed to be some constant multiple (called the *competition radius factor*) of d.b.h., in inches. As there were no *a priori* grounds for estimating the appropriate radius factor(s) to use, the entire study was rerun for a succession of eleven different factors, ranging from 0.25 to 2.75 inclusive. Those which produced the strongest regressions for the growth model studied were selected as optimum radius factors. Detailed analyses were confined just to regressions based upon these particular factors.

The particular regression model used to represent the basal area growth response of individual trees was given the form:

$$\begin{aligned} G = {} & b_0 + b_1 D + b_2 D^2 + b_4 S + b_5 C + b_6 C^2 + b_7 \rho + b_8 \rho^2 \\ & + b_9 DS + b_{10} DC + b_{11} DS + b_{12} SC + b_{13} S\rho + b_{14} C\rho \end{aligned}$$

where D was the d.b.h. at the start of the observed growth period, S was a measure of relative site quality, called red oak ratio, C was one of four alternative competition indices studied, and ρ was the change in the value of competition quotient caused by partial cutting.

Altogether, 220 different regression analyses were performed, based upon this particular model. The three measures, besides competition quotient, used alternatively as the variable C in the equation were; Newnham's competition index C_2, a modification of Spurr's point density called C_3, and Spurr's point density C_4. Separate regressions were run, not only for all eleven radius factors, but also for each of five different groups of species; red oak; white oak; black oak; bitternut, pignut, and shagbark hickories; and red and sugar maples. Models containing Spurr's point density produced results so similar to those for C_3 that, in the interest of computer economy, evaluation of Spurr's measure was confined to radius factor 1.00.

The contributions to the regressions of the concomitant variables D and S were examined before anything else. Diameter proved highly significant in all five species groups, *explaining* between one-third and one-half of the total variation in each. Red oak ratio, the measure of site, offered little improvement over this, although its contribution was significant at the 1 per cent level in the cases of red oak, black oak, and hickories.

Percentages of additional variation removed by the final ten-term subsets of each regression equation were plotted over radius factor separately by species groups and by competition index. Different radius factors appeared to be optimal for different species and indices. Further comparisons were confined strictly to regressions pertaining to optimum factors. Of these, the significant regressions producing the strongest correlations were those containing competition quotient. Spurr's point density appeared to be the measure least sensitive to competition.

Of the five groups of species studied, only the maples displayed a pronounced effect, and even this was unimpressive, representing a mere ten per cent improvement over the effects of d.b.h. and site.

Tests of individual terms within each model disclosed that most of the variation removed per model was attributable to the variable ρ, the measure of release. This was to be expected.

A number of small but real effects were detected by the analysis, enabling us to answer at least those questions which prompted the investigation. It was observed that competition radius factor does attain different optimal values in relation to different competition indices, and that these optima vary considerably from one species to another. Furthermore, it was found that, of the four expressions considered, competition quotient consistently produced the strongest correlations with basal area growth. Finally, the analysis revealed a marked difference in response to release among different species, with the maples (predominantly red maple) displaying the most pronounced effect. The ability of competition quotient to measure competition is reflected in the extent of this response.

None of the effects observed in the study was sufficiently large to have much practical significance. From this it would seem that further investigations along this line should be directed at pure stands, preferably plantations, wherein the factors controlling the performance of individual trees are far less numerous and more susceptible to measurement.

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APPENDIX I. Derivation of the formula for the area common to two intersecting circles.

(a) <u>The segment of a circle</u>:

In Figure (a), the area of the sector

$$ABCD = \left(\frac{\Theta}{2\Pi}\right)\Pi r^2$$

$$= r^2\left(\frac{\Pi}{2} - \alpha\right)$$

$$= \frac{\Pi}{2}r^2 - r^2\sin^{-1}\left(\frac{x}{r}\right)$$

Since the area of

$$\Delta ABD = x\sqrt{r^2 - x^2}$$

Therefore, the area of segment

BCD

$$= \frac{\Pi}{2}r^2 - r^2\sin^{-1}\left(\frac{x}{r}\right) - x\sqrt{r^2 - x^2}$$

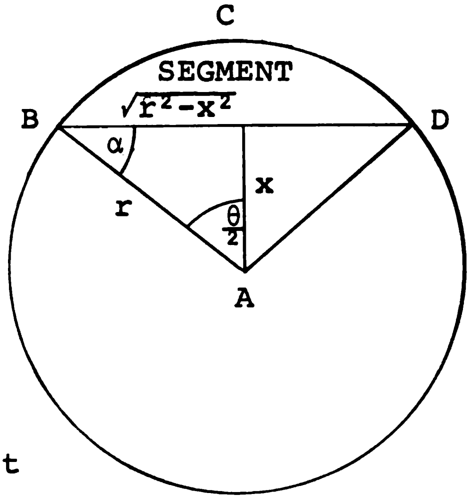

Figure (a)

(b) <u>The sum of two segments</u>:

In Figure (b), the area of overlap of the two circles is the sum of their two segments.

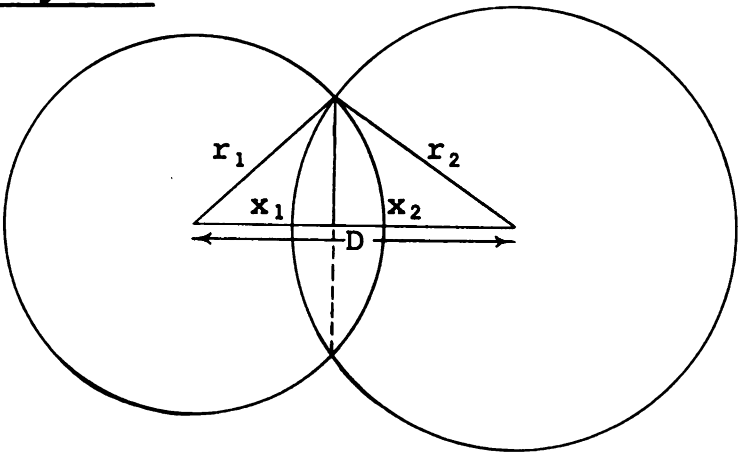

Figure (b)

Area of overlap

$$= \frac{\Pi}{2}(r_1^2+r_2^2) - \left[D\sqrt{r_1^2-x_1^2} + r_1^2\sin^{-1}\left(\frac{x_1}{r_1}\right) + r_2^2\sin^{-1}\left(\frac{x_2}{r_2}\right)\right]$$

where $x_1 = \dfrac{r_1^2 - r_2^2 + D^2}{2D}$ and $x_2 = D - x_1$

APPENDIX II. Botanical names of species referred to in the text.

Common Name	Botanical Name
White oak	*Quercus alba* L.
Red oak	*Quercus ruba* L.
Black oak	*Quercus velutina* Lam.
Bitternut hickory	*Carya cordiformis* (Wangenh.) K. Koch
Pignut hickory	*Carya glabra* (Mill.) Sweet
Shagbark hickory	*Carya ovata* (Mill.) K. Koch
Red maple	*Acer rubrum* L.
Sugar maple	*Acer saccharum* Marsh.
American elm	*Ulmus americana* L.
White ash	*Fraxinus americana* L.
Black cherry	*Prunus serotina* Ehrh.
Largetooth aspen	*Populus grandidentata* Michx.
Cottonwood	*Populus deltoides* Bartr.

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