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# Crown Geometry of Plantation-Grown American Sycamore and Its Simulation

John R. Schutt
H. H. Shugart
J. W. Ranney

Environmental Sciences Division
Publication No. 2574

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ENVIRONMENTAL SCIENCES DIVISION

# CROWN GEOMETRY OF PLANTATION-GROWN AMERICAN SYCAMORE AND ITS SIMULATION[1]

John R. Schutt,[2] H. H. Shugart,[3] and J. W. Ranney

Environmental Sciences Division
Publication No. 2574

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# ABSTRACT

SCHUTT, J. R., H. H. SHUGART, and J. W. RANNEY. 1985. Crown geometry of plantation-grown American sycamore and its simulation. ORNL/TM-9721. Oak Ridge National Laboratory, Oak Ridge, Tennessee. 290 pp.

Branching variables were measured on plantation-grown American sycamore (*Platanus occidentalis* L.) as part of a study to describe and model branch-level crown geometry. The analyses were assumed to define a complete description of sycamore crown geometry.

Results show that sycamore produces two types of primary proleptic branches: those that develop either the current year (Type I) or the subsequent year (Type II). Several subsequent analyses treated these branch types separately. Type I branching potential varied with tree and through time, and the number formed was associated with extension growth. Type I branches form on the lower trunk annual growth increment (AGI), form at a slightly more acute angle than Type II branches, and, after the first year, do not differ in extension growth from Type II branches.

Environmental and genetic factors affected extension growth. Leader growth was predicted from either calculated soil moisture values or one of three drought indices, and from class variables which were assumed to represent fertilization/cultivation and tree genetics. Variables related to crown geometry and crown growth history were used to analyze relative branch growth (branch AGI/leader AGI). Node density was examined. Node position analysis revealed three phases of growth: increasing, almost constant, and declining internode distance. One or more phases were absent on many branches.

Phyllotaxis was studied. For leaves or primary branches, the mean angle of divergence was 145.7 degrees. The direction of the spiral reversed on 27.5% of the tree AGIs; a phenomenon independent of tree and time. Second- and higher-order branches formed at mean angles of 90 and 270 degrees. On these AGIs, the circular variance increased acropetally to 13 nodes, or 90 cm, at which point the phyllotaxis appeared spiral. The number of daughter branches formed, their angle of divergence from the mother section, and their subsequent inclinations were predicted from variables related to branch geometry, crown position, and tree genetics.

Results of the branching analysis were used to develop a FORTRAN computer model which simulates the three-dimensional development of sycamore crowns. The model was validated by comparing output for leader growth and branching characteristics with field observations. Future model uses are discussed.

# CHAPTER 1

## INTRODUCTION

> The growth of a particular plant in the forest depends upon its capacity to express its genetic potential through physiological functioning within the environment to which it is exposed. --- Daniel et al. 1979

The study of plant geometry and growth has ancient foundations. In his excellent review, Studhalter (1955) recorded early concepts of plant growth and subsequent developments in this field. The earliest citation to a botanical work that he found was a fragmentary reference to writings by the Greek author Empedoclese of Agrigentum (ca. 450 BC) contained in Aristotle's works. The earliest written observation on tree growth was part of a Hippocratic collection discussed in Cohen and Drabkin (1948). This interesting passage discusses the grafting of a bud from one type of tree onto another and the observation that fruit later produced from that union is unlike the tree on which it was grafted. This was thought to occur in the following manner:

> First the bud sprouts, for it has nourishment originally from the tree from which it was taken and then in that upon which it was grafted. When it has sprouted in this way it sends out tender roots to the tree and at first derives nourishment from the moisture of the tree upon which it has been grafted. Then after a time it sends roots into the ground through the tree upon which it has been grafted and derives nourishment from the soil, drawing up moisture. It is from this source that it has been fed.

The similarity between this explanation of the process of bud-grafting and the current analogy of the "pipe-model" (Shinozaki et al. 1964) is striking.

In the modern literature, tree geometry and growth studies take one of two approaches. In the first, the crown is examined at a fixed point in time or over a season to identify within-tree correlations and trends of growth. An early example of this approach is the work of Friesner (1943-44) on red pine (*Pinus resinosa* Ait.) and Eastern white pine (*Pinus strobus* L.). In March 1942, he marked the terminal bud of 30 lateral branches on one Eastern white pine and 130 branches on two red pine trees. The elongation growth of these branches was measured through the growing season. Friesner discovered several facts. First, whereas most studies prior to his had shown elongation to follow a "grand period" sigmodal curve, he found three distinct waves of growth. Secondly, he found current growth to decrease from tree top downward; the leader grew more than 1-year-old primaries, which grew more than 2-year-old primaries, and so on down the stem. He also found older second-order branches to elongate less than younger ones, even though they may be found on older primaries. These differences were primarily due to differences in rates of growth, rather than in the duration of elongation.

Another example of this approach is Duff and Nolan's (1953) work in which they examined radial and apical growth of the bole in red pine. This example differs from the first in that single measurements were made on each experimental unit producing a

"snapshot" view of stem growth. They found three observable trends. Their first (Type 1) trend examined all stem radial growth increments formed in a given year. As they examined the annual growth rings from tree apex to base, they observed that the mean growth increment increased to a maximum and then declined from that point to the tree base. They found this same pattern as they examined radial growth from pith to current growth at a fixed internode (Type 2). Their Type 3 sequence examined the $n^{th}$ ring from the pith from tree apex to base. No pattern was found in the variation of the mean along this gradient. A Type 1 decline in organ size from tree tip to base has also been observed for bud size (Kozlowski et al. 1973, Owston 1969), branch elongation (Cannell 1974, Fraser 1962, Friesner 1943-44, Forward and Nolan 1964, Jensen and Long 1983, Norman and Jarvis 1974, and Powell 1977), and branch weight (Kohyama 1980). It is to be noted that all these studies have been on conifers. Further examples of Type 2 and Type 3 sequences will be mentioned in Chapter 5.

Ward's (1964) work is another example of the snapshot approach. He measured approximately 150 shoots on thirty 10-year-old red oak (*Quercus rubra* L.) trees. From these data, he demonstrated that both the number of buds formed and the number of branches formed were a function of the length of the "mother" shoot.

In many studies of tree crown geometry, the number of variables measured is limited; very few studies measure more than one. One reason for this fact is that studies of this type are very labor intensive. Jensen and Long (1983) noted this fact, and their study

on Douglas fir (Pseudotseuga menziesii (Mirb.) Franco) was confined to measuring most of the branches from within a 90 degree quadrant (285 -015 degrees azimuth). Hutchinson et al. (submitted) also noted the amount of labor needed to measure the geometry of woody elements in a forest canopy.

The second method used to study tree geometry and growth involves an examination of the processes which produce a given tree geometry. This type of study may follow directly from the approach mentioned above. Many excellent reviews of these processes have been published (e.g., Brown 1971a, Jankiewicz and Stecki 1976, Kramer and Kozlowski 1979, Wareing 1970, and Wilson 1970). Aging, one such process, was described and examined by Moorby and Wareing (1963). They observed three predictable changes with increasing tree age: (1) the branch annual growth increment (AGI) decreases markedly with age (this is similar to a Duff and Nolan Type 2 sequence for branches), (2) apical dominance ("control," sensu Brown et al. 1967) is lost so that a leader can not be clearly identified, and (3) older shoot systems show a weak, if any, response to gravity. All of these processes are reversible. Their work examined these changes in Scots pine (Pinus sylvestris L.) and Japanese larch (Larix leptolepsis (Sieb. & Zucc.) Gord.) and explored the mechanisms governing these changes.

Apical control is another process governing the growth of trees. Foresters and botanists assumed for a long time that the presence of a single leader in excurrent trees was the result of strong apical dominance and that the multi-leader condition of

decurrent trees was the result of weak apical dominance. Upon closer examination, Brown et al. (1967) noticed that the uppermost buds on excurrent trees do grow the year they are formed, whereas the buds in decurrent trees are usually (see Chapter 4) completely inhibited. During the second year, the top buds of decurrent species are released, and may grow to compete with the leader, whereas in excurrent trees, the apex maintains control over the amount of extension growth. This newly described phenomenon was called apical control. Brown (1971) speculated that the misunderstanding of this situation probably resulted from an attempt to transfer results form the work on apical dominance by Thimann and Skoog (1933, 1934) on the herbaceous Vicia faba L. directly to woody plants.

In many of these studies of tree geometry and its development, results have been presented as word models (e.g., Jankiewicz 1972), graphs (e.g., Figure 13.2 in Fisher 1978, Friesner 1943-44), or as means (e.g., Table 1 in Baxter and Cannell 1978, Table 1 in P. White 1984). Few mathematical models have been fit to any of the observed trends. One clear exception is the paper by Cochrane and Ford (1978). In this study several branching variables were measured on five Sitka spruce (Picea sitchensis (Bong.) Carr.) trees, and other variables were later measured on an additional 10 trees. Statistical models were fit for the leader and branch annual growth increment, number of branches formed, branch azimuth, branch inclination, proportion of interwhorl buds, and mean relative length of interwhorl branches. This paper contains the most complete

statistical description of branch geometry known to the author. The fact that the primary author of this paper is a member of a department of actuarial mathematics and statistics demonstrates the complexity of these analyses.

Plant crown processes, such as photosynthesis, respiration, transpiration, and gas exchange, depend upon tree attributes (crown structure and physiological status) as well as on environmental factors. For this reason, the accurate description of tree geometry is important. In his 1976 paper, Helms reviewed plant and environmental factors influencing tree net photosynthesis. He asserted that foliage position is of great importance to plant productivity. Many other papers, both theoretical and empirical, have examined the geometry of both trees and stands and evaluated the importance of crown geometry to productivity (e.g., Kira et al. 1969, Monsi et al. 1973, Monteith 1965, deWit 1965).

Light interception is another process influenced by tree and stand geometry. Lemur and Blad (1974) reviewed modeling approaches used to estimate plant canopy radiation interception. They found two classes of models: geometrical and statistical. Geometrical models assume that the stand is composed of regularly arranged shapes of objects with characteristic dimensions. These models usually deal with individual plant types which are simulated as cones, spheres, cylinders, etc., and are used to predict light interception on a daily, seasonal, or yearly basis. Geometrical models may be further subdivided into models that consider individual plant shapes and those that consider arrangements of

shapes. A current study that uses this approach is Oker-Blom and Kellomaki (1982). Statistical models, on the other hand, do not explicitly consider the position of canopy elements, but assume that the canopy display can be described as a statistical distribution. They are often used to study light penetration through a canopy. The probability of light interception by any canopy layer is a function of the statistical distribution assigned to the canopy and includes such elements as the number of leaf layers and the distribution of their inclination (e.g., Duncan et al. 1967).

Each of these modeling approaches has its limitations. Geometrical models assume that the crowns are a monolayer, ignoring the theory developed by Horn (1971). Descriptive geometrical models which include Horn's theory are given in Brunig (1976). Statistical models simulate plant canopies, but ignore individual plants. For these reasons, neither model type can be used to understand light interception by individual trees. Another approach (Gates 1980) develops analytical models to examine factors affecting the energy budgets of leaves and plants and photosynthesis of leaves. This approach is also limited in that it ignores crown structure.

A new class of models is now being developed which may be considered as another type of geometrical model. These models simulate the growth of the branching system and, as such, demonstrate a tremendous potential for use in understanding the relationship between crown geometry and crown processes. The first model of this type (Honda 1971) examined the minimum number of variables needed to simulate tree-like objects. In a later paper,

Fisher and Honda (1977) used this modeling approach to simulate branching in Terminalia catappa L. from data previously collected by Fisher (1978). This model was later used to examine the equitable distribution of leaf clusters on a branch system (Honda and Fisher 1979) and the branch angle which maximized light interception (Honda and Fisher 1978, Fisher and Honda 1979a). Work on this model continues (Fisher and Honda 1979b, Honda et al. 1981, Honda 1982).

Terminalia branching is fairly easy to simulate because its branching follows several well defined rules. Branches are produced in whorls with the whorls in a plane. Branching is dichotomous, with a constant mother/daughter length ratio and angles. This species also produces leaves in whorls at the end of each branch. In most of the work with the model of this species, competition occurs only among branches in the same tier, although in one paper (Honda et al. 1981) inter-tier competition was considered.

Hofmann (1981) studied the three-dimensional branching of rubber trees (Hevea brasiliensis (Willd. ex A. Juss) Mull-Arg.) with the purpose of identifying selection characteristics for resistance to wind damage. As part of this work, he also developed a three-dimensional branching model for this species.

Since canopy processes are determined by crown geometry as well as crown physiology and environmental conditions, a detailed description of crown geometry is needed. This description could then be reduced to a model describing branch development, and this model, in turn, could then be used to examine crown processes (e.g., light interception, branch mortality, etc.,) as well as crown branch

dynamics. For this work, the branching of open-grown trees should be studied first, and this should be followed by an examination of the effects of competition on crown branching.

The present research was undertaken to accomplish the following goals:

1. To quantify the geometry of plantation-grown sycamore (*Platanus occidentalis* L.).
2. To develop statistical models which integrate known mechanisms of branching and which describe the processes involved in sycamore growth.
3. To integrate the branching variables analyzed under goal 2 into a FORTRAN model which simulates crown development in sycamore.

The "ideal" method to study crown geometry would begin by examining open-grown trees. Here, the architectural model (Halle et al. 1978) of the tree develops with only intracrown competition. The effects of intra- and interspecific competition on crown geometry would be examined next and added to the model. In the current study, competitive effects were minimized by examining young, plantation-grown trees.

Sycamore was chosen for study for a variety of reasons, For one, it is an economically important species and has been studied intensively as a source of fiber using the "silage" (McAlpine et al. 1966) silvicultural system (e.g., Bellanger and Pepper 1978, Crandall and Luxmoore 1982, Geyer 1981, Saucier et al. 1972, Steinbeck 1971, and Wood et al. 1976). Because of this fact, a

fairly well developed literature has developed which examines the effects of fertilization, spacing, rotation length, genetics, soils, etc., on the growth (usually height and diameter) and carbon allocation (to roots, bole, or branches) of this species. From a practical standpoint, this means that plantations of several ages and cultural treatments already exist. Also, many of the studies of tree crown geometry have been done on trees with low branching densities (e.g., *Aralia spinosa* L., P. White 1984) or on trees with very regular branching patterns (e.g., *Terminalia catappa* L., Fisher 1978). The branching of sycamore is intermediate in branch density and complexity between trees such as *Aralia* and, for example, that of *Betula nigra* L. Sycamore is also a long-lived, early-successional tree and will experience a variety of environmental conditions throughout its lifespan. Trees in this category may be the most plastic in their developmental geometry and, therefore, the most interesting to study (P. White, pers. comm.).

# CHAPTER 2

## MATERIALS AND METHODS

The study site is part of a hardwood plantation established by Union Camp, Inc. in Sussex County, Virginia along the Nottoway River (Figure 2.1). An overview of Union Camp's site selection criteria and hardwood plantation management techniques is given in Malac and Heeren (1979). The soil at the site used in this study is in the Riverview series. This is a well drained fine loam that forms along floodplains of rivers located in, or originating in, the Piedmont. The typical pedon consists of a silt loam surface layer overlying a thick (84 cm), loamy B horizon. This soil is well drained and is flooded during the spring of most years. The topography is nearly level to gently rolling.

Since this site had not previously been under agricultural use, it was prepared for planting by clearcutting. This was followed by shearing any material remaining and piling it into windrows.

Seed for this Union Camp plantation was collected from an area which ranged from just south of Franklin, Virginia, north to the study site (within a 64 km radius of the site). At each location, better than average trees were selected by criteria which was later used to select mother-trees to establish a seed orchard. To qualify for selection a tree must have been producing seed and had a good form (i.e., straight bole and good crown). Since sycamore self-pollinates to produce sterile seeds, seed was collected from only one tree in a given stand (although other trees had to be

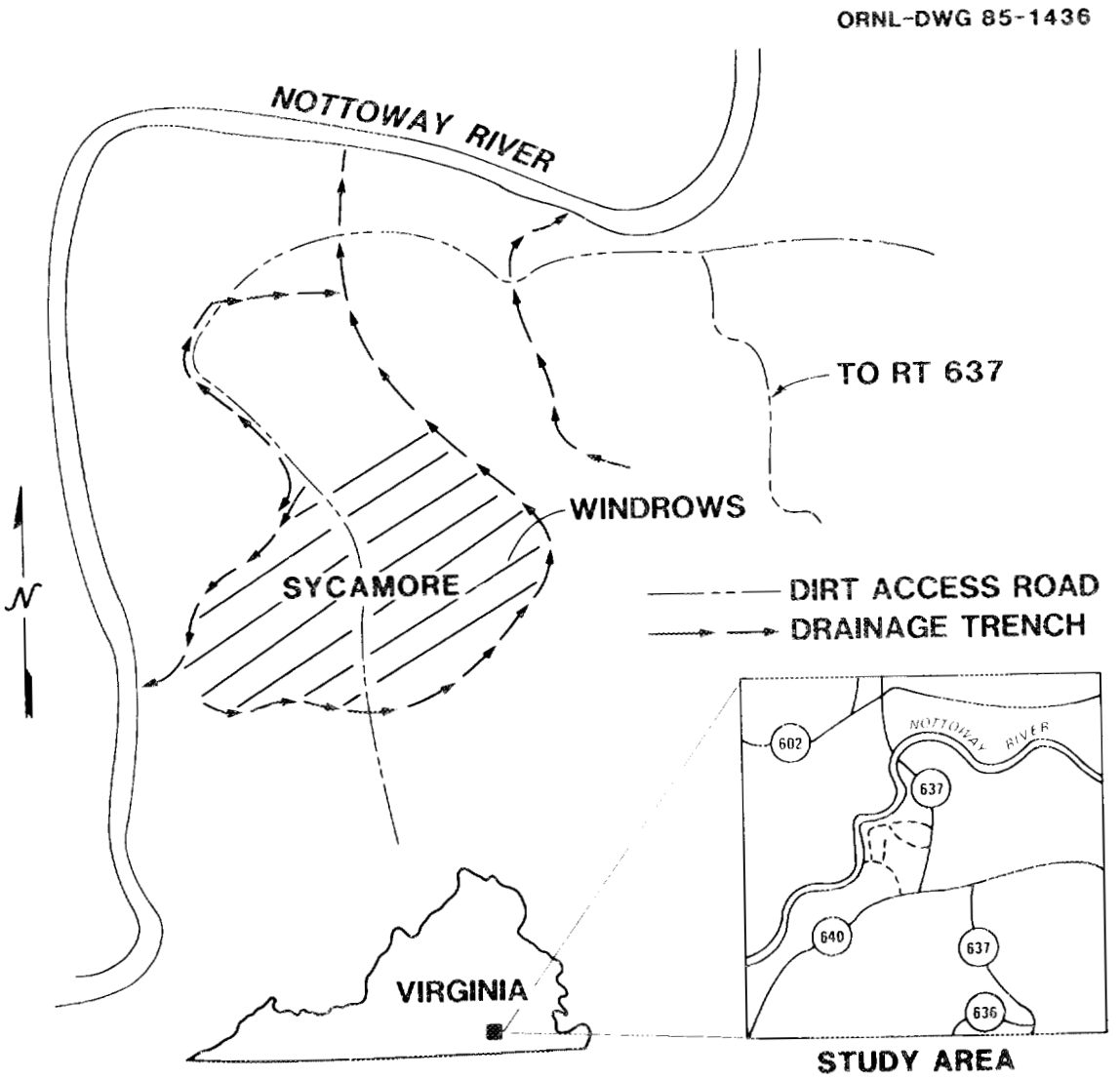



Figure 2.1. Map of the study area showing the location of the sycamore plantation.

visible) and from only one tree in a given drainage system (R. Heeren, pers. comm.). These seeds were then grown for one year in Union Camp's nursery. Healthy seedlings (minimum root collar diameter of 0.95 cm and a height of 60.96 cm) were selected and planted at the study site in the winter of 1976/77. The trees were planted at a spacing of 3.05 m in rows that were 3.66 m apart. The gross area planted in sycamore this year at this site was 38 ha. Vegetative competition was reduced by cultivating with offset cultivator disks. This machinery was designed to throw a mound of soil along the row to cover emerging weeds not reached by the disks. The study site was cultivated in May and June of 1977 and twice in 1978. Union Camp's site fertilization depends on soil analysis and the expected response of weeds to fertilizer application. At the study site, a banded application of diammonium phosphate was added in June 1977 at a rate of 280.23 kg/ha (250 lbs/a). A mid-rotation fertilization of 280.23 kg/ha of ammonium nitrate was made by helicopter. The trees will be harvested between ages 12 and 15 and will be allowed to coppice for two rotations.

The study site was naturally divided into blocks by the presence of both an access road and windrows. Each block contained approximately 10 rows of trees. To estimate the number of trees in each block, the number of tree positions was counted for one row. The term position is used here instead of tree because it was easy to determine where each tree had been planted, even though it may have subsequently died. Tree selection began by assigning tree

numbers to each block of trees. To minimize edge effects along the end of the rows, the first and last 10 trees in each row were not included. Each block was then assigned a three digit range of numbers, the length of which was equal to the number of positions in that block; this was done to ensure that each position had an equal probability of being selected. A three digit random number was then chosen to select a tree position. The row number was selected next. This was done by first excluding the two rows neighboring the windrows to minimize any edge effects and then randomly choosing a row number. A position was selected for study if it met the following criteria:

1. a tree was present at the study position;
2. the trunk was unforked with only one stem;
3. the tree was surrounded by two living trees in all directions (i.e., the tree was in the center of a group of 25 living trees formed by five trees in each of five rows).

If the tree at the study position (n) did not meet these criteria, the next 10 trees (n + 10) in that row were examined, searching for the first tree that met all the criteria. If one was not found, the search continued in the opposite direction for up to 10 trees (n -10). If this procedure failed to identify a suitable tree, the process was repeated; another block and row were randomly selected until a study tree was found.

After the first three trees had been measured and the fourth one had been selected, it appeared that the study site was not homogeneous; trees in different areas of the plantation seemed to differ in height and survival. At this point one of the blocks was

randomly chosen, and all subsequent study trees were measured in this block. Since two of the three previously measured trees were not from this block, they were not included in the analysis.

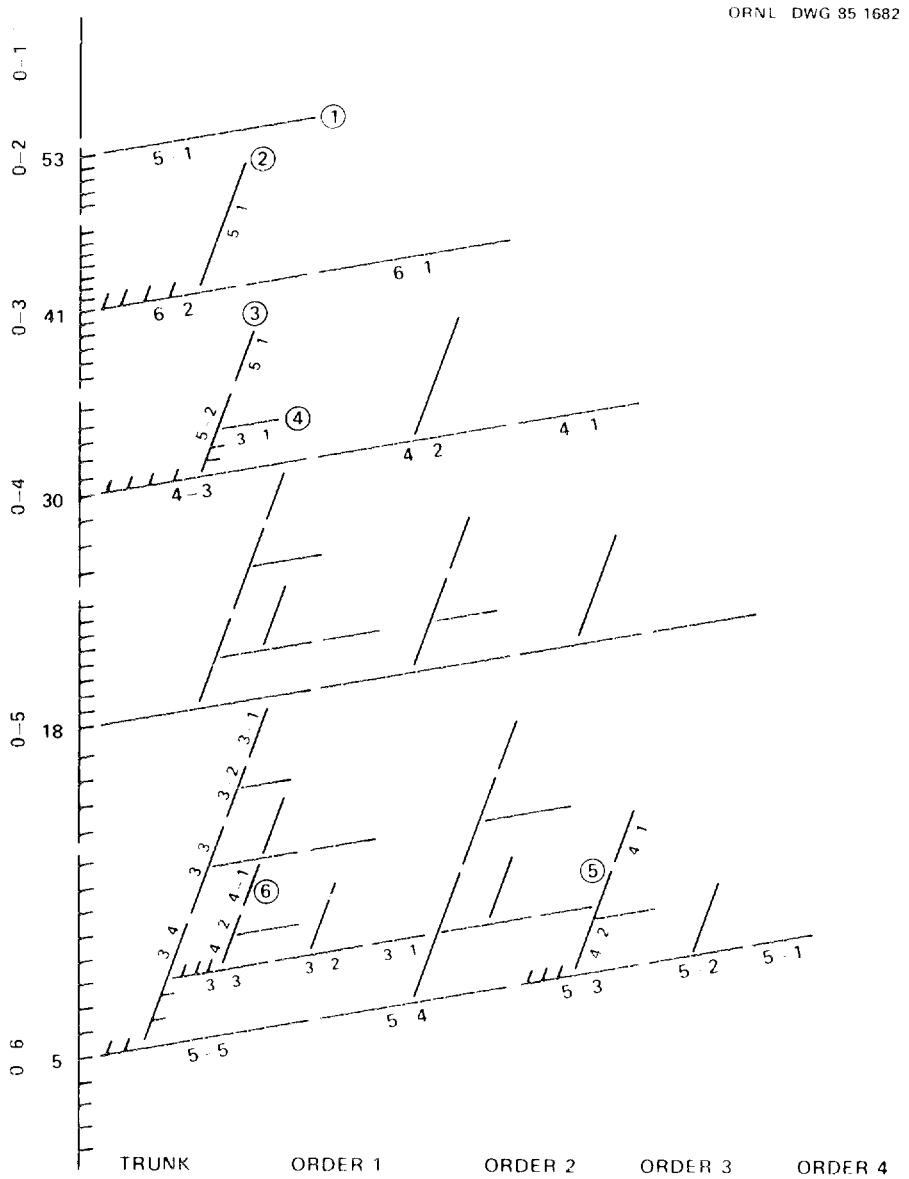
Data were collected in two phases: leaf data were collected in the late summer of 1982 and branch data were collected in the winter of 1982. Leaf measurements were made after branch elongation was almost complete. Each branch was identified temporarily by assigning it a number counting from tree base to tip and every fifth primary branch was marked with flagging tape for easy location. Since a previous study (Schutt, unpub. man.) had indicated that branch competition may be greatest in the row direction, the azimuths were divided into four quadrants with quadrants 1 and 3 being centered on the row azimuth (75/255 degrees). The azimuth of each live primary branch was recorded and its quadrant number was determined. On each stem annual growth increment (AGI) four branches were randomly chosen for study from each quadrant. Leaf measurements were then made on the current leader and on these randomly selected primary branches. If the primary branch had second-order branches attached to it, a second-order branch from each primary branch AGI was randomly chosen for measurement. This technique was followed for all higher-order branches. On some trees it was difficult to distinguish between the two lower stem AGI's because radial growth had obliterated the pseudo-terminal bud scale scars and because sycamore (*Platanus occidentalis* L.) forms Type I proleptic branches (Chapter 4). This position was tentatively located and was verified later (p. 28).

A method was needed to assign an identification (ID) to each branch. An example of the numbering system used is given in Figure 2.2. A two digit code was used to record the node number of the branch from the AGI base, and a one digit code was used to record the age of the branch section being measured. If the branch was a second- or higher-order branch, the ID of all ancestor branches was also included in the ID for that branch.

After a study branch was chosen and given an ID, the distance to each node was recorded to the nearest cm. If a branch had two nodes within the first cm, they were counted as only one node. For each leaf on the branch section, the following measurements were made:

1. The angle between the branch and the petiole. This angle, called the parent angle (PANG), was measured with a protractor to the nearest degree.
2. The angle formed between the petiole and a plane containing both the branch section and the line of gravity. This is called the parent "azimuth" (PAZ) because of the correspondence between this angle and the bird's-eye view of the primary branches measured relative to north. This angle was measured to the nearest 5 degrees with a protractor which had a line level attached to it.
3. Lamina inclination (ANG) relative to gravity. This angle was measured to the nearest degree with a protractor which had a weighted string attached to its focus.

Figure 2.2. Diagram showing potential branch positions and giving examples of branch identification (ID). 01B is the number of the study branch from tree base. In the other ID variables, the "O" stands for branch "order" and the number following the "O" gives the order of the study branch. In the last letter, "N" represents the "node number" of the parent to which that branch is attached and the "A" represents the "age" of the annual growth increment.




| BRANCH | TRUNK TREE | TRUNK TA | ORDER 1 O1B | ORDER 1 O1N | ORDER 1 O1A | ORDER 2 O2N | ORDER 2 O2A | ORDER 3 O3N | ORDER 3 O3A | ORDER 4 O4N | ORDER 4 O4A |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ① | 1 | 2 | 53 | 5 | 1 | | | | | | |
| ② | 1 | 3 | 41 | 6 | 2 | 5 | 1 | | | | |
| ③ | 1 | 4 | 30 | 4 | 3 | 5 | 1 | | | | |
| ④ | 1 | 4 | 30 | 4 | 3 | 5 | 2 | 5 | 1 | | |
| ⑤ | 1 | 6 | 5 | 5 | 3 | 4 | 2 | | | | |
| ⑥ | 1 | 6 | 5 | 5 | 5 | 3 | 4 | 3 | 3 | 4 | 1 |

Figure 2.2

4. Lamina azimuth (AZ) relative to gravity. This was measured to the nearest 5 degrees with a compass numbered counterclockwise from north so that the face did not have to be rotated for each measurement.
5. Petiole length was measured to the nearest cm.
6. Lamina length was measured to the nearest cm.
7. Lamina width was measured to the nearest cm.

Figure 2.3 gives a diagram showing how several of these variables (which have corresponding measurements for the branches) were measured.

After all leaves had been measured on the selected branches of all orders on the first tree, it became apparent that the amount of information gained from measuring the innermost leaves on the lowest branches was small in relation to the time taken to measure them as each of these branches typically held only one or two very small leaves. To allocate time optimally, subsequent measurements were made only on leaves attached to the three most recent years of branch growth. At the end of the measuring period, leaves were collected from various quadrants, branch ages, and branch orders to develop a regression equation predicting branch area from lamina length and width. Leaves were dried in a plant press and their areas were measured to the nearest 0.1 $cm^2$ using a LI-COR Incorporated model LI-3100 area meter. While the present study does not include an analysis of leaf variables, a description of the methods used to collect the data have been given because these branches are included in the branch data set.

Figure 2.3. Diagrams showing methods used to obtain several of the variables. (a) Parent angle (PANG) between the petiole (or daughter branch) was measured with a protractor. For curved branches, this angle was the angle formed between a tangent to the mother at the point of daughter insertion and a line connecting daughter base to tip. (b) Parent azimuth (PAZ) was measured by holding a protractor at 90 degrees to the axis formed by the mother branch. The 0 degrees mark on the protractor lies in a plane formed by the intersection of the line formed by the mother branch and a line of gravity. (c) Inclination relative to gravity (ANG) for leaves and branches was measured with a protractor with a weighted string attached to its focus. Leaf inclinations are measured from the horizontal and branch inclinations are measured from the vertical. (d) Azimuth relative to gravity (AZ) was measured with a compass that had the face numbered counterclockwise. (Leaf azimuth is the azimuth of the normal of the lamina. (e) Petiole length and lamina length and width.

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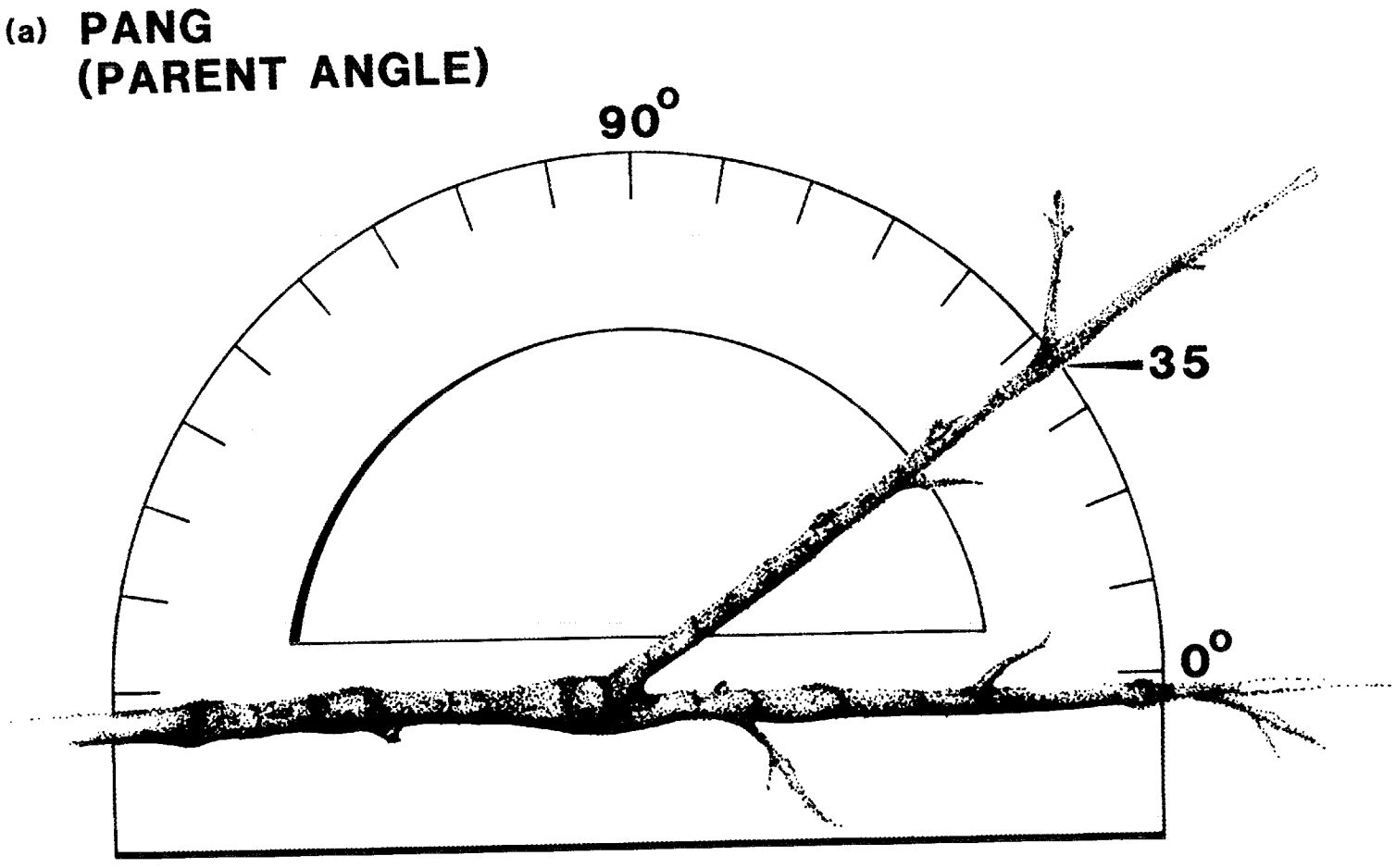


Figure 2.3

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(b) PAZ

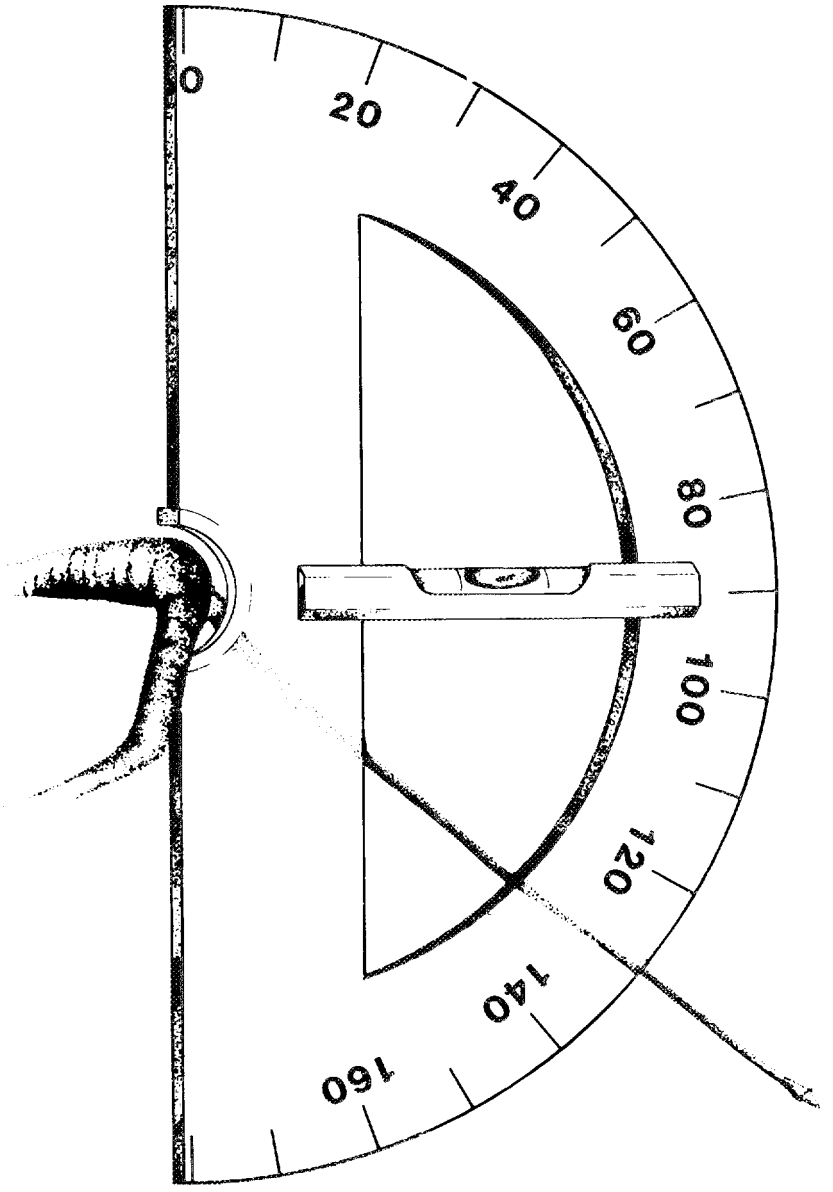


Figure 2.3 (continued)

**(c) ANG**
**(RELATIVE INCLINATION TO GRAVITY)**

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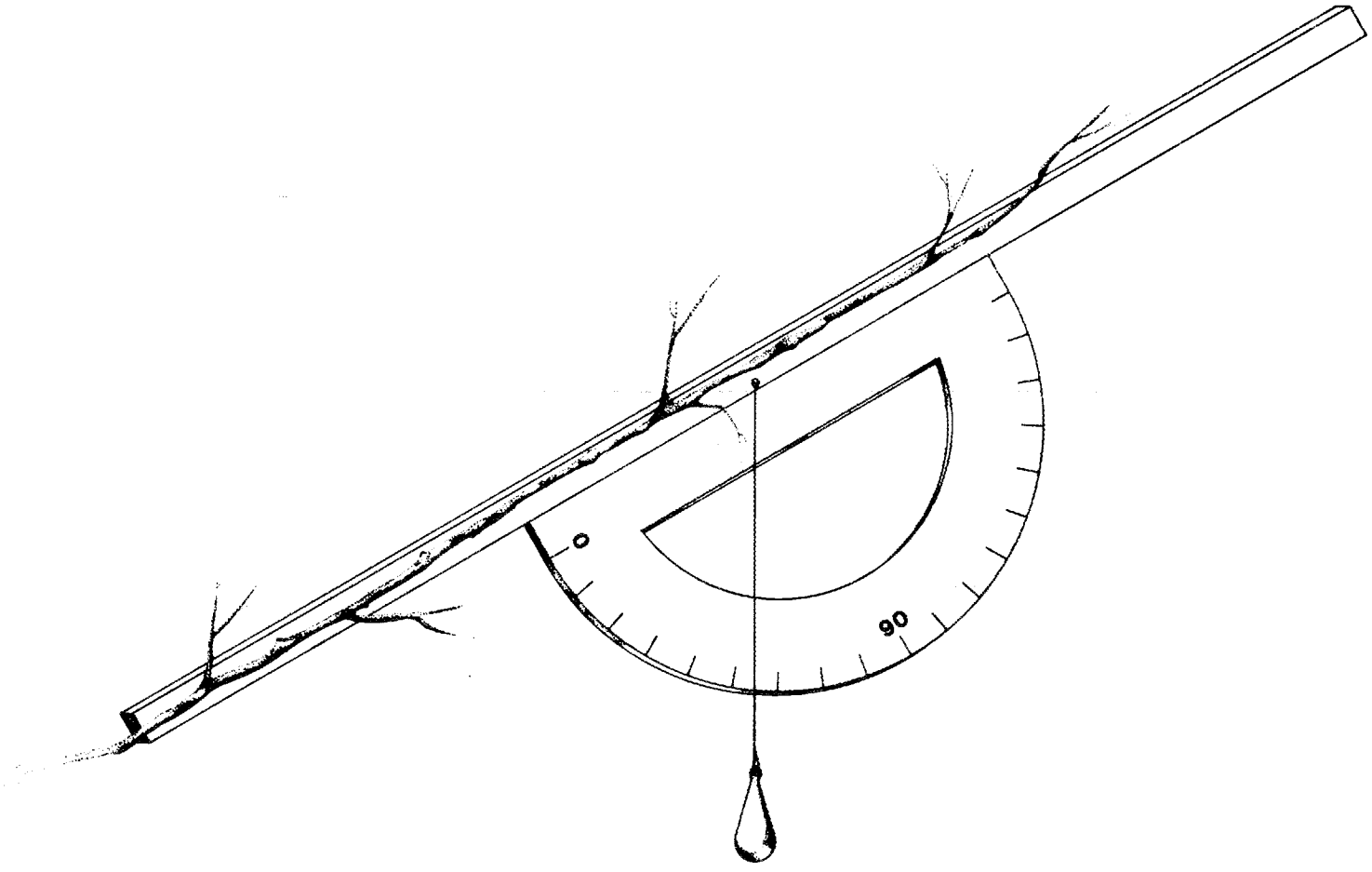


Figure 2.3 (continued)

(d) **AZ**

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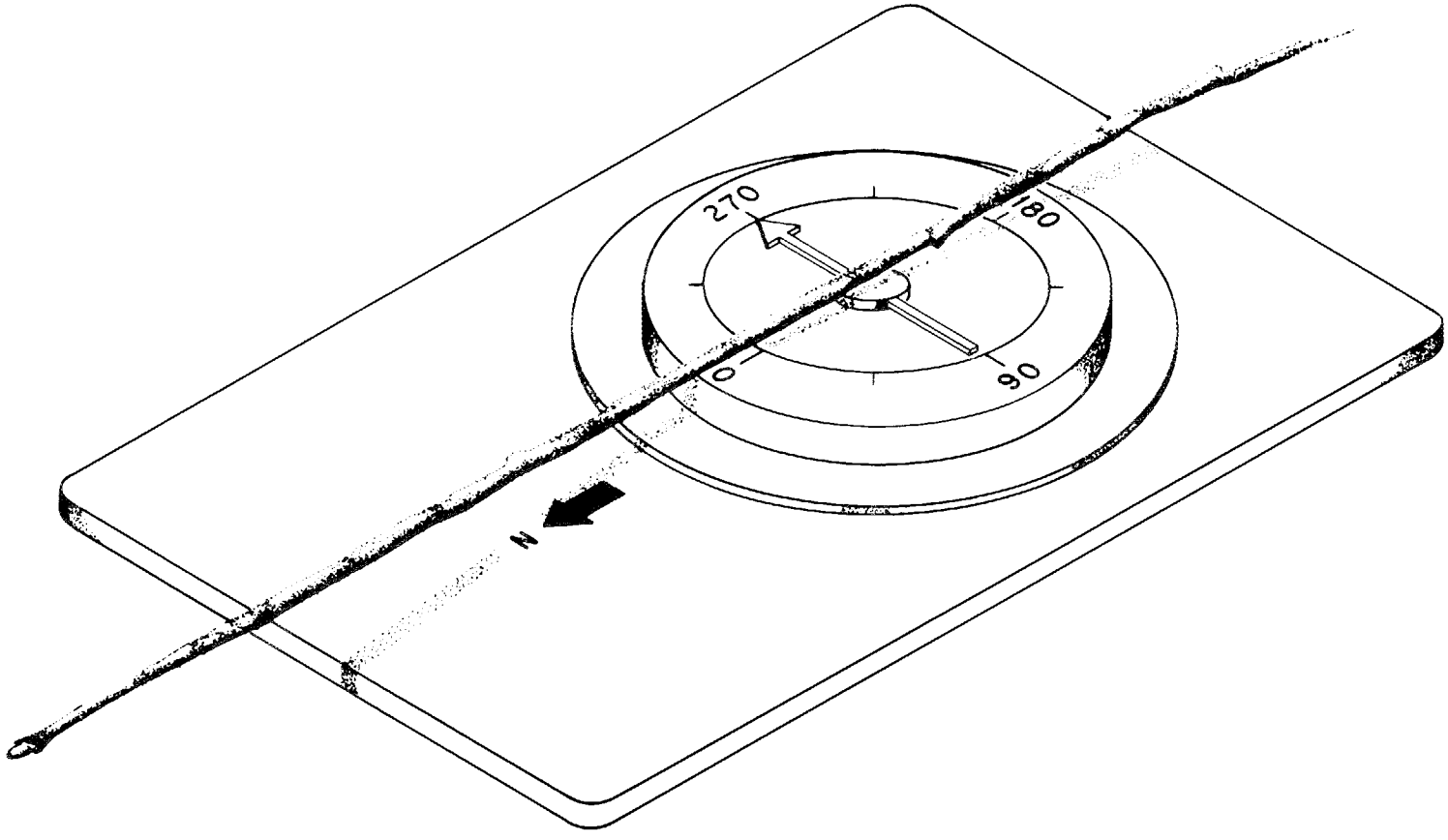


Figure 2.3 (continued)

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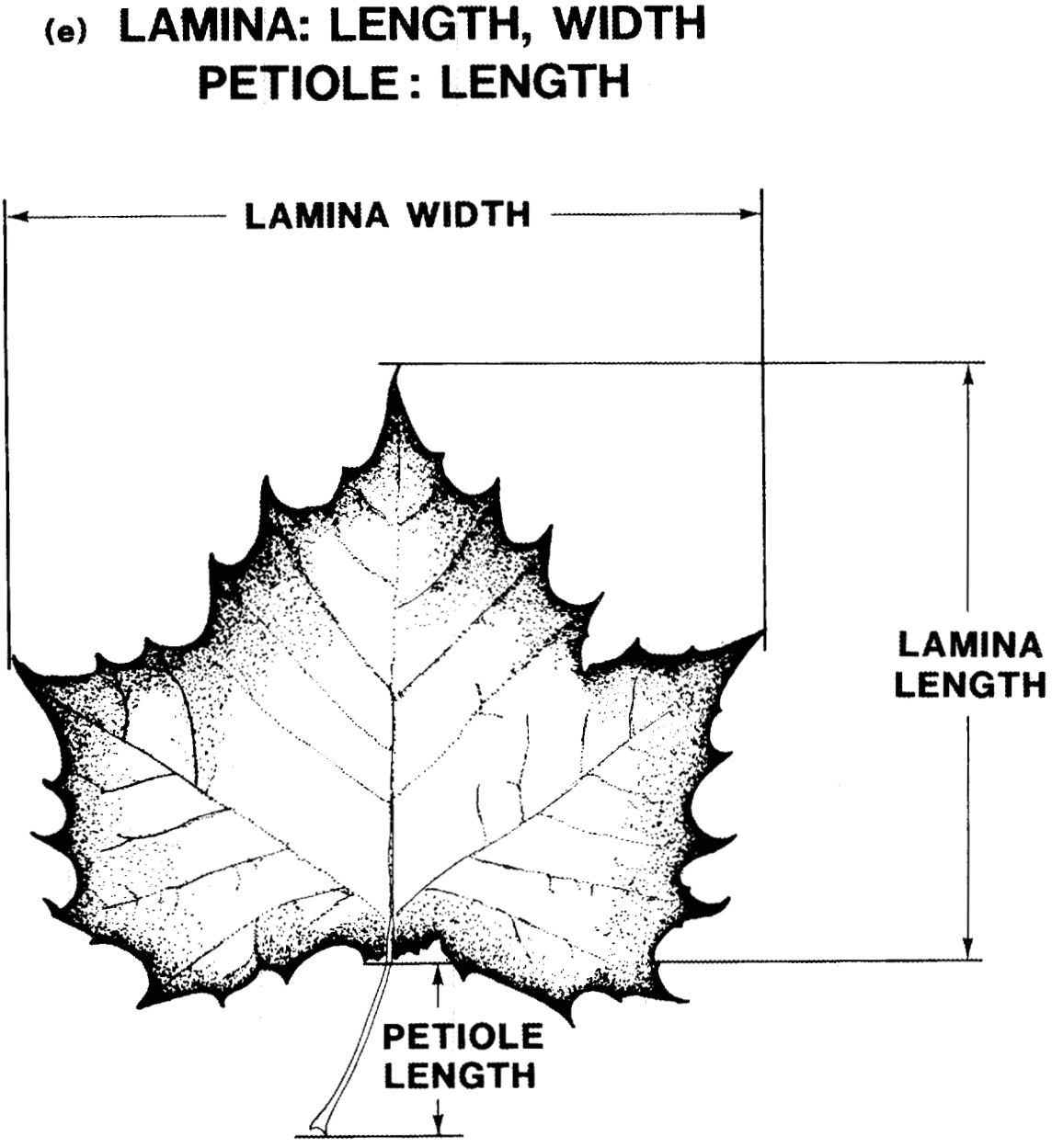


Figure 2.3 (continued)

Branch data were collected in the late fall/early winter of 1982. On each trunk AGI, the distance to each node was measured to the nearest cm. At this time the temporary branch numbers were replaced with actual node numbers. Because radial growth had obliterated both leaf and stipule scars at the base of some trees, the original node numbers could not be determined for the lowest branches and their temporary numbers were retained. (Note: these branches were not included in any analysis requiring node number). Measurements made on the primary branches are similar to those made for the leaves (Figure 2.3). They include:

1. The inclination of the basal branch segment relative to its mother (PANG) was measured to the nearest degree. For primary branches, the bole was assumed to be vertical; therefore the angle was the same as the angle relative to gravity.
2. Branch section inclination relative to gravity (ANG) was measured for each AGI to the nearest degree.
3. Compass azimuth (AZ) was measured to the nearest five degrees. Only one reading was made for for each primary branch assuming that the azimuth did not change.
4. Branch section length of each AGI was measured to the nearest cm.

Similar measurements were made for each AGI on all higher-order branches. The one measurement that differs for higher-order branches is the azimuth, which is now measured relative to the plane formed with the branch segment and the line of gravity. This

measurement was called parent azimuth (PAZ) in the leaf data set. Measurements were made on all branches which held leaves that were measured for the leaf data set. In addition, branches were also sampled from branch AGI's older than three years.

For both the leaf and the branch data sets, missing values were coded with either a 0, 99, or 999.

Another data set was needed to predict the summer branch inclinations from the winter inclinations. The assumption was made that changes in branch orientation were due to changes in the primary branch inclination and that the relationship of the higher-order branches to their mother branch did not change. This assumption may be violated in the case of long second- or higher-order branches, but it is probably accurate for short branches. In the late-summer of 1983, 10 trees were randomly selected in the study block according to the criteria described above. On each tree, one primary branch from each stem AGI was selected, and the inclination of each primary branch AGI was measured. These branches were remeasured in autumn 1983 after leaf-fall.

All data were punched onto cards for statistical analysis. While the branch data were being collected, several errors were found in the branch ID. These were usually due to miscounting the node number (e.g., the branch was at node 5, not at node 4). These corrections were made. Two data sets were then created: one (PARENT) contained the master data set with all branches listed relative to their mother branch and the second (DAUGHTER) contained

a separate data line for each branch. Several statistical programs were written using the Statistical Analysis System (SAS Institute Inc, 1982) to check for errors in the data. One such program determined if the numbers for the observations on each variable in the PARENT data set were equal. Errors of this type were usually found in pairs and were caused by writing a data point on the wrong line. These errors were easy to correct. In the original data set, broken branches were marked and the inclinations of the broken segments were measured. A second program was written to locate these values and set them to missing (= 999). A third program was written to check for missing values in the DAUGHTER data set. Errors of this type were often caused by recording a data value in the wrong column (e.g., at node 9 instead of at node 10). These were also corrected.

As mentioned above, on some trees it was not possible in the field to distinguish between year 1 and year 2 trunk growth. For most temperate tree species, this position can be estimated by examining branch ages. This is not possible for sycamore because it forms Type I proleptic branches so that branches of two ages are found intermixed on one AGI. To solve this problem, plots were drawn which show trunk annual height growth, branch annual growth, and branch age (Figure 2.4). A more detailed description of the problem and a solution was given in Schutt (unpub. man.) and in the brief summary which follows:

1. Within an AGI, branch length increases with increasing distance from the AGI base.

Figure 2.4 Side profiles of the study trees. Lines to the left of the y-axis show tree height at various tree ages. Lines to the right of the y-axis show branch annual growth increments (AGI) and age for all primary branches. Within an AGI, Type I proleptic branches are identified by their older age.

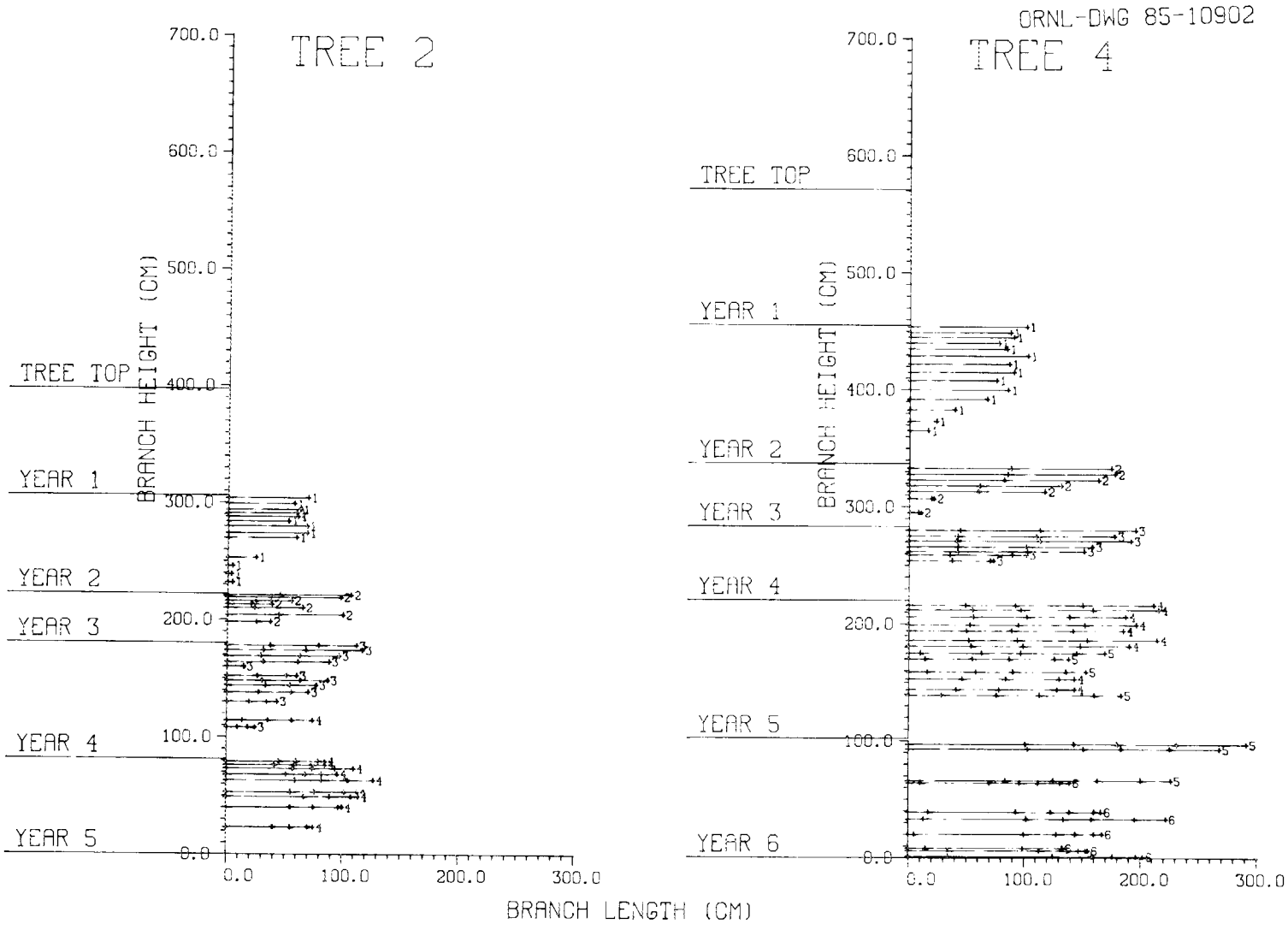
ORNL-DWG 85-10902
TREE 2
TREE 4
TREE TOP
YEAR 1
YEAR 2
YEAR 3
YEAR 4
YEAR 5
YEAR 6
BRANCH HEIGHT (CM)
BRANCH LENGTH (CM)
0.0
100.0
200.0
300.0
400.0
500.0
600.0
700.0

Figure 2.4

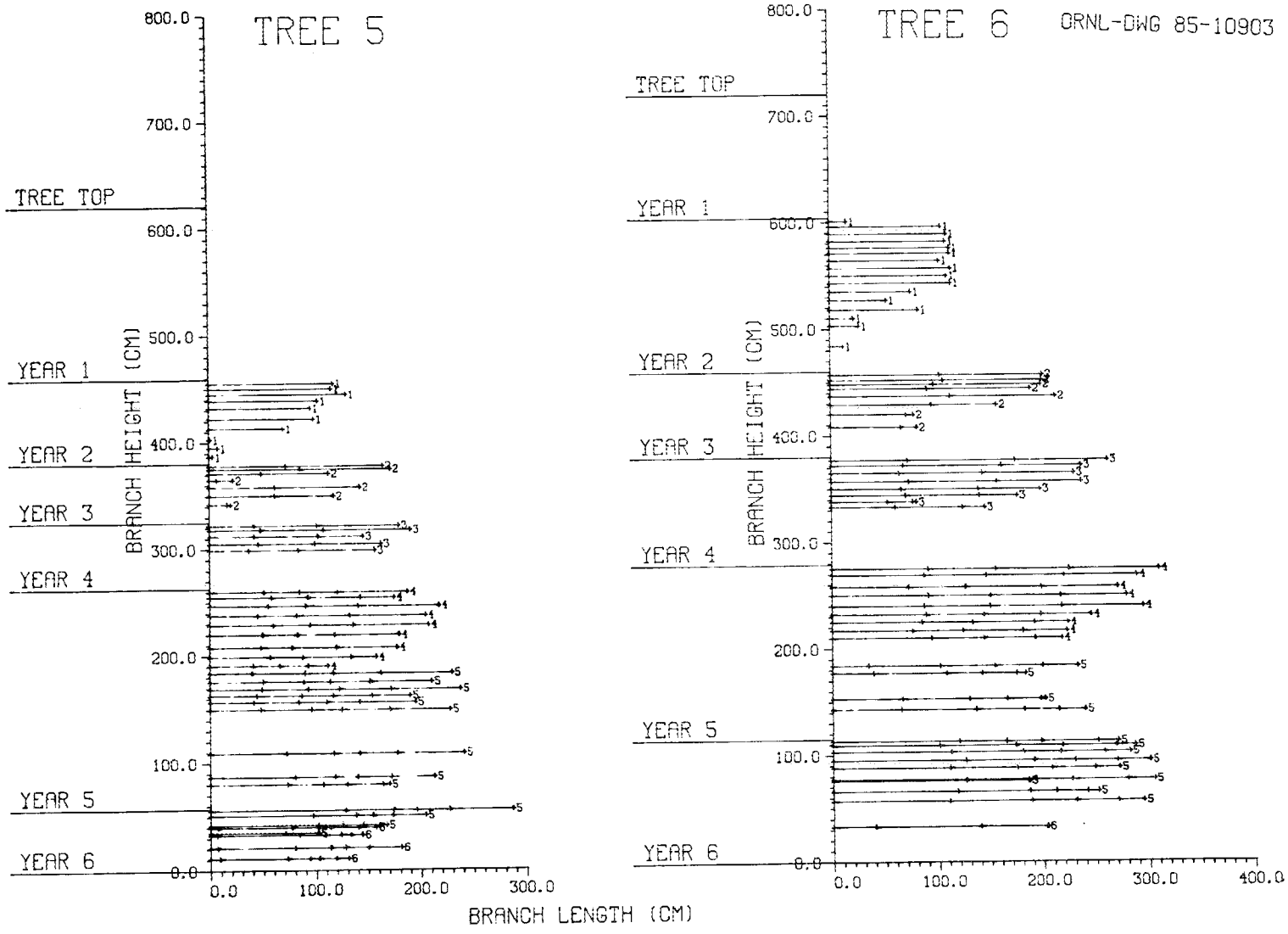


Figure 2.4 (continued)

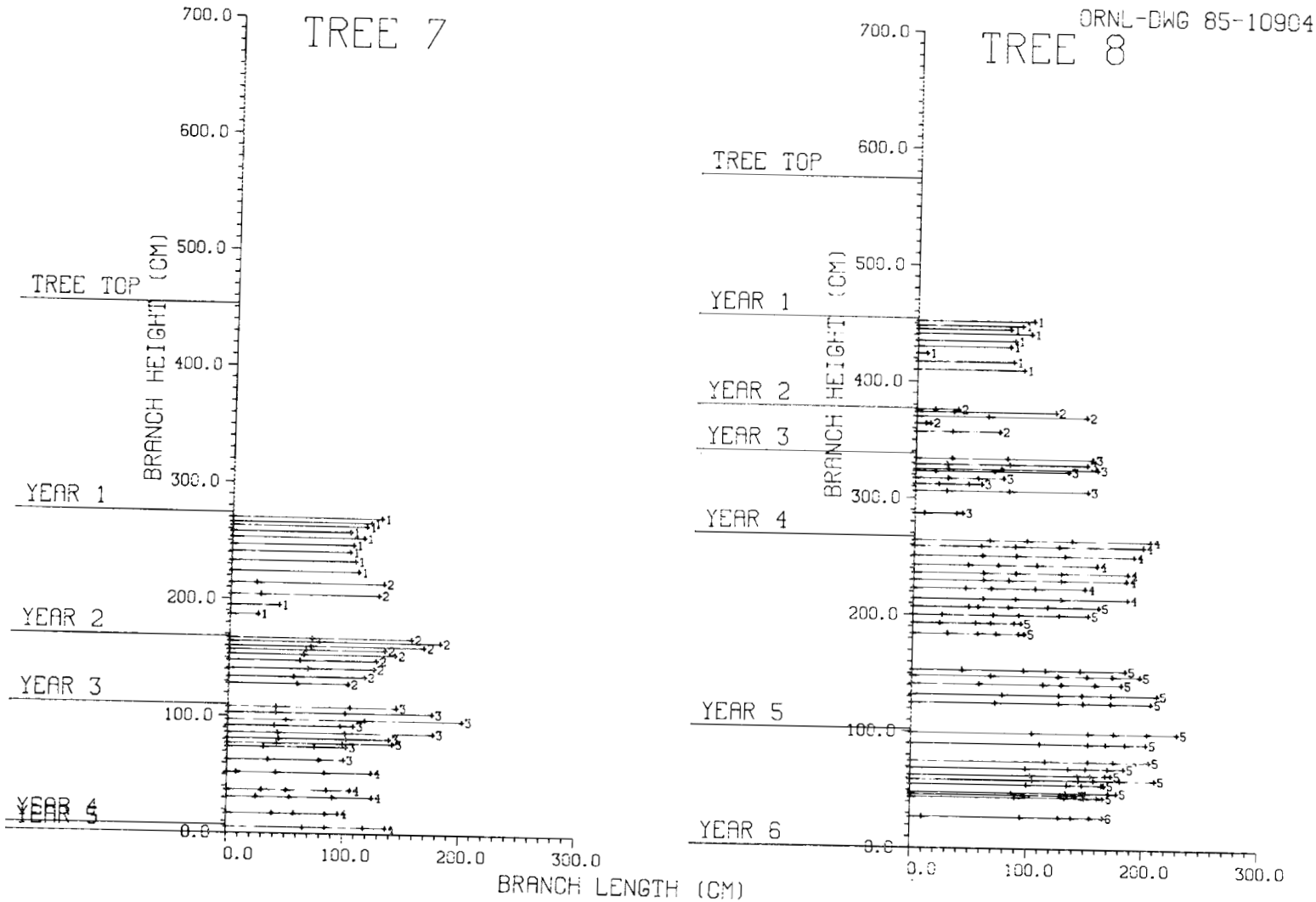


Figure 2.4 (continued)

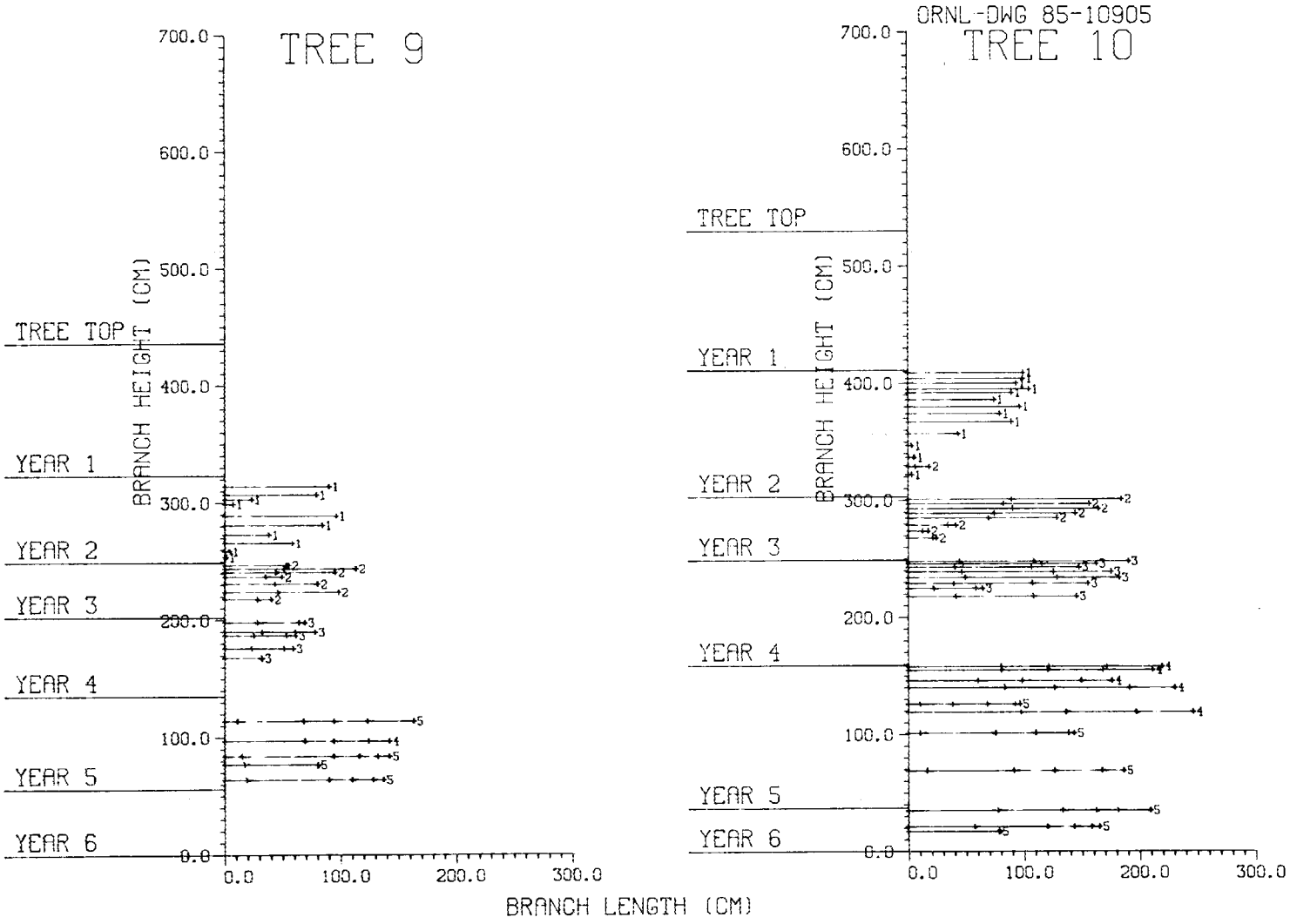


Figure 2.4 (continued)

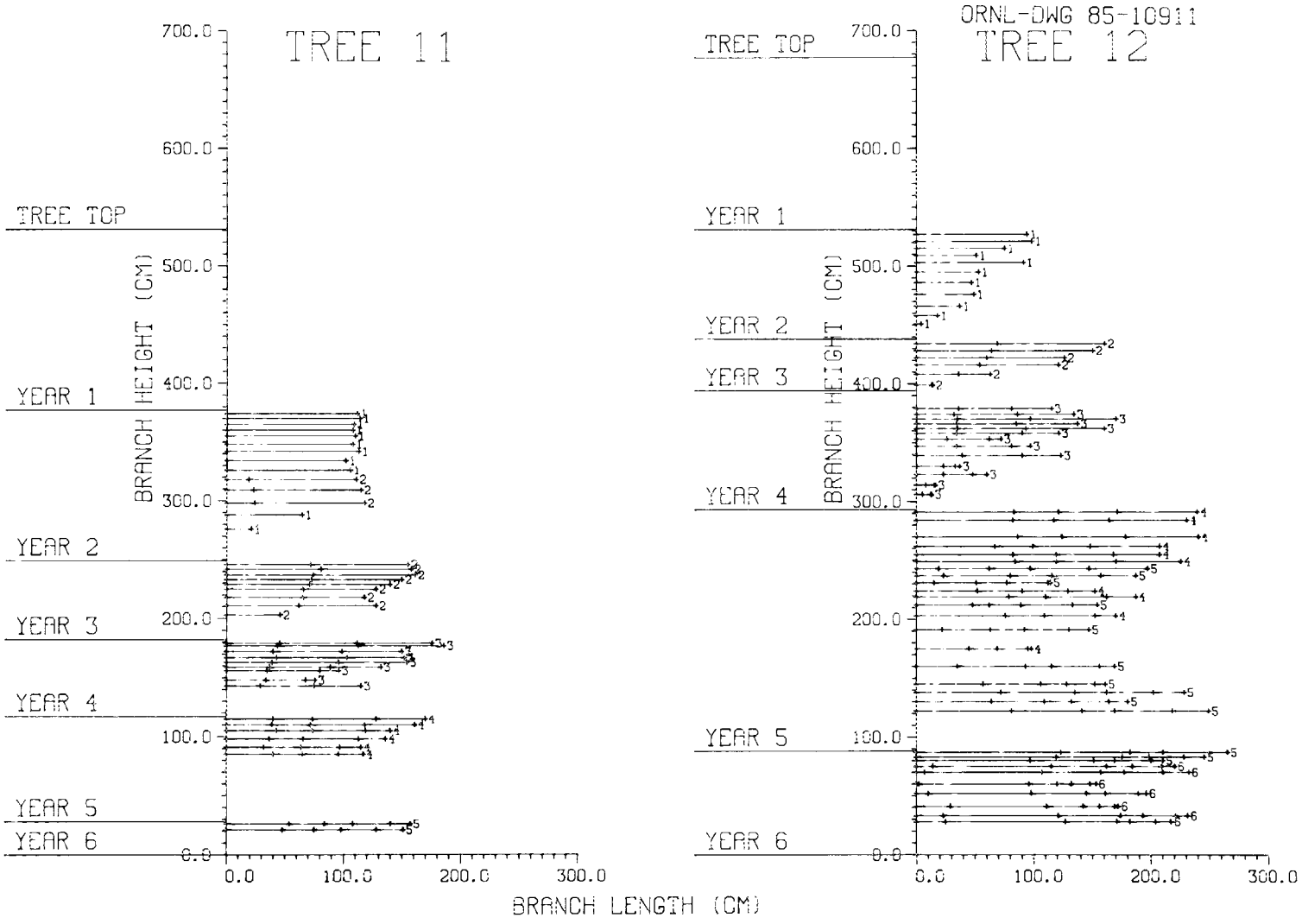


Figure 2.4 (continued)

2. In subsequent years, the lower, smaller branches die, leaving a section of the bole which is free of branches.
3. When Type I proleptic branches occur, they occur on the lower section of a stem AGI.
4. First year growth of Type I proleptic branches is usually shorter than growth of subsequent years (see pages 93-95).

With these observations (which can do be made on Figure 2.4), it was possible to identify the last year 1 branch formed. Other data sets were then used to determine the mean distance from the last branch formed to the end of that season's growth. This value was 2.55 cm (N = 44). The division mark between year 1 and year 2 growth was then set at 3 cm (the mean value rounded to the nearest cm) above the last year 1 branch. To verify the assignment of this location, increment cores were taken at various heights from any tree where there was a question about the year 1 and year 2 division mark to determine tree age at that height. These data verified this procedure. The relative node numbers for the AGI for years 1 and 2 were then determined and added to the data set.

# CHAPTER 3

# HEIGHT GROWTH

## Introduction

Patterns and phenology of extension growth will be discussed in Chapter 5. This chapter will address the topic of environmental effects on the total amount of seasonal extension growth.

Plant extension growth is the result of the complex interaction between a plant's genetic potential and a host of environmental resource levels and regulators. Kramer and Kozlowski (1979) listed the principal resources needed for plant growth as light, water, oxygen, carbon dioxide, and mineral nutrients. Physical space should be added to this list. Environmental regulators include temperature, wind, gravity, pH, water, and biochemicals. Analysis of plant growth is further complicated by interactions among the environmental resources, the environmental regulators, and the growing plant. Indeed, plant growth is usually not limited by a single, simple factor as was proposed by Liebig (1843) and later modified by Blackman (1905). Therefore, any attempt to model plant growth from a single environmental factor should be undertaken with a healthy dose of optimism. Even so, a significant amount of the variation in plant growth can be explained from an analysis of environmental factors. For example, in his review, Brown (1971a) summarized our current understanding of the effects of mechanical forces, light, water stress, and temperature on plant form.

Lockhart (1961) related extension growth in pinto beans to light intensity, demonstrating that maximum length was obtained at less than full sunlight; elongation growth was inhibited by gibberellin deficiencies in full sunlight. Wilson and Fisher (1977) also found that light intensity determined the amount of extension growth in striped maple (Acer pensylvanicum L.) as well as the fate of bud primordia. Biro et al. (1980), Jaffe (1973), Neel and Harris (1971), and Turgeon and Webb (1971) all found touch to inhibit terminal elongation in the species they studied. Hunt and Jaffe (1980) found an interaction between temperature and wind (one type of touch) while explaining the amount of elongation growth in Phaseolus vulgaris L.

Perhaps the area of environmental physiology most thoroughly studied is the effect of water supply on plant growth. Relatively few papers have examined the effects of moisture surplus on plant physiological processes. In one review of this topic, Kozlowski (1982) discussed the effects of flooding on tree growth and concluded that trees vary both in their flood tolerance and in the methods used to survive a flood. A topic studied more thoroughly than water surplus is the effects of water deficits on plant growth. Brown (1971a) concluded that water is the single most important factor limiting tree growth and distribution. Kramer and Kozlowski (1979) also concluded that water supply is the primary environmental resource controlling the occurrence of trees in places where temperature will allow their existence.

Many physiological processes are affected by water deficits. A recent review of this topic was supplied by Hsiao (1973). He wrote that, although studies on this topic abound, few authors have concurrently examined the progress of more than one physiological or metabolic process in plants undergoing increasing, gradual water stress. Because of this fact, it is hard to place the various processes in a sequence of increasing sensitivity to stress. With the limited data available to him, he tentatively concluded that cell growth is the most sensite process. His evidence came from a variety of sources. One was the fact that turgor pressure has long been considered crucial for cell expansion. Another was that the rates of change in cell enlargement with water stress proceed too rapidly to be caused by metabolic changes. He cited a study by Acevedo et al. (1971) which demonstrated that short, mild water stress in maize did not alter total elongation. This implied that metabolic processes continued uninterrupted during the period of stress. A last line of evidence came from the fact that root growth is resisted by soil water potential and soil mechanical resistance. An increase in soil water potential or mechanical resistance should reduce root pressure potential and, subsequently, root growth. This has been found to be the case (Greacen and Oh 1972).

Zahner (1968) reviewed the effects of water deficits on tree extension, diameter, root, and reproductive growth. He concluded that:

> Botanists, foresters, and horticulturalists in every decade since the middle of the eighteenth century (reviewed by Studhalter et al. 1963) have reported increasingly

> convincing evidence that tree growth responds more to natural changes in sap flow, and therefore environmental water stress than to any other normal, perennial factor in a forest or an orchard (emphasis added).

This statement can be coupled with Hsiso's assertion about the importance of cell turgor pressure to growth to conclude that there is a correlation between cell water potential and soil water potential, although the two are not equivalent. Zahner continued by stating that differences exist even within the soil and that the average soil moisture stress of a volume of soil differs from the moisture stress at the root/soil interface, the later being much greater. The magnitude of this soil/plant water potential difference increases with height above the water table. Spatial and temporal variations in water potential in the soil-plant-atmosphere continuum have been described by Hinckley et al. (1978). They reviewed studies of field-grown forest trees and included the following topics: the environmental control of stomatal activity, transpiration and water movement in tree stems, tissue capacitance, interspecific variations, and ecological considerations.

The amount of extension growth also varies with site, year, and tree species. Zahner (1968) reported that hundreds of papers have been published which demonstrate that height growth is less on dry sites than on moist sites. He formed the general conclusions that soil water is the key to forest site productivity and that soil characteristics which determine the amount of water available to a tree account for most of the

variation between sites. Although this is so, forest soil characteristics have been poorly studied (Hinckley et al. 1978), and problems such as site heterogeneity make this work difficult. The amount of extension growth at a given site also varies between years. Many authors have correlated extension growth with rainfall (Zahner 1968) resulting in the general conclusion that, for trees on upland sites, growth is greatest in wetter years. The effect of climate on extension growth also varies with species at any given site. In trees such as tulip poplar (*Liriodendron tulipifera* L.) and loblolly pine (*Pinus taeda* L.), which grow throughout the season, extension growth is reduced by current season water deficits, whereas in species with preformed leaf primordia, water deficits of previous years reduce the number of leaf primordia formed and current deficits reduce leaf size and internode distance (Zahner 1968). Doley (1970) has proposed an alternative explanation to account for the amount of extension growth in *Liriodendron*. He simulated drought experienced by *Liriodendron* seedlings by reducing atmospheric humidity in a growth chamber from 95% to 45% and reducing soil water potential from -0.4 to -11.0 bars. He found that humidity reduced growth more than the water potential of the root medium. In the field, these variables probably interact to produce the observed growth.

Bassett's (1964) work is an early study attempting to quantify soil moisture availability and its effect on tree growth. He used a previously developed method to estimate soil

moisture content for each day in the growing season from the following data: field maximum, field minimum, minimum storm, accretion regressions, depletion curves, transition dates, and a daily record of rainfall. This technique was used for the 0 to 15.24 and 15.24 to 30.48 cm (0 to 6 and 6 to 12 inch) soil layers. He then created two indices to relate soil moisture levels to tree growth: no-growth and growth days. He defined a no-growth day as a day in which the mean moisture tension in the surface 30.48 cm (foot) reached or exceeded -4 bars. The index was the sum of these daily values. To calculate the growth day index, soil-moisture tension and potential evapotranspiration (PE) were combined as:

$$\text{Growth-day unit} = 1.0 - (P \times T)$$

where P is the daily value of PE in inches of water and T is the mean moisture tension of the surface 30.48 (foot) of soil in bars. The product of P and T represents the interaction between these terms, which is tree water stress. These two indices were regressed against basal area growth ($ft^2$) and cubic-foot growth of a second growth forest composed of loblolly and shortleaf (*Pinus echinata* Mill.) in mixture with upland southern hardwoods, mainly southern red oak (*Quercus falcata*). The linear regressions were significant ($p \leq 0.01$) and explained 95 to 97% of the variation in the data.

Zanner and Stage (1966) have also developed a tool to predict tree growth from daily moisture stress. Their technique is based on Thornthwaite's technique of determining the difference between

potential evapotranspiration and precipitation and, in the case of a deficit, calculating soil moisture depletion. In one analysis, they explained 72% of the variation in red pine (Pinus resinosa Ait.) shoot growth from water deficits of the current year shoot elongation period, deficit sums for the previous year's needle-elongation plus food-storage periods, and the square of sum of deficits for the preceeding year. This was an improvement on the 52% of the same variation given by a regression on total precipitation and average temperature for the same growing periods. They also were able to describe 78% of the variance in the deviation from normal basal area growth in western white pine (Pinus monticola D. Don) by an orthogonal polynomial regression using mean daily temperature, daily precipitation, and six coefficients describing moisture stress.

Many equations have been developed to predict evapotranspiration on time scales varying from one day to one month (Veihmeyer 1964). The most widely used technique for calculating water balance is that developed by Thornthwaite and Mather (1955, 1957). Input to this model includes:

1. mean monthly (or daily) air temperature,
2. mean monthly (or daily) precipitation,
3. information about the water holding capacity of the soil, and
4. plot latitude.

The first step in this technique is to calculate a temperature efficiency (TE) index as the sum of the twelve monthly temperatures ($T_i$) from the empirical equation:

$$TE = \sum_{i=1}^{12} (T_i/5)^{1.514} .$$

Next, potential evapotranspiration (U) is calculated as:

$$U = 1.6(10T_i/TE)^a$$

where:

$$a = 0.000000675(TE)^3 - 0.0000771(TE)^2 + 0.01792TE + 0.49239.$$

This value is then modified to correct for varying day lengths with increasing latitude and also for different month lengths. The difference between precipitation and potential evapotranspiration is calculated next. If this value is positive, water is added to the soil until it is at field capacity, at which point runoff occurs. If the value is negative, moisture is withdrawn from the soil.

Soil water depletion does not occur in a linear fashion but along a soil-moisture characteristic curve (Hillel 1971). At increasing tensions, soil moisture is held more and more tightly by the soil. Soil wetting occurs by a different process, and this curve differs from the soil depletion curve. This phenomenon is an example of a hysteresis. In Thornthwaite and Mather's 1957 paper, soil moisture values were found in tables for different soil available water holding capacity and from values for accumulated

potential water loss (ACCPWL). Pastor and Post (1984) observed in Dunne and Leopold (1978, Figure 8-3, p. 241) that soil moisture is related to ACCPWL by a negative exponential and that the slope of this function is determined by field capacity (FC in mm). They then selected random values from Thornthwaite and Mather's tables as data which was used to develop the following summary equation:

$$\text{Soil water} = FC \times e^{(0.00046 - 1.10559/FC)} (ACCPWL) \quad .$$

They obtained an $R^2$ of 0.9993.

Several indices have been developed to quantify the severity of soil moisture stress on plant growth. Palmer (1965) used Thornthwaite and Mather's approach to develop the Palmer Drought Severity Index (PDSI) which averages the current weather conditions with conditions for part of the previous month. A map showing PDSI values for the 48 continental states can be seen in the Weekly Weather and Crop Bulletin. This index has been used successfully to account for much of the variation in tree-ring chronologies and to reconstruct droughts (Cook and Jacoby 1977).

Mann and Post (1980) developed another index for soil moisture stress, and a description of their method can be found in Solomon et al. (1984), and Pastor and Post (in press). Soil moisture values were calculated by the Thornthwaite and Mather approach. Their drought index (D) is the number of days in the growing season that soil moisture falls below the -15 bar tension level. Tree diameter growth is reduced by a factor $(1 - D/D_i)$ where $D_i$ is the "maximum drought days" that species i can tolerate during the growing season.

This parameter was estimated by comparing the western-most extent of a species' range with maps of calculated maximum drought days for the eastern United States. They used Bassett's 1964 paper to assume that the shape of the function relating tree diameter growth to a "drought day" climatic index is linear.

The purposes of this chapter are: to parameterize a soil moisture model for the study area based on Thornthwaite's methodology, to develop several indices which describe soil moisture deficits, and to develop an equation to predict sycamore bole extension growth from these soil moisture indices and from calculated soil moisture values.

## Materials and Methods

Mann and Post's FORTRAN computer code was used to determine the monthly soil moisture values from observed temperature, precipitation, soil, and latitude data. Growing season length was determined as the number of days between the mean last spring frost and the mean first autumn frost. These values were obtained from the Climatic Atlas of the United States (1968). Soil moisture values were estimated by the following procedure. Union Camp, Inc. had previously classified and mapped the soils at the study site (Chapter 2). Values for the depth and texture of each soil horizon of the Riverview soil were taken from the "typical pedon" description given on the Soil Series sheet by the U.S. Department of Agriculture, Soil Conservation Series. Field capacity (FC) for each texture was obtained by multiplying soil moisture values by weight

found in Table 1 of Broadfoote and Burke (1958) by bulk density estimates found in their Table 7. Soil moisture values for -15 bar tensions (DRY15) were read directly from Figure 6 of the same publication. The values for both field capacity and -15 bar tension for each soil layer were then multiplied by the depth of that layer to estimate the available water holding capacity of the soil. Mean monthly temperatures and total monthly precipitation data for the 53 most recent years were obtained for the tidewater climatic division of Virginia from the publication Climatological Data. A weather station exists in Stony Creek, Virginia (which is near the study site), but data from this station was not used alone because Blasing et al. (1981) have shown that climatic division data is preferred over single station observations for predicting tree diameter response to climate. This is due to the fact that data averaged over several stations reflects the regional climate better than that of a single station due to dampening of local, anomalous fluctuations.

Three indices were created to describe drought severity for each year (Figure 3.1). The first expressed the growing season date (GSD) that the soil moisture potential reached the -15 bar level and was expressed as a fraction of the growing season length. The second was calculated by subtracting the duration (DUR) of the drought (also expressed as a fraction of the growing season) from 1.0. This index is the same as that calculated by Mann and Post (1980), scaled by the length of the growing season. The third index represented the fraction of the potential water available for plant

Figure 3.1. Rainfall, evapotranspiration, soil moisture, and three climate indices for 1980. GSD is the growing season date that the soil moisture curve drops below the 3-bar tension level expressed as a fraction of the growing season length. DUR is the duration of the drought expressed as a fraction of the growing season length. FPOT is the fraction of the potential soil water available for extensive growth calculated as (field capacity - 3-bar tension) x length of the growing season.

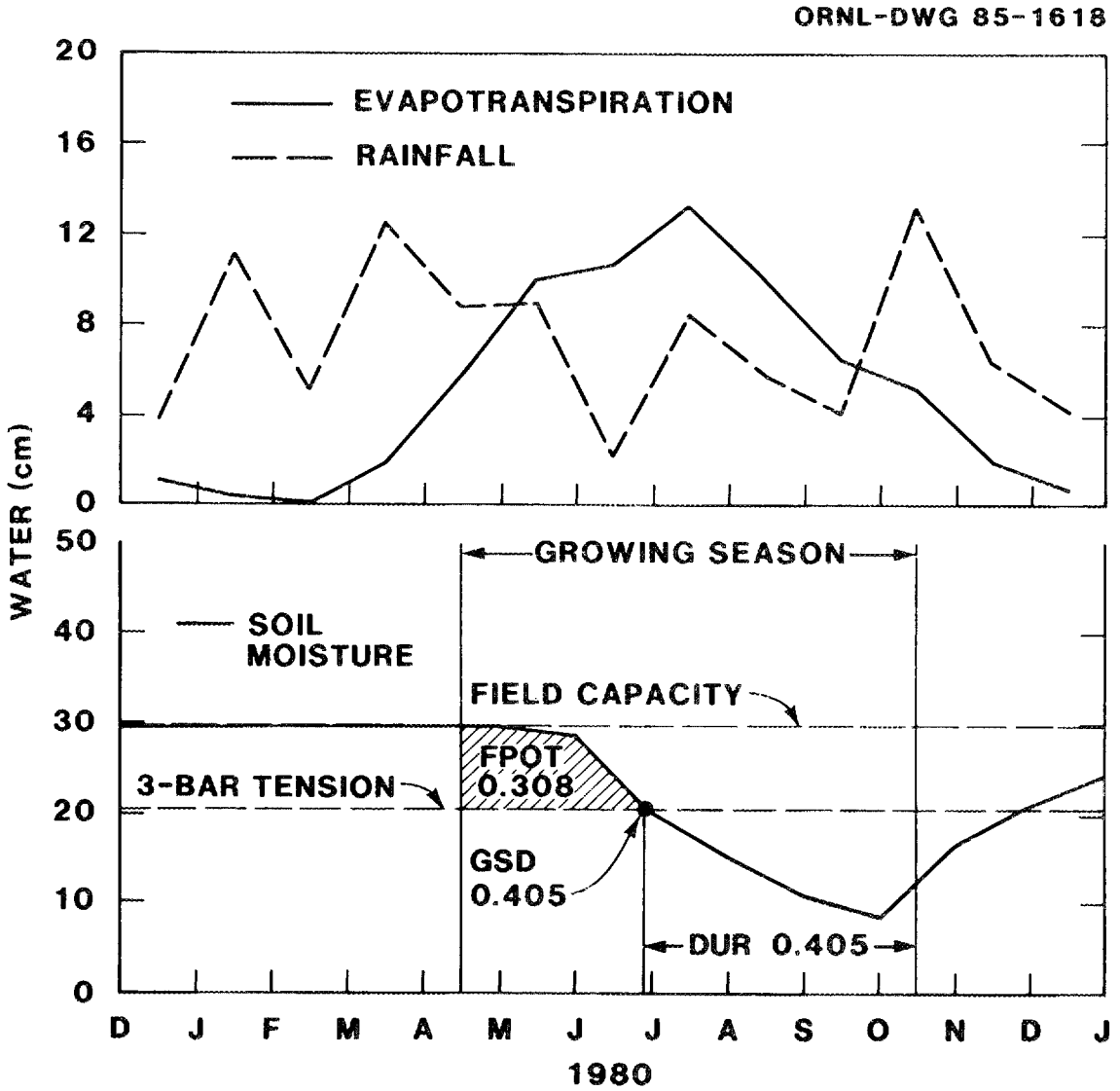
ORNL-DWG 85-1618
EVAPOTRANSPIRATION
RAINFALL
WATER (cm)
20
16
12
8
4
0
50
40
30
20
10
0
GROWING SEASON
SOIL MOISTURE
FIELD CAPACITY
FPOT 0.308
3-BAR TENSION
GSD 0.405
DUR 0.405
D J F M A M J J A S O N D J
1980

Figure 3.1

growth (FPOT). This potential is the product of the number of days in the growing season and the available water holding capacity (AWHC = FC - DRY15). These indices all ranged between 0.0 (representing total drought) and 1.0 (representing no soil water deficit).

All input data were added to the model which was run to calculate monthly soil moisture values and the DUR index. For the 53 years of input data, the DUR index was less than 1.0 in only one year. Therefore, this index was not sensitive enough to explain the variation in sycamore extension growth.

The fact that cell growth is one of the processes most sensitive to moisture stress was noted above (Hsiao 1973). Hsiao summarized information showing that growth ceased at leaf water potentials of -4 bars in sunflower, -7 bars in maize, and -12 bars in soybeans. Table 1 in his paper indicates that this process may be sensitive to tissue water potentials of a fraction of a bar. Stransky and Wilson (1964) found that shoot extension in loblolly (Pinus taeda) and shortleaf pine (Pinus echinata) was totally inhibited by a soil water potential of -2 bars. Doley (1970) found a 70% reduction in Liriodendron stem elongation with a reduction of leaf water potential from -6 to -7 bars. Bassett (1964) cited Kramer and Kozlowski (1960) who stated that, theoretically, soil water potentials greater than -1 or -2 bars reduce growth, and Bassett used a DRY value of -4 bars in his work. These examples have been given to demonstrate that cell expansion is sensitive to soil water potentials above -15 bars, the value taken as representing the permanent wilting point. Because of this fact, the DRY value was

reset at -3 bars. Values for this soil moisture potential were given in Holtan et al. (1968) and was calculated for the current study by the following procedure. First, the seven study sites closest to Stony Creek, Virginia were located. These were: College Park, Maryland; Moorfield, West Virginia; Blacksburg, Virginia; Americus, Georgia; Watkinsville, Georgia; Beemerville, New Jersey; and Marlboro, New Jersey. Soil water tension values were obtained for each layer of the Riverview series from silt loam soils at these sites. Since an adequate sample size was obtained only for the surface horizon, values for the subsurface horizons were obtained from soils at the same sites but with other surface horizons. Data for the loamy fine sand subsurface layer were still too few, so values were obtained from the description of other eastern United States soils. From these data the mean -3 bar moisture values was calculated for each layer, and these values were then multiplied by the depth of that layer in the Riverview series to get the soil -3 bar moisture value.

Preliminary data analysis indicated that an additional tree height measurement was necessary. The original study trees could not be remeasured because the tops of several of these trees had to be removed to measure them. In the autumn of 1983, fifteen trees were randomly selected from throughout the plantation described in Chapter 2. Tree height was measured for each of the seven years of growth, and in addition, two increment cores were extracted at random azimuths from the base of each tree. To determine if these trees differed in mean annual height from the 10 study trees, they

were compared by t-tests. These analyses failed to reject the null hypotheses ($p > 0.05$) and confirmed that the ten study trees are a random sample of the larger population. Figure 3.2 shows the mean height and diameter growth for the 7 years of stand growth, as well as soil moisture and Palmer Drought Severity Index values for the same time period.

The growth curve of many species is not linear over time but sigmoidal (Leopold and Kriedmann 1975). Because the shape of this curve affects the form of the regression equation, tree height was plotted against time for the trees at this study site, for trees at other sites planted by Union Camp, Inc., and for values published in Belanger and Pepper (1978) for two stands with densities similar to those in the present study. These curves (Figure 3.3) are linear over the age of the study. Others (Cochrane and Ford 1978) have observed linear extension growth in young plantations.

Several other factors had to be considered during model development. First, the first year of tree height growth is not only a function of tree genetic potential, environmental conditions, and cultural management techniques, but is also a function of seedling size and the depth to which it is planted. Because of this, the first year's growth was not included in the analysis. Second, as mentioned in Chapter 2, the trees were fertilized during the first year of growth and cultivated twice during each of the first two years. The trees were also fertilized at mid-rotation (age 7). Early-rotation fertilizer effects last two years (J. Jones, pers. comm.) with 2/3 of this effect occurring in the first year.

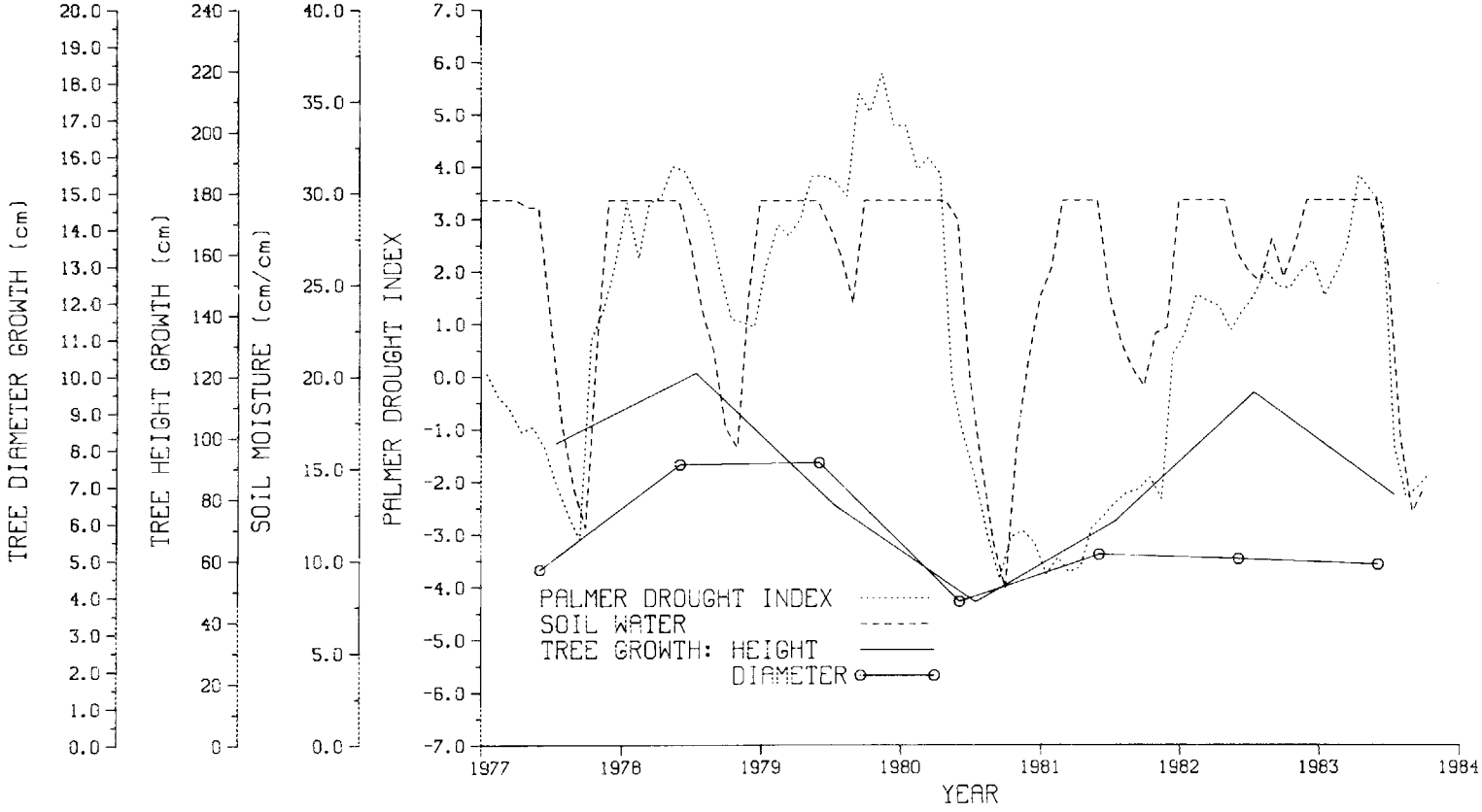


Figure 3.2. Mean tree extension and diameter growth, calculated soil moisture values, and Palmer drought index values for 1977-1983. Values for tree extension and diameter growth are means for 15 trees and are plotted in mid-year.

ORNL-DWG 85-10913

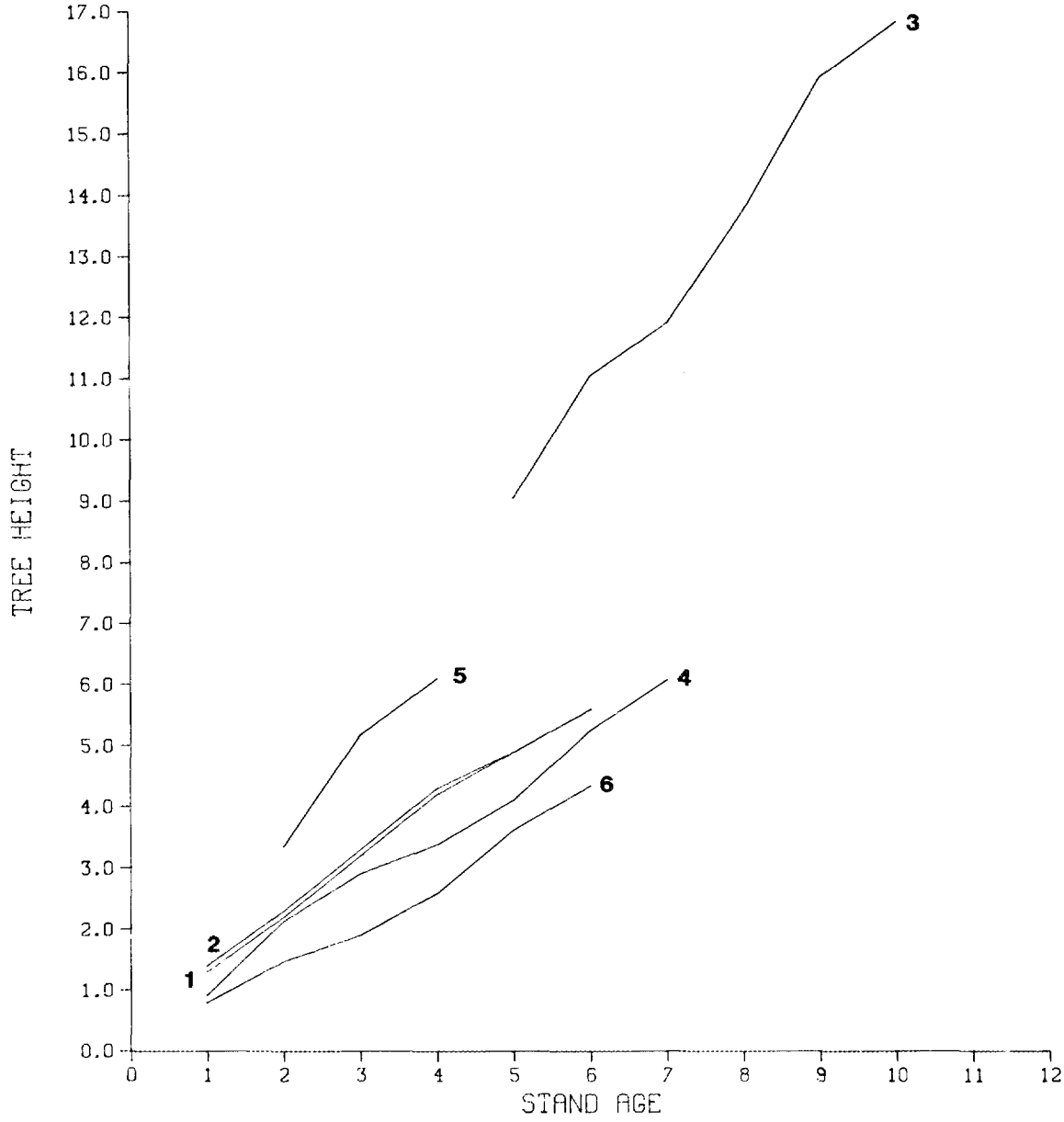


Figure 3.3. Mean tree height at various ages. Curves 1 and 2 are from data in Bellanger and Pepper (1978), curves 3 and 6 are from data collected by the author in other Union Camp plantations, curve 4 is for the trees at the study site, and curve 5 is from data in Saucier et al. (1972).

The combination of year 2 fertilizer and cultivation effects was coded as a FERT = 2 class effect and the mid-rotation effect was added as a FERT = 3 effect. A last complication is that repeated observations were made on the same tree, violating the regression assumption of independence. One technique used to avoid the potential correlation among observations is the growth curve analysis procedure developed by Grizzle and Allen (1969). Another analytical approach suggested by Draper and Smith (1981) for growth data is to fit a model "in as common sense a manner as possible, and then to examine the residuals from the fit to see if they exhibit characteristics that give clues of invalid assumptions." In the present study there were two extremes in a continuum of potential methods that could have been used in the analysis. An anti-conservative procedure would have treated all observations as completely independent, which they clearly are not. A conservative method would have treated the observations on a tree as completely dependent, and the six observations could then be collapsed into one. The model chosen assumes that tree growth is linear over the course of the experiment and that the population mean height is lognormally distributed. Any dependencies present in the data can then be treated as a random effect due to "tree." By this procedure, any tree whose growth is above the mean in its first year of growth will be above the mean all other years. For the relatively short growth period analyzed in this study, this assumption is appropriate. However, for analyses covering longer growth periods or for different genotypes or silvicultural

treatments, the shape of the growth curve may change (Daniel et al. 1979) and another model may be needed. This term is considered as a random effect in the analysis because the study trees are a random sample of the larger population. The equation to be analyzed was:

$$HT = e^{b_0} \cdot (\text{SOIL MOISTURE INDEX})^{b_1} \cdot e^{\text{FERTILIZER}} \cdot e^{\text{TREE}}.$$

After taking logs this became:

$$\ln(HT) = b_0 + b_1 \ln(\text{SOIL MOISTURE INDEX}) + \text{FERTILIZER} + \text{TREE}.$$

Separate analyses were run for all three soil moisture indices as well as for monthly soil moisture values. Since the April soil moisture value was the same for all years, it was deleted. It was also necessary to combine the soil moisture values for the months of May and June, July and August, and September and October because of the small number of years in the data set.

## Results and Discussion

Results from the regression analyses (Table 3.1) show that all regressions are significant ($p \leq 0.05$). In the regression with May and June soil moisture (lnWAT5/6), the significance level is less than in other regressions, and in this model the soil moisture term is not significant ($p > 0.05$). Above, it was mentioned that the April soil water value was the same for all years. Figure 3.2 shows that the soil is recharged to field capacity each year and is still at field capacity early in the growing season. As such, it is not surprising that unless a very hard drought develops early in a

Table 3.1. Parameter estimates, F-values, and coefficients of determination for the multivariable regressions predicting ln (ΔHT) from climate, fertilizer, and tree variables. The significance levels given over the parameter estimates are from the type III F-tests.

| Intercept | Climate | Fertilizer class 0 | Fertilizer class 2 | Fertilizer class 3 | Tree Variance | F | $R^2$ |
|---|---|---|---|---|---|---|---|
| -12.446 | 2.243 ln WAT 5/6$^{ns}$ | -0.009* | 0.380 | 0.000 | 0.0119$^{ns}$ | 2.13* | 0.334 |
| -4.627 | 1.272 ln WAT 7/8*** | -0.327*** | 0.042 | 0.000 | 0.0217* | 5.04*** | 0.543 |
| -0.038 | 0.675 ln WAT 9/10*** | -0.308*** | 0.209 | 0.000 | 0.0214* | 4.94*** | 0.539 |
| 4.813 | 0.765 ln GSD*** | -0.355*** | 0.080 | 0.000 | 0.0221* | 5.21*** | 0.552 |
| 4.809 | 0.761 ln DUR*** | -0.358*** | 0.083 | 0.000 | 0.0219* | 5.15*** | 0.549 |
| 4.928 | 0.677 ln FPUT*** | -0.259*** | 0.221 | 0.000 | 0.0203* | 4.47*** | 0.514 |

$^{ns}$Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

season, this early-season water value would add little to the regression. After June, the soil moisture values are highly significant, indicating that this is the time of year when tree growth is most sensitive to soil moisture stress. It should also be noted that the three climatic indices are highly significant and that the magnitudes of the parameters are similar. They all do a good job of measuring soil moisture stress. This in not surprising as all three are highly correlated ($p < 0.0001$, $n = 53$).

The fertilizer effect is also highly significant. The value of 0.0 for the mid-rotation (FERTilizer = 3) class level is a result of the algorithm that SAS uses to solve the normal equations, and other FERTilizer class level values should be compared to this value. The model was able to detect that both the early fertilization/cultivation treatment and the mid-rotation treatment increased sycamore height growth. The combination of early fertilization and cultivation (FERT = 2) resulted in the greatest increase in height growth. With the exception of the first regression, the magnitude of the parameters are strikingly similar. As the purpose of these cultural techniques is to reduce direct competition by herbs and to increase height growth, it appears that they are successful.

The random TREE effect is also significant, although less so than the other terms. This implies that the trees have little differences among them. This is not surprising in a monoculture established from similar genetic stock. This term was assumed to be lognormally distributed with a mean of 0.0 and the calculated

variance given in Table 3.1. Once again, there is a striking similarity in the magnitude of this term among regressions.

This TREE effect could represent one of two factors: microsite or genetics. A microsite effect would represent variables related to the environment (e.g., small-scale changes in soil fertility, soil texture, or soil depth) or biotic effects on tree growth (e.g., insect attack). These environmental variables would influence growth throughout the tree's life and would probably affect the growth of several trees in an area. Biotic effects would probably be important only for early tree growth (affecting subsequent years), although an acute, late-season attack may affect the parameters for this variable. A second possibility is that these TREE differences are related to genetics and that trees differ in their growth potential. Because the study area was over a small, apparently homogeneous area of the sycamore plantation, and because the mean tree height for these 10 study trees did not differ from the height of the rest of the plantation, the TREE effect is probably not due to microsite effects. For the remainder of this paper, the TREE effects will be assumed to be due to genetics. Indeed, trees do differ in their height growth potential.

Because the results from several of the models were so similar, any one of the regressions could have been used in the simulation model to predict height growth. The regression with the DUR variable was chosen because of its similarity with previous work by others.

# CHAPTER 4

# OPPORTUNISTIC BRANCHING

## Introduction

To temperate foresters and botanists, it has long been considered "normal" for trees, shrubs, and herbs to make their total annual extension growth in a single flush which follows a sigmoid "grand period of growth" shape curve (Studhalter 1955). Modifications of this pattern were considered the exception, not the rule. This chapter will examine some of these so called "exceptions" and their significance for sycamore (*Platanus occidentalis* L.).

Bell et al. (1979) developed a model to simulate two-dimensional branching patterns of plants. In this model, the developmental geometry of a plant was simulated from parameters modeling meristem fate (time of birth and death), potential (or type), and position (location and orientation). Meristems have one of three initial fates: they may grow into a shoot, abort, or become dormant (often as a bud which may develop later). Growing and dormant meristems may later be damaged and die, or may die naturally. A considerable botanical literature has developed to name and describe these meristem fates. For example, Studhalter (1955) listed over twenty terms that describe late-season growth flushes; the two most common are the German "Johannistrieb" and the English "lammas" (Brown 1971b, Halle et al. 1978, Rudolph 1964). Another branching phenomenon is prolepsis.

Spath (1912, in Halle et al. 1978) defined syllepsis and prolepsis as (in translation):

> Sylleptic shoots are such as develop regularly on a leafy unmodified shoot, without consideration of the season, during continuous extension growth of the terminal bud from newly formed lateral auxiliary buds - mostly without forming bud scales first - therefore without a preceding rest period and developing independently of other factors. Therefore they belong to the normal shoot system of the plant, but they are to be found frequently and regularly in young plants only and may be lacking occasionally in old ones.
>
> True proleptic shoots are those which develop irregularly on a leafy unmodified shoot, without consideration of the season after complete conclusion of extension growth, therefore from already closed (almost always terminal) buds after an appreciable resting period. Therefore they do not belong to the normal shoot system of the plant.

Kozlowski (1964) wrote that sylleptic shoots are "less well known" and "often are unnoticed because they form during the early part of the growing season when normal shoots develop (emphasis added)." He cited Szczerbinski and Szymanski (1957) who found that "shoots in young *Pinus sylvestris* trees formed frequently from newly formed, scaleless buds that had not passed through a period of rest (emphasis added)."

Multiple tip flushes have long been known. Theophrastus wrote of two types of multiple flushes, end-on-end from terminal buds and lateral growth from lateral buds (in Studhalter 1955). This distinction has been retained up to the present. Rudolph (1964) defined lammas growth as "the type of terminal shoot elongation characterized by one or more periods of growth following the first

elongation of the terminal shoot earlier in the season" and prolepsis as "the condition in which at the end of the normal seasonal growth, one or more lateral buds at the base of the terminal bud break dormancy and add another flush of growth." He further limited the definition of prolepsis to include only branching at the base of the terminal bud of the main stem. Kramer and Kozlowski (1979) further added that these are "abnormal late-season bursts of shoot growth from opening of recently formed buds which are not expected to open until the following year (emphasis added)."

Halle et al. (1978) have also reviewed the historical usages of the terms syllepsis and prolepsis. They retained Spath's original definition of syllepsis but adopted Tomlinson and Gill's (1973) modification to his definition of prolepsis. Their definition reads, "Prolepsis is the discontinuous development of a lateral from a terminal meristem to establish a branch, with some intervening period of rest of the lateral meristem." Their contentions with Spath's definition are two. The first is that he did not differentiate between the growth of the terminal and lateral buds (lammas and prolepsis as described above).
In their words:

> These definitions indicate that no distinction is made between activity of terminal and lateral buds, i.e., the terms do not relate only to branching "prolepsis." Spath thus clearly means "precocious" breaking of a bud which would "normally" be expected to overwinter, a sense in which it is still commonly used, especially with reference to specialized shoot systems like that of *Pinus*, e.g., Rudolph (1964).

Their second disagreement is with the fact that many definitions state that this is an unusual phenomenon (note the emphases added to the above quotations). Again, in their words:

> Now that we have a more cosmopolitan understanding of tree growth and especially now that we can appreciate that synchronization of shoot extension is neither a necessary, nor the most common condition for tree growth, as tropical observation demonstrates, we can apply Spath's terminology strictly to branch expression in the way we have established ... without treating it as a special case. This leaves the field clear for "lammas shoot" and its equivalents to describe a normal but only infrequently expressed phenomenon. We thus invert the whole of the philosophy behind the forester's thinking, by saying "temperate trees are anomalous, lammas shoots of various kinds are normal phenomena of growth."

They suggested that this normative viewpoint developed because most studies have been made on temperate trees and emphatically stated that this viewpoint "has to be changed."

In the literature, the terms prolepsis and lammas have sometimes been used interchangeably. Rudolph's (1964) definition of lammas growth was restricted to terminal shoot growth and his definition of prolepsis was for lateral bud growth. Kozlowski (1964) and Kramer and Kozlowski (1979) agree with this terminology. Carvell (1956) described lammas growth on red pine as shoots which originated from lateral buds surrounding the leader. As such, his lammas growth is equivalent to Rudolph's proleptic growth. Halle et al. (1978) also use the term lammas to refer to shoot growth.

Morphologically, sylleptic branches can be identified by the presence of an extended internode (hypodium) below the first leaf or

pair of leaves (Halle et al. 1978, Tomlinson 1983). Proleptic branches can be recognized by the presence of basal bud-scales and a gradual transition (of size and shape) towards adult foliage. Many factors have been put forth to explain the frequency of late-season growth flushes. In his review, Rudolph (1964) found that soil, weather, light, heredity, and auxin relationships have been postulated as primary factors influencing the formation of these shoots. Because his own work had shown that jack pine (Pinus banksiana Lamb.) from the more southern Lake States had a higher frequency of late-season shoots than more northerly seed sources, he attributed the difference to genetics. Brown (1971b) gave excess late-season rainfall as the primary cause for lammas shoots. Borchert and Slade (1981) observed them more frequently on "vigorous saplings." Carvell (1956) also found that lammas shoots were found "almost entirely...[on] the largest and most vigorous [red] pines."

Rudolph (1964) mentioned another type of branch growth which he called "long buds" in which terminal buds elongate but do not break. These differ from lammas shoots of pine in that lammas shoots have needles along their length, whereas long buds do not.

Syllepsis, prolepsis, and lammas growth are examples of buds which grow either immediately after formation or shortly thereafter. Buds may also remain suppressed for much longer periods of time. The terminology "suppressed" adopted here is that of Brown (1971b) who prefers its use to "dormant" because the buds are continually producing new leaf and scale primordia, and are growing

with the radially expanding cambium. If stem cross sections are made, vascular traces can be seen (Brown 1971b, Figure I-18a and b). In some tree species, auxiliary buds may produce additional buds in the axils of their basal bud scales (Brown 1971b). These buds may then exist as suppressed buds. Epicormic branches, also called "water sprouts" (Kramer and Kozlowski 1979), result from the release of suppressed buds after an increase in light intensity received by tree trunks or branches (Daniel et al. 1979). Huppuch (1961) observed epicormic branches on sycamore trees after a reduction in stand basal area and his data suggest that the frequency is proportional to residual basal area. Stump sprouts are another example of the release of suppressed buds on lower tree stems (Kramer and Kozlowski 1979).

In addition to buds that form in leaf axils, buds may develop which have no connection with apical meristems. These are called adventitious buds (Kramer and Kozlowski 1979). All buds on roots are adventitious (Brown 1971b), and stems that originate from them are called root sprouts or "root suckers" (Kramer and Kozlowski 1979). Adventitious buds may also arise from stem meristematic tissue on stumps, and these "stool sprouts" are usually short lived (Kramer and Kozlowski 1979).

The present study will adopt Halle et al.'s (1978) definitions of syllepsis and prolepsis. Use of their term prolepsis is, however, not without problems when it is applied to tree branching in seasonal environments. In temperate climates, their "period of

rest" may occur within one growing season, over the winter, or over several years (e.g., epicormic branches). No terminology has developed to separate the first two of these situations. Branches formed from buds that form, rest, and break during the same growing season were called "proleptic" by Spath. Halle et al. wrote (p. 45) that he meant "precocious." Elsewhere (p. 45), Halle et al. (1978) imply that these should be called lammas shoots, but the problem with their use of this term is that they use it elsewhere (p. 273) where they apparently mean "epicormic." A term to describe the branches of temperate trees that form from overwintering buds is also lacking. Both of these branch types were observed on sycamore. In the present study, branches that form along the current leader growth will be called Type I proleptic branches or Type I branches, and those that form from overwintering buds will be called Type II proleptic branches or Type II branches. The terminology is easy to remember for temperate trees in that Type I proleptic branches form on 1-year-old branch sections and Type II branches form on 2-year-old branch sections.

The presence of epicormic branching in sycamore has already been mentioned. The purpose of this chapter is to examine other branching strategies exhibited by in American sycamore.

## Materials and Methods

A description of the sampling techniques has been given in Chapter 2. In addition to the main data set, data were collected on

plantations established in 1974, 1977, 1978, 1981, 1982, and 1983. In each of these, 15 trees were randomly chosen. On these trees, the amount of height growth was measured and the number of Type I and Type II branches formed each year were counted. Two diameter measurements were also recorded. For the older plantations, two increment cores were extracted near the base of each tree. In the plantation established 1974, extension growth was measured for as many years as possible.

## Results

On several trees the branches appeared to stop and then continue growing within the same year. This was evident from the presence of pseudo-terminal bud scale scars and, in some cases, by the presence of the bud scales. In the 1982 growing season this trait was observed on one branch of one tree, at 11 places in another, and 15 times on a third tree. Only two examples were observed on 1981 tree growth. The mean number of nodes produced before bud set (for the 1982 data) is 3.55, and the mean number after bud set is 1.37 nodes. The high frequency of occurrence on only a few trees suggests that this trait is genetically determined. One of these trees was the smallest one measured, and the other was of average height.

On the study trees, two instances were observed where two primary branches were attached to the same node. The population

frequency of this event, and the mechanisms causing it are unknown. Red oak (Quercus rubra L.) is another species with this trait (Ward 1964).

In many instances, one or more new branches had formed on an older section of a primary branch. It is unknown whether these branchlets were newly formed after branch damage or whether this is an example of the process mentioned above where suppressed buds which formed in the axils of basal bud scales may later be released (Brown 1971b).

Sycamore also forms Type I primary branches, and the number formed on each annual growth increment (AGI) of each study tree is shown in Table 4.1. They can also be identified in Figure 2.4 (see pages 29-34). No second- or higher-order branches were observed. The "X" under TA6 for trees 2 and 7 indicates that these trees appeared to be only five years old, presumably due to dieback which probably occurred their first year of growth. Many factors may be proposed to explain the presence of Type I branches on these trees. Among these are: genetics, tree age, climate, spacing (competition), site fertility (natural and added), and interactions between these factors. To determine the effect of tree age on Type I branching, all observations for trees 2 and 7 were shifted left one column in the table so that TA6 represented year 1 growth for all trees, TA5 represented year 2 growth, and so forth. At this point it should be noted that this test is not simply a test for age dependency. Climate, fertilization, and cultivation may have a confounded effect

Table 4.1. The number of Type I proleptic branches on each annual growth increment (AGI) for the ten study trees. The "X" under Trunk Age 6 for trees 2 and 7 indicates that these trees had shown dieback.

| | Trunk Age | | | | | | |
|---|---|---|---|---|---|---|---|
| Tree Total | 1 | 2 | 3 | 4 | 5 | 6 | |
| 2 | | | | 1 | | X | 1 |
| 4 | | | | | 4 | 7 | 11 |
| 5 | | | | | 9 | 4 | 13 |
| 6 | | | | | 4 | 1 | 5 |
| 7 | | 2 | | 4 | | X | 6 |
| 8 | | | | | 9 | 1 | 10 |
| 9 | | | | | 4 | | 4 |
| 10 | | 1 | | | 3 | | 4 |
| 11 | | 3 | | | | | 3 |
| 12 | | | | | 10 | 7 | 17 |
| Total | | 6 | | 5 | 43 | 20 | 74 |

with age. A G-test (Sokal and Rohlf 1969) was performed to test the null hypothesis of independence between age and tree effects. The G value of 104.802 is much greater than the $\chi^2$ ($p = 0.05$) value of 61.582, so the null hypothesis of independence is rejected. It is clear from Table 4.1 that some trees formed more Type I branches at a given age than others. The column totals indicate that they produced more Type I branches early in their life. This may have occurred through a variety of mechanisms. One is that physiological age does affect Type I branch formation. Climate may also have been favorable for Type I branching during early tree growth and less favorable in later years. These stands were also fertilized and cultivated during these first two years. It has been shown that these factors affected tree height growth (Chapter 3), and it will later be shown that they also increased node density (Chapter 5) and, therefore, increased the number of potential daughter branches formed. Unfortunately, data are not available to distinguish among these factors. Union Camp, Inc. does have plantations of various ages, but these plantations could not be used to sort out the climate, fertilizer, and cultivation effects because they were planted on different sites.

The significant interaction between the age/climate/fertilization/cultivation effect and the tree effect indicates that Type I branching is genetically inherited. This hypothesis was tested on the other data sets described in the Materials and Methods section of this chapter. To average out any climate effect in these

data sets, they were divided into two classes: even and odd years. It was mentioned above that two of the trees showed evidence of dieback the first year. Since it was not possible to determine tree age in the oldest plantation by counting pseudo-terminal bud scale scars, these trees were assumed to be the same age. Results of this analysis are shown in Figure 4.1. According to notes in the SAS (1982a) output, these tests may be invalid due to small sample size in some of the blocks. Yates' correction for continuity has been frequently recommended for small sample sizes (Sokal and Rohlf 1969), but this results in an unduly conservative test. Since this is the case, the chi-square results were accepted as calculated. In all three plantations, trees with Type I branches in even years show a frequency of Type I branch formation in odd years that is higher than expected. The same is true for trees with no Type I branches. These differences are significant for the plantations established 1974 and 1977 and almost so for the one established 1978. To obtain a larger sample size, data from these three sites were pooled, and the test was rerun. The $X^2$ value of 13.792 is highly significant ($p = 0.0002$). This indicates that the significance level for the individual sites would probably have been higher with larger sample sizes. For both the plantation established 1977 and the one established 1978, one tree had experienced dieback during one year. When these trees were deleted, the $X^2$ value increased for both of these cases. These analyses demonstrate a genetic basis for Type I branching.

Plantation established 1974

| | | | Even years: Absent | Even years: Present | Total |
|---|---|---|---|---|---|
| Odd years | Absent | Observed | 6 | 3 | 9 |
| | | expected | 3.6 | 5.4 | |
| | | $X^2$ | 1.6 | 1.1 | |
| | Present | | 0 | 6 | 6 |
| | | | 2.4 | 3.6 | |
| | | | 2.4 | 1.6 | |
| | Total | | 6 | 9 | 15 |

$X^2$ = 6.67 p = 0.0098

Plantation established 1977

| | | | Even years: Absent | Even years: Present | Total |
|---|---|---|---|---|---|
| Odd years | Absent | Observed | 11 | 1 | 12 |
| | | expected | 9.6 | 2.4 | |
| | | $X^2$ | 0.2 | 0.8 | |
| | Present | | 1 | 2 | 3 |
| | | | 2.4 | 0.6 | |
| | | | 0.8 | 3.3 | |
| | Total | | 12 | 3 | 15 |

$X^2$ = 5.10 p = 0.0239

Plantation established 1978

| | | | Even years: Absent | Even years: Present | Total |
|---|---|---|---|---|---|
| Odd years | Absent | Observed | 5 | 6 | 11 |
| | | expected | 3.7 | 7.3 | |
| | | $X^2$ | 0.5 | 0.2 | |
| | Present | | 0 | 4 | 4 |
| | | | 1.3 | 2.7 | |
| | | | 1.3 | 0.7 | |
| | Total | | 5 | 10 | 15 |

$X^2$ = 2.73 p = 0.0986

Figure 4.1. Chi-square test for independence in Type I proleptic branch formation in even and odd years for three sycamore plantations.

Next, the hypothesis was made that the number of Type I branches formed was related to the amount of tree leader extension growth. Data for this analysis were taken from measurements on plantations established in 1974, 1977, 1978, 1981, and 1982. This potential data set was subset to include only those trees which are genetically Type I branch forming trees, defined as those which formed Type I branches in at least one year. The mean annual leader extension growth for this group was 96.6 cm. Trunk sections were divided into two classes: those greater than or equal to this mean and those shorter than this mean. The association between branch length and presence/absence of Type I branches was then tested. A chi-square test for independence strongly rejected the hypotheses of no association ($X^2 = 7.214$, $p = 0.0072$, $N = 151$). Frequencies were higher than expected for the long shoot/Type I branches present and the short shoot/ no Type I branches present classes. This result provides evidence for the case that conditions which result in increased leader elongation (e.g., adequate soil moisture, fertilizer application, or cultivation) also increase the frequency of Type I branches. In Chapter 3 it was assumed that tree growth was relatively constant across years (i.e., no age effect) over the course of this study. Differences in extension growth across years were predicted from fertilization/cultivation and climate effects. It appears that these same effects can be invoked to explain the number of Type I branches formed through their combined effect on the amount of leader growth.

Since Type I proleptic branch formation is related to extension growth, a regression analysis was performed to predict the number of Type I branches formed from the amount of leader length. Because the data consist of counts, some of which are zero, they were transformed by adding 0.5 to each observation and then taking the square root (Sokal and Rohlf 1969). The ANOVA table is given in Table 4.2. While the significance level is very high, the prediction power of the model is low. This shows that the number of Type I branches formed is greater on longer mother sections, but it is also determined by other, as of yet unknown, factors.

Next, Type I proleptic branches were compared to branches attached to the same AGI and also to branches of the same age. In sycamore, primary branch length is a function of the distance from the base of the annual growth increment to the branch (Schutt, unpub. man.). As such, the first step in this analysis was to test for differences in position of attachment. The distance from the AGI base to the branch could be used to compare branches attached to the same mother trunk section, but this measure could not be used to compare branches of the same age due to differences in amount of extension growth. To make this second comparison, the relative position (RELPOS = node distance /AGI length) was used. As in the regression analysis of Chapter 3, a random class variable (TREE) was added to account for differences among trees, assuming that this accounted for any dependencies in the data.

Results are shown in Tables 4.3 and 4.4. In five of the six ANOVAs, the F-value is highly significant. The TREE term is highly

Table 4.2. ANOVA for the regression predicting the number of Type I proleptic branches formed from mother branch length.

| Source of Variable | df | SS | MS | F |
|---|---|---|---|---|
| Length (cm) | 1 | 4.080 | 4.080 | 18.56*** |
| Error | 147 | 32.326 | 0.220 | $R^2 = 0.112$ |
| Total | 148 | 36.407 | | |

***Significant at 0.001 level.

Table 4.3. Results from the ANOVA analysis examining for differences in position of attachment between Type I and Type II proleptic branches attached to the same trunk section.

| | Mean node distance | | Type III F-value | | Full model | |
|---|---|---|---|---|---|---|
| Trunk age | Type I | Type II | Proleptic class | Tree | F | $R^2$ |
| 2 | 47.67 cm | 66.27 cm | 7.92** | 6.05*** | 5.72*** | 0.336 |
| 4 | 28.40 | 60.81 | 32.53*** | 5.61*** | 6.90*** | 0.479 |
| 5 | 70.64 | 114.07 | 99.21*** | 14.74*** | 18.69*** | 0.656 |
| 6 | 36.33 | 68.93 | 31.20*** | 7.47*** | 11.71*** | 0.672 |

$^{ns}$Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

Table 4.4. Results from the ANOVA analysis examining for differences in position of attachment between Type I and Type II proleptic branches of the same age.

| | Mean relative node position | | Type III F-value | | Full model | |
|---|---|---|---|---|---|---|
| Branch age | Type I | Type II | Proleptic class | Tree | F | $R^2$ |
| 2 | 0.401% | 0.678% | 9.46** | $0.59^{ns}$ | $1.50^{ns}$ | 0.183 |
| 5 | 0.418 | 0.774 | 58.47*** | $1.02^{ns}$ | 8.60*** | 0.522 |

$^{ns}$Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

significant for the comparisons of the branches on the same mother section, but is not significant for the comparison of branches of the same age. In all analyses, Type I branches form much lower along the trunk than Type II branches. The lengths of Type I and Type II branches were also compared. In Chapter 5 a model will be developed to predict the annual growth of branches of all orders. This model was rerun with the addition of a term to examine for differences between Type I and Type II branches. Before interpreting the results of this analysis, two further considerations are necessary. First, the model was designed to describe the exponential decay in branch annual growth with increasing age. Because the first year growth of Type I branches is shorter than the following year's growth, it was not included in the analysis. Second, the full model included branches of all orders, whereas it was stated earlier in this chapter that only primary (first-order) Type I proleptic branches are formed. The analysis showed that the PROLEP term was not significant ($p = 0.05$). Therefore, after the first year of growth, the growth increment of a Type I branch does not differ significantly from that of a Type II branch formed at the same node distance.

An attempt was made to run an ANOVA to compare the length of each year's growth between Type I and Type II branches with node position (or relative position) as a covariable. The results were ambiguous, and no clear pattern emerged. Some analyses showed an interaction between the slopes of the two branch classes. In some, one or more year's growth differed among the classes but in others

it did not. Some of this confusion may be due to small sample size or to a confounding of tree and proleptic class variables. Because of these difficulties, these results will not be presented.

The angle of divergence between a branch of one order and the next (PANG) were also compared for these two branch classes. As with the analysis for length, the model will be given in Chapter 5. This analysis showed that Type I branches form at an angle 1.0 degrees more acute than Type II branches.

## Discussion

Many attempts have been made to relate the size and shape of organisms to their structure. If the process of survival is seen as a game, then the organism's "strategy" is to survive by performing various biological tasks with minimum energy expenditure within a given environment. Leopold (1971), drawing upon his earlier work with stream drainage systems, made the analogy that tree branching structures are governed by the opposite tendencies of providing efficient sunlight interception while minimizing energy expenditures on branch and stem lengths. Rashevsky (1961) stated the principle of optimal design as:

> For a set of prescribed biological functions of prescribed intensities, an organism has the optimal possible design with respect to economy of materials used and energy expenditures needed for the performance of the prescribed functions.

He then defined the principle of adequate design as above, substituting the word "adequate" for "optimal." Organisms may not have optimal design, but they must have adequate design.

Attempts have also been made to develop theories which explain the functions performed by organisms, and then to evaluate these theories by a comparison with data. Rashevsky (1943a, b, 1944) was one of the first investigators in this field.

This process has been applied to the design of tree crowns and forest canopies. Paltridge (1973) developed an analytical model to examine the effects of leaf water potential (through its effect on photosynthetic rate) on tree geometry. His model was later applied to forest canopies after it was expanded to include light interception. He examined the effects of tree height, soil water availability, and tree shape on the photosynthetic rate of forest trees.

Horn (1971) developed a theoretical model to explain strategies of leaf distribution by individual trees. His theory consisted of two tree crown types: the monolayer, in which all leaves are held in one layer at the periphery of the crown, and the multilayer, in which leaves are held throughout the crown with "gaps" between individual leaves. He then predicted that multilayer trees would be found in early successional stages and also in late successional stages on xeric sites, and that monolayer trees would be found in late successional stages and also in the understory. He also predicted that early successional, multilayer trees would have small or lobed leaves, be tall and thin as a sapling, have soft wood, and a conical shape in the open. Late successional, monolayer trees would be flat and spreading as saplings and would be tall and ellipsoid to cylindrical in the open.

The shape of individual plant parts has also been analyzed by this process. Parkhurst and Louck's (1972) model predicted leaf size by assuming that leaves are designed to produce maximum water-use efficiency. Their results agree well with observed large-scale trends. Givnish and Vermeij's (1976) model predicted leaf size by comparing gains due to enhanced gas exchange with losses of water and predicted leaf shape from mechanical efficiency and proper orientation to light.

Of course, tree canopy shape is also limited by physical laws. Greenhill (1881), one of the first to examine these "limiting rules," predicted the greatest height to which a tree of a given diameter could grow without buckling. D'Arcy Thompson (1952) was another explorer in this field and investigated the growth and form of a variety of organisms. Other early investigators in this field were Opatowski (1944a, 1944b, 1945) and Esser (1946a,b). Work along this line continues to the present (Cobble 1971, McMahon 1973, McMahon and Kronauer 1976).

Various authors have examined the methods used by trees to achieve a canopy shape. Halle et al. (1978) have developed a series of architectural models which describe the genetic pattern of branching. Their models use attributes such as the amount of stem branching (branches or unbranched) and pattern of shoot elongation (continuous or rhythmic) to classify trees. More recently, Fisher and Hibbs (1982) have demonstrated that these models can not be tied with any successional stage because the same architectural model may give rise to different canopy geometries and different architectural

models may give rise to the same geometry. They concluded that the adaptive geometry of a tree and its architectural model are not synonymous, nor even comparable. Brunig (1976) has also developed a series of tree "ideotypes" based on the aerodynamic properties of leaves and the exposure of mature leaves to wind and radiation. Marks (1975) examined the correlation between extension growth and successional status in the northeastern United States. He found that early successional trees have indeterminate growth that allow for large amounts of extension growth and allow growth to continue through the growing season. Late successional species produced small amounts of extension growth over a short time period through determinate growth patterns. P. White (1983) examined the correlations among leaf size, leaf shape, twig cross-sectional area, leaf number per twig, and branching density for 74 eastern tree species. He found that leaf size is positively correlated with twig area and negatively correlated with branch density. Early successional trees also tend to have smaller leaves than late successional trees at the same twig diameter, more leaves per twig, and larger total area per twig. They also have longer extension growth per year and either compound leaves or high bifurcation ratios. Trade-offs among leaf size, leaf number per shoot, and branching density exist, so that overall tree form is better correlated with successional status than single canopy attributes. Recent work by John Sperry (Tomlinson 1983) has shown that conductivity values of the vascular system of proleptic and sylleptic branches are lower in young proleptic branches than in

young sylleptic branches. This situation is reversed as the trunk/branch union thickens. Tomlinson suggested that young proleptic unions are less efficient but safer, whereas mature proleptic unions are more efficient but less safe. He further suggested that from the point of view of hydraulic conductivity, temperate trees may have selected the safest union between branch and tree. These examples demonstrate that the genetic potential of a tree species is a result of a series of trade-offs among several developmental patterns and in some environments, species which are genetically diverse have a survival advantage.

Sycamore is usually classified as intolerant to intermediate in tolerance and competitive ability (Fowells 1965). Seedlings must have direct light to survive. When they do, they can grow 91.4 to 121.9 cm in height the first year and continue this fast growth throughout their life. Apical growth is indeterminate, continuing throughout the growing season. This species also sprouts readily when young. The crown of the trees is open, conforming to Horn's multilayer strategy. These facts confirm the status of this species as early-successional. Sycamore has many developmental attributes which allow it to be successful in this role, and these traits were observed and discussed in this chapter. It may form more than one branch at a node, may form new branches when old ones are damaged, may stop and then continue growth, and may form Type I proleptic branches. While not previously discussed as an adaptive strategy, these traits are clearly beneficial to early-successional species. As will be discussed in Chapter 5, branching is by acrotony: within

a given trunk AGI, longer branches form towards the branch apex. This phenomena is advantageous for it produces leaf area through the length of the trunk, while concentrating that leaf area near the top of the bole. For an early-successional species, height growth is tantamount to survival. The same argument is true of Type I proleptic branching. A species which can develop its leaf area along the current year's leader growth has an advantage for light interception. The combination of traits which allow sycamore to develop its canopy throughout the growing season, to develop leaf area in the same year as extension growth, and to repair damage gives this species an advantage over other trees and allows for its survival.

From a management point of view, if prolepsis is genetically determined and found on longer stems, then selection for this trait may be useful in giving these trees an advantage when they are grown in plantations with competition with herbs.

The presence of all these features permits sycamore to survive, and thrive, as an early successional species.

# CHAPTER 5

# CROWN DEVELOPMENT

## Introduction

Chapter 1 discussed the fact that very few studies exist which give a complete description of crown branching for any tree species. At that point, however, a list of the variables needed for such a "complete description" was not given. Since branching occurs over a two year interval for most temperate tree species (see the "exception" discussed in Chapter 4), these processes can be classified by year. A description of first year growth of both trunk and branches includes the following variables:

1. the amount of extension growth at all crown positions,
2. the number of nodes formed,
3. the distance to each node, and
4. the azimuth of each node.

If the crown description is to include leaf display as well as branching, the following variables are also needed:

1. petiole length,
2. the angle of divergence between the petiole and the mother branch,
3. leaf size,
4. leaf inclination relative to gravity, and
5. leaf azimuth relative to gravity.

The azimuth of the leaf lamina must also be measured if leaf weight and petiole flexibility cause it to differ from the node azimuth.

And, if leaf inclination and azimuth are measured relative to the mother branch rather than relative to gravity, a measurement of the torque of the petiole and lamina must also be made. In the second year of branch formation the following variables are needed:

1. the number of daughter branches produced,
2. the node number of each daughter, and
3. the angle of divergence between the mother and daughter branch.

If, as is usually the case, the branches are not straight, then the azimuth relative to the mother should be remeasured as it will differ from the node azimuth. All variables describing year one growth must also be measured for each daughter. These second year branching variables must also be measured on any Type I proleptic branches formed during the first year. Cochrane and Ford (1978) have categorized these variables into three phases of branch growth: (1) production, which includes the number of branches produced; (2) dispersion, which includes branch azimuth and inclination; and (3) extension, which predicts the length of each branch.

What follows is a brief review of the processes governing these aspects of crown development.

## Elongation Growth: Pattern and Phenology

For a long time, it was assumed that plants made their total amount of seasonal extension growth in a single spurt which could be described by a sigmoid curve (Studhalter 1955). Richards (1969) attributed the first clear description of this "grand period of

growth" to Sachs (1874). Many of the earlier papers on tree extension growth used this terminology. For example, Friesner (1941-42) found that the growth of four species of Indiana pines "illustrated a grand-period type of behavior," and he then subset these curves into nine types. He mentioned that the "essential character" of the curves was not affected by the environment, but that environmental factors do affect curve shape. In a later paper (1943-44) he observed that growth of eastern white pine (Pinus strobus L.) and red pine (Pinus resinoa Ait.) departed from a "grand period" shaped curve. In his words:

> All previous studies of these species have shown the elongation of the primary axis to exhibit essentially a grand period type of curve while in these three trees each curve shows 3 waves of intensity, which do not have a very close resemblance to the grand-period type of curve.

After this work, other researchers questioned whether all trees follow this "grand period" type of curve, and indeed, they found a variety of types of growth curves. These shapes vary with species, individual, and crown position and are further modified by environmental factors (Kozlowski and Ward 1961).

Brown (1971b) classified elongation growth patterns of different species into four patterns. Growth may occur: (1) in a single flush followed by the formation of a resting bud, (2) in several flushes each of which is followed by the formation of a resting bud, (3) in a growth flush followed by shoot-tip abortion,

or (4) by a sustained growth flush in which late-formed leaves expand before terminal bud formation.

The growth curves of individual branches on a tree are also affected by crown position. For example, Friesner (1943-44) observed that: (1) current growth on primary branches decreased from tree tip to base (Trend 1 in Chapter 1), (2) second-order branches elongated less than primary branches, (3) second-order branches on older first-order branches elongated less than second-order branches on primaries above them, and (4) older second-order branches grew less than younger second-order branches, even though the younger second-order branches may have been on older primary branches. Although the duration of elongation varied between branches, the rate of elongation varied much more. Kozlowski and Ward (1961) found a decrease in amount of elongation growth with increasing branch order. Others have observed a decline in the duration of elongation growth with increasing branch order. Fraser (1962) and Forward and Nolan (1964) found that elongation growth at the tree tip began earlier, and ended later, than at the tree base.

Studies on tree extension growth have continued to the present. Critchfield (1960) examined heterophylly in Populus trichocarpa T. & G. and found two distinct peaks in internode lengths; the first internode formed between the early and late leaves was longer than those below or above it. He also found (1971) a distinct hiatus in leaf production and internode expansion between early and late leaf formation in red maple (Acer rubrum L.),

Borchert (1973) proposed a model to explain endogenous rhythms in shoot growth which assumed that this phenomenon was caused by feedback between two potentially limiting reactions. His predicted results (1975) agreed with observed patterns of shoot growth in pin oak (Quercus palustris Muench.). He later developed a computer program to aid in analysis of shoot growth patterns (1976).

Phyllotaxis

Leaves may be arranged along the stem in one of three phyllotaxes: they may form singly at an angle of 180 degrees from each other (distichous), form in pairs which are 90 degrees from each other (decussate), or form spirally around the stem. Of these three patterns, spiral phyllotaxis has received the most attention. As an interesting historical aside, Leonardo da Vinci (McMurrich 1930, MacCurdy 1936, both cited in Studhalter 1955) made an unsuccessful attempt to determine branch age from phyllotaxis. Braun (1831) and Schimper (1836) are credited with putting the study of phyllotaxis on its modern basis (Sinnott 1960). They proposed the rule that the angle of divergence between two consecutive leaves is a rational fraction of 360 degrees (Snow 1955). This fraction is determined by connecting the centers of leaves in the order of their formation (Snow 1955) to form the ontogenetic, or genetic spiral. After a fixed number of turns have been made in the spiral, a leaf will be reached which is directly above the first leaf in the series. This phyllotaxis is expressed as a fraction in which the numerator gives the number of turns of the spiral between

overlapping leaves and the denominator gives the number of leaves encountered in the process. Distichous phyllotaxis is represented as the Braun-Schimper fraction 1/2. Other observed fractions are 1/3, 2/5, 3/8, and 5/13. These fractions form a series in which both the numerator (or denominator) is the sum of the numerators (or denominators) of the previous two fractions. The numbers used in this series (1, 1, 2, 3, 5, 8,...) are the numbers of the Fibonacci series in which each number is the sum of the preceeding two.

A second approach used to study phyllotaxis examines leaf primordia in the bud, or in other specialized circumstances where the phyllotactic spiral can be observed clearly (e.g., at the base of a pine cone or in a sunflower head). Snow (1955) used this technique to observe that the angles of divergence between leaf primordia do not support Braun and Schimper's rule. Angles of divergence do not fall into clearly defined groups but approach the number 0.382 (the "golden mean") which defines the angle 137.5 degrees. It can be observed that, with the exception of a few special cases, all the Braun-Schimper angles are practically the same.

By this second approach, two intersecting logarithmic spirals are observed. Beginning with the most recently formed plant part (e.g., leaf primordia, cone scale, or seed), the number of elements in each of these spirals (parastichies or contact parastichies) are counted up to the plant part where the two curves intersect, and these numbers are then expressed as a fraction (e.g., 3/5). Fractions formed by this method also use the numbers of the

Fibonacci series, but these fractions differ from the Braun-Schimper series in that the denominator of one fraction becomes the numerator of the next (e.g., 2/3, 3/5, 5/8, etc.). Several researchers have noted that this series converges to 0.618, the complementary fraction formed by the "golden mean" (1.0 -the "golden mean"). Some have speculated that the angle (137.5 degrees) formed by the "golden mean" optimizes leaf display. Thompson (1952) disagrees. In his words:

> While the Fibonacci series stares us in the face in the fir-cone, it does so for mathematical reasons; and its supposed usefulness, and the hypothesis of its introduction into plant-structure through natural selection, are matters which deserve no place in the plain study of botanical phenomena.

Reviews of phyllotaxis can be found in Richards and Schwabe (1969), Sinnott (1960), and Snow (1955). A recent work in this area is Williams (1975).

Branch Inclination

Branch inclination is the angle (measured from the vertical) that a branch, or branch section, forms with a line of gravity passing through the point of measurement. Several terms have been used to describe these angles, and these depend on the location of the measurement on the branch. Burtt (1899, in Brown 1971a) called the angle formed in the middle course of growth the "angle of inclination" and the angle formed by the branch tip the "geotropic angle." Polk (1974) defined the "angle of origin" as the angle made by the branch at its point of insertion along the stem and defined

the "angle of termination" as the angle formed by a line connecting the branch tip to its origin. Jankiewicz and Stecki (1976) have illustrated that the angle of origin or "crotch angle" may change with tree age simply because the branch becomes embedded in the trunk. A complete description of branch curvature would include branch inclinations at all branch positions. Recently, Burk et al. (1983) developed a method to model branch inclination by assuming constant curvature.

Branch angles are under genetic control but are also influenced by environmental factors. Genetic variation may be seen among cultivars and even within the same tree (Kramer and Kozlowski 1979). Many morphological processes have interacted to produce the branch inclination observed at any given time, and information on these processes has been summarized by Brown (1971a), Jankiewicz and Stecki (1976), and Kramer and Kozlowski (1979). Jankiewicz and Stecki reported that the direction of branch growth is determined by the angle the branch forms with the trunk and the amount the branch will bend. In pines, crotch angles often widen during the first year of growth. This is accomplised through two mechanisms. First, newly formed tissue in the branch crotch exerts a mechanical downward pressure on the branch. Second, reaction wood is formed, perhaps as a response to basipetally transported auxin produced by the leader (Jankiewicz and Stecki 1976, Wareing 1970). This influence of the leader on branch inclination is an example of epinasty. These downward forces exerted at the base of the branch are opposed by reaction wood formation on the lower side of older branches and also

by branch thickening. At the branch apex, growth is upward in response to gravity (negative geotrophism). The net result of these processes produces the branch inclination observed at any given time. This angle may increase in winter due to the weight of any snow load. In subsequent years, branch inclination increases under the weight of new needles, and this force is countered by reaction wood formation.

Similar processes determine branch inclination in woody angiosperms. One difference in this group is that negative geotropism is often countered by geo-epinasty. This process causes downward branch growth (Jankiewicz and Stecki 1976), and its strength is correlated to branch order (higher-order branches are less geotropically active, Brown 1971a).

Branch inclination, in turn, affects branch physiology. Horizontal branches have less extension growth and greater reproductive growth, a fact well known by fruit growers. Another effect of inclination on physiology is the fact that after displacement from the vertical, buds on the underside of a stem are often released (an example of reiteration, sensu Halle et al. 1978).

Branch angles also change with tree age and competition. Moorby and Wareing (1963) described three processes associated with tree aging. The first of these, reduced annual growth, was mentioned above. The second, loss of apical dominance, may affect branch angles through a decreased epinasty. The third, change in geotropic response, results in increased branch angles. As an example of this third effect, it is often observed that top branches are often

vertically oriented and that branch angle increases basipetally (similar to the Type 3 Duff and Nolan sequence discussed in Chapter 1). This is true for both woody angiosperms (e.g., Quercus rubra L., Ward 1964) and conifers (e.g., Picea sitchensis (Bong.) Carr., Cochrane and Ford 1978). Competition also affects branch angle. Nelson et al. (1981) observed an increased angle of origin and a decreased angle of termination at wider spacings with Populus clones.

The purpose of this chapter is to give a "complete description" of sycamore branching. Statistical models will be developed which describe each aspect of branch growth listed in the Introduction to this chapter. These models will then be used as the basis of the simulation model developed in Chapter 6. Where possible, variables which represent the processes discussed in the introduction to this chapter will by entered into the analyses.

## Materials and Methods

Chapter 2 discussed the procedures used to select study trees and branches, and also listed the variables measured on each branch. The methodology used to analyze these data will be given in each of the following sections.

## Results and Discussion

### Extension Growth

Figure 5.1 shows the annual growth of the primary branches on the study trees. In this figure, the 1-year-old section (current

Figure 5.1. Branch annual growth increments (AGI) for all primary branches. (a) Trunk age = 2 (TA2). (b) TA3. (c) TA4. (d) TA5. (e) TA6. Type I branches are marked with a boxed "X" and Type II branches are marked with an "X."

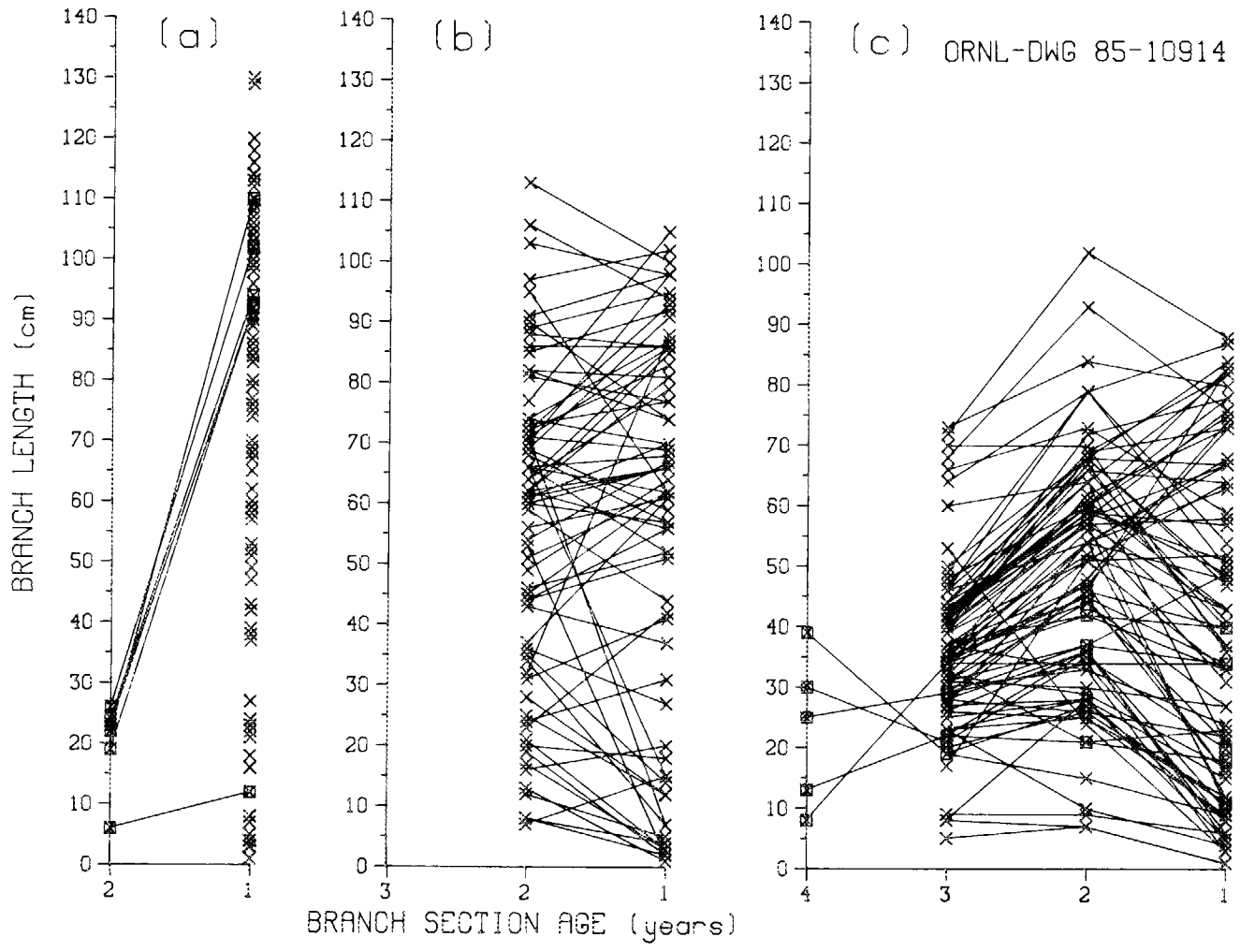
(a)
(b)
(c)
ORNL-DWG 85-10914
BRANCH LENGTH (cm)
BRANCH SECTION AGE (years)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
1
2
3
4

Figure 5.1

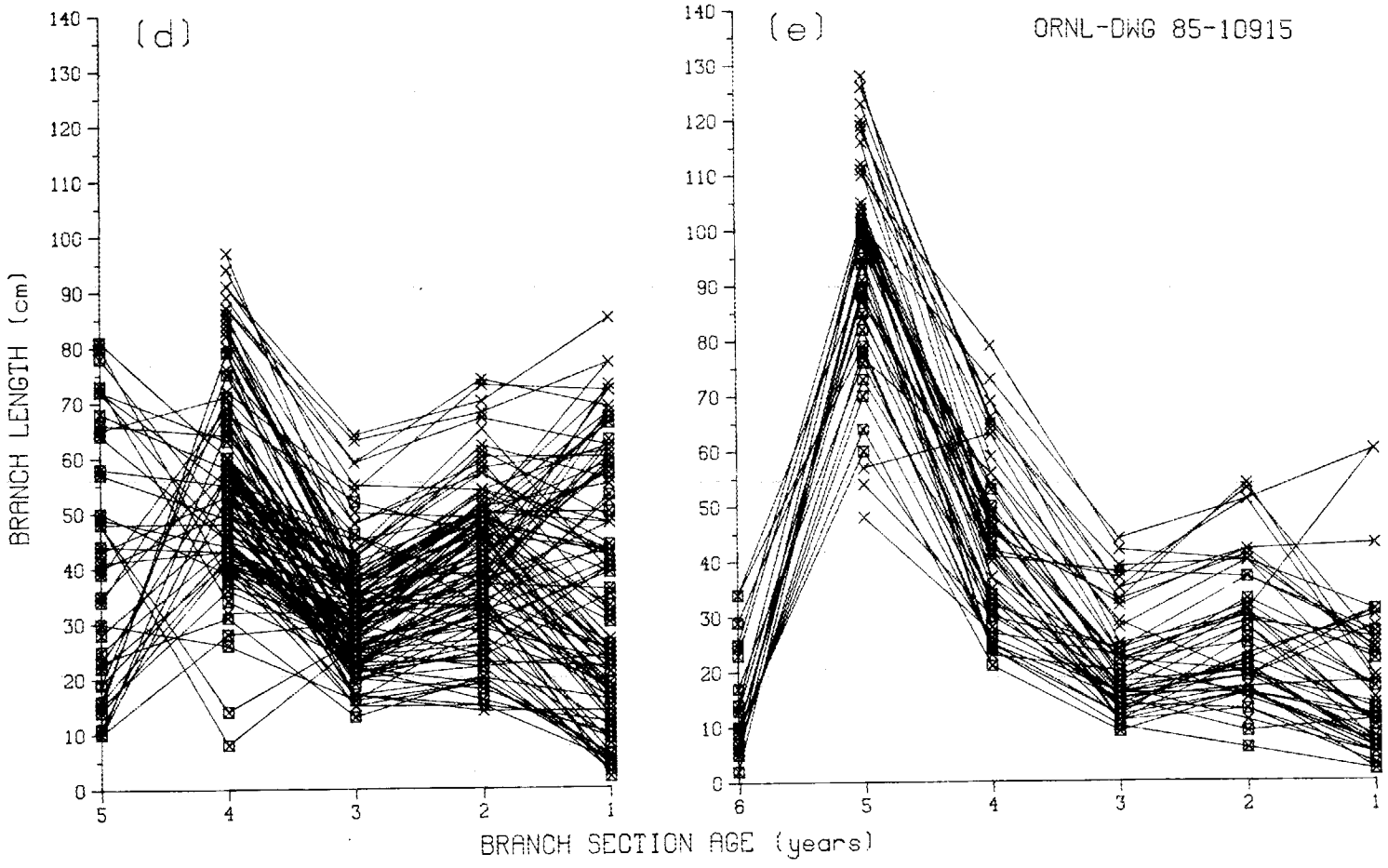


Figure 5.1 (continued)

growth) of a branch is marked Branch Section Age = 1, the 2-year-old section is marked Branch Section Age = 2, and so forth. All measurements on a given branch have been connected with a solid line. Observations on Type II proleptic branches (Chapter 4) have been marked with an "X," and those on Type I proleptic branches have been marked with a boxed "X." Several generalizations can be made from this figure. First, in most cases, the length of Type I proleptic branches is much less in their first year of growth than in the following year. This is probably due to the fact that these branches could elongate for only part of the growing season; some time had elapsed before the bud had formed and more time lapsed during the (brief) rest period. Second, the decrease in length of successive annual growth increments (AGI's) is exponential. This is especially evident for the 5-year-old branches. A third observation is that climate affects branch elongation growth. Chapter 3 discussed the theory behind this concept and demonstrated that sycamore height growth is related to soil moisture. Values for the DUR soil moisture index (see Chapter 3) for years 1978 to 1982 are: 0.74, 1.00, 0.42, 0.85, and 1.00. The reduction in elongation growth due to the 1980 soil moisture deficit can be clearly seen in Figure 5.1.

A multivariable regression analysis was performed to model mean branch growth. Soil water availability, cultivation, and fertilization affect extension growth (Chapter 3). These whole-tree effects were accounted for by scaling (dividing) branch AGI length

by the length of the tree leader AGI. This technique implicitly adds these environmental effects to branch growth through their effect on leader growth. Previous work (Schutt, unpub. man.) has shown that the amount of first-year extension growth of the primary branch is a function of the distance from the base of the trunk AGI to that branch; branches near the tip of a trunk AGI section are longer than those below it. This can be observed in Figure 2.4 (see pages 29-34). Because several observations were taken on each branch, the regression assumption of independence was violated. This difficulty was circumvented by assuming that the relationship between branch length and distance to that branch (mother node distance (MN)) held for other years of branch growth. This model is more flexible than the previous work in that it allows the curve shape to vary. The further hypothesis was made that this branch position effect also holds for extension growth of second- and higher-order branches. This was accounted for in the model by including all "ancestor" node distance terms (grandmother (GN), great-grandmother (GGN), great-great-grandmother (GGGN)). It will be shown later in this chapter that branch length is a good predictor of the number of nodes or the number of daughters formed on a branch section. Because of this relationship, mother length (ML) may also affect subsequent daughter branch length. This hypothesis was also tested by the regression. The exponential decay observed in Figure 5.1 was entered as the variable branch age (BA). Further hypotheses were made that the slopes and intercepts of these variables differed with branch order and with branch section age

(parent age = PA) within order. These variables were added to the model. A multiplicative model was chosen and analyzed by taking the natural logarithm (indicated by the prefix LN on the variables) of all variables. The full model contained the following terms: branch order (ORDER); parent age (PA); mother, grandmother, great-grandmother, and great-great-grandmother node distances (LNMN, LNGN, LNGGN, LNGGGN); ancestor lengths (LNML, LNGL, LNGGL, LNGGGL); and branch age (BA).

Results from this analysis are shown in Table 5.1. The full model is highly significant ($p \leq 0.0001$) and accounts for 79% of the variation in the data. Several interesting observations can be made from this table. One is that the predictive power of the "ancestor" variables decreases with each generation from the daughter branch. This says, for example, that if a primary branch can survive to produce a fourth-order branch, the position of the fourth-order branch on the third-order branch is a better predictor of the length of that fourth-order branch than the position of its first-order ancestor on the trunk. This table also demonstrates that branches of different orders and branches on different parent ages within each order differ in their slope and intercept. A partial explanation for this may be the nature of the data in that it contains branches of different ages. For example, 1-year-old primaries vary in length from small branches near the AGI base, to longer branches near the AGI tip (this is an example of the mother node position effect described above). On the other hand, the measured 5-year-old primaries are those which have undergone several

Table 5.1. Results from the regression predicting branch growth (expressed as a percent of leader growth) from branch order, percent age, "ancestor" node distances, "ancestor" lengths, and branch age. See the text for an explanation of the terms.

| Source of Variation | df | Sum of squares: Full model | Sum of squares: Type III | MS | F |
|---|---|---|---|---|---|
| Model | 79 | 5999.843 | | 75.947 | 162.22*** |
| ORDER | 3 | | 30.595 | 10.198 | 21.78*** |
| PA (ORDER) | 6 | | 15.817 | 2.636 | 5.63*** |
| LNMN (ORDER) | 4 | | 490.334 | 122.584 | 261.84*** |
| LNGN (ORDER) | 3 | | 6.460 | 2.153 | 4.60** |
| LNGGN (ORDER) | 2 | | 2.549 | 1.274 | 2.72$^{ns}$ |
| LNGGGN (ORDER) | 1 | | 0.464 | 0.464 | 0.99$^{ns}$ |
| LNML (ORDER) | 4 | | 25.074 | 6.269 | 13.39*** |
| LNGL (ORDER) | 3 | | 2.477 | 0.826 | 1.76$^{ns}$ |
| LNGGL (ORDER) | 2 | | 1.017 | 0.509 | 1.09$^{ns}$ |
| LNGGGL (ORDER) | 1 | | 0.497 | 0.497 | 1.06$^{ns}$ |
| BA (ORDER) | 4 | | 190.117 | 47.529 | 101.52*** |
| LNMN (PA * ORDER) | 9 | | 90.873 | 10.097 | 21.57*** |
| LNGN (PA * ORDER) | 5 | | 4.642 | 0.928 | 1.98$^{ns}$ |
| LNGGN (PA * ORDER) | 0 | | - | - | - |
| LNGGGN (PA * ORDER) | 0 | | - | - | - |
| LNML (PA * ORDER) | 9 | | 37.809 | 4.201 | 8.97*** |
| LNGL (PA * ORDER) | 5 | | 3.552 | 0.710 | 1.50$^{ns}$ |
| LNGGL (PA * ORDER) | 2 | | 0.385 | 0.193 | 0.41$^{ns}$ |
| LNGGGL (PA * ORDER) | 0 | | - | - | - |
| BA (PA * ORDER) | 6 | | 8.538 | 1.423 | 3.04** |
| Error | 3359 | 1572.584 | | 0.468 | $R^2$ = 0.792 |
| Total | 3438 | 7572.426 | | | |

$^{ns}$Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

years of branch death, and in this process the probability of survival is greater for longer branches (Schutt, unpub. man.). Consequently, these older branches will probably have a more homogeneous length (at least for their oldest lengths) than will the 1-year-old branches. Branches of all ages are needed to estimate the effect of mother length. The 5-year-old branches add more information on the shape of the decay curve, whereas the 1-year-old branches yield more information on the effect of position on first year growth. Repeated measurements made on the annual extension growth a cohort of branches are needed to develop a better model for this variable.

To parameterize the equation for the tree branching model, the regression was rerun, deleting all terms that were non significant in the first analysis. The parameter estimates for the LNMN term for order 1 to order 4 branches are: 1.47, 1.27, 0.84, and 0.08. An exponent greater than one indicates that the branches near the AGI tip dominate; branches get proportionately longer with increasing distance to the AGI base. The small exponent for order 4 branches may be due to small sample size. This analysis confirms the observation that branch length increases with distance from the AGI base.

This pattern of decreasing organ size with increasing distance from the tip has been observed by others. It has been found for inter-whorl branch lengths among conifers (Baxter and Cannell 1978, Cochrane and Ford 1978, Jensen 1976, Powell 1977), for branch length in woody angiosperms (Caesar and Macdonald 1984, Isebrands and

Nelson 1982, Jankiewicz and Stecki 1976, Nelson et al. 1981), and for bud size (Gill 1971). The pattern of increasing branch length within an AGI is called acrotony and appears to be due to differences in bud size and/or ability to attract assimilates (Jankiewicz and Stecki 1976). At one extreme in the range of expression of acrotony, some species, such as Ailanthus altissima (Mill.) Swingle and Aralia spinosa L., may produce only one or two daughter branches which are located near the AGI tip. Acrotony probably is advantageous in that it allows for display of photosynthetic surface throughout the stem while concentrating most of that surface near the crown periphery. In woody angiosperms, these long primary branches often grow to compete with the leader (Brown 1971a).

Trees have many trade-offs available to them to develop an optimum photosynthetic area and mechanical support of that area. P. White (1983) has shown that correlations exist between twig thickness, leaf size, and branching density in trees of the eastern United States. Whitney (1976) has suggested that the rachis of a compound leaf may be the functional equivalent of the long, slender shoot produced in some species. The rachis may differ from those shoots in that it is a "disposable" organ in the sense that it does not contribute to the final geometry of the tree. Acrotony may be another advantageous branching strategy. The lower, shorter shoots may also be disposable, yet unlike the compound leaf's rachis, it may function for more than one year. The longer shoots have a longer life expectancy and may function in crown expansion.

Previous work (Schutt, unpub. man.) has confirmed that primary branch death in sycamore (Platanus occidentalis L.) is concentrated on the lower, shorter branches on an AGI. This previous work also confirmed the observation that the amount of annual branch growth declines with increasing branch age.

Other researchers have observed a decrease in branch AGI length with increasing branch age (e.g., Powell 1977) and three have modeled it. Jensen (1976) predicted branch length in Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) with the equation:

$$Y = 438.0 - 319.0(\log X)$$

where Y is internode length (AGI) and X is internode number from the bole (BA). Fisher and Honda (1977) modeled the dichotomous branching of Terminalia catappa L. as the ratio of the daughter branch length to the mother length. Their branching ratios of 0.94 and 0.87 can be translated into the equation:

$$Y = a^X$$

where Y and X are as above, and a is the branching ratio. Cochrane and Ford (1978) defined the relative extension rate (G(I)) of whorl and interwhorl branching as:

$$G(I) = \frac{\text{Branch increment in the } i^{th} \text{season}}{\text{Average length of branch in } i^{th} \text{season}}$$

where:

$$G(I) = (0.6250)(1.1377)^{-I} \qquad 2 \leq = I \leq 8$$

for whorl branches and:

$$G(I) = (2.1727)(1.7082)^{-I} \qquad 2 \leq = I \leq 4$$

for interwhorl branches. The current analysis is an improvement over these models in that it includes branches of all orders and in that it also scales branch growth by leader growth (and in doing so includes the effects of climate, cultivation, and fertilization on branch extension growth).

Physiological explanations have been given to describe the decrease in annual branch growth with increasing branch age. Moorby and Waring (1963) described the "marked reduction in the annual increments of extension growth" as a defining characteristic of tree aging. In Scots pine (*Pinus sylvestris* L.) this was observed first on higher-order branches, and it spread in an acropetal direction until the whole branch was affected. Grafting experiments have shown that this is a reversible process. Moorby and Wareing also conducted pruning experiments to demonstrate that this phenomenon is a result of increasing intra-branch competition for available nutrients with increasing branch complexity. Apical dominance ("control," sensu Brown et al. 1967) also modifies nutrient distribution. Many observations are present which support the hypothesis that this intra-crown competition is for root-originated metabolites (Jankiewicz and Stecki 1976). Jensen (1976) hypothesized that the decrease in annual branch growth was due to physiological changes occuring in the branch as well as to changes in the relative position of the growing tip with respect to the

tree's leader. He listed potential physiological changes as: increasing apical age, mechanical changes in the transport system, and reallocation of growth substances from extension to radial growth. He argued that competition from neighboring trees or self-shading was not the cause because this trait was observed on even the youngest branches.

The decrease in annual branch extension growth has also been explained from a metapopulational (sensu J. White 1979) viewpoint. J. White (1980) generalized that module size decreases with increasing module number. Borchert and Slade (1981) have shown that branching rate must also decline with plant age to avoid intra-tree competition. These two principles have been validated from field observations. For example, Gunckel et al. (1949) observed a reduction in the long shoot/short shoot ratio in *Ginkgo biloba* L. They attributed this to inhibition of sub-terminal branch growth by terminal long shoots, an effect controlled through auxin production. Wilson (1966) observed this same phenomenon in red maple. P. White (1984) also noted a decrease in extension growth with increasing annual growth number in *Aralia spinosa*. Observations of this type have led J. White (1980) to conclude that the number of branches on a tree becomes asymptotic with increasing plant age.

## Number of Nodes

The number of nodes borne on a branch increases with branch length. The density of those nodes (number of nodes/branch increment

length) may also change with branch length. Data presented in P. White (1984) suggest that this is true for Aralia spinosa. He found the node density of the first mean annual increment to be 0.13 nodes/cm (10 leaves/75cm) whereas the density of later increments was 0.24 nodes/cm (6 nodes/25 cm). Only two regressions were found in the literature which predict number of nodes from branch length (Powell 1977, Ward 1964). In both of these regressions, the number of nodes formed was a linear function of branch length.

The purpose of this section is to develop a model to predict node density. Since this density may vary with branch length, a logarithmic multiplicative model was chosen because of its flexibility. The effect of branch length on node density was included by adding the logarithm of branch length (LNLEN) as an independent variable. Chapter 3 demonstrated that both fertilization/cultivation and climate influence height growth. Node density may also vary with these effects. To test this hypothesis, the early rotation fertilization/cultivation effect was added as a FERT = 2 class effect and the absence of this effect was entered as FERT = 0. The DUR soil moisture index developed in Chapter 3 was also used in this analysis to account for climatic effects. Another random class variable (TREE) was added to account for any data dependencies due to differences in trees.

Table 5.2 gives the ANOVA for the regression equation. The parameterized equation is:

$$\ln(\text{NNODES/LENGTH}) = e^{0.390} \cdot \text{LENGTH}^{-0.440} \cdot e^{b_2} \cdot \text{DUR}^{0.103} \cdot e^{b_4}$$

Table 5.2. ANOVA table for the regression predicting the node density (ln (number of nodes/branch length)) from branch length (LNLEN), fertilizer (FERT), climate (LNDUR), and tree (TREE) effects.

| Source of Variation | df | Sum of squares: Full model | Sum of squares: Type III | MS | F |
|---|---|---|---|---|---|
| Model | 12 | 230.272 | | 19.189 | 843.69*** |
| LNLEN | 1 | | 203.090 | 203.090 | 8929.17*** |
| FERT | 1 | | 1.289 | 1.289 | 56.69*** |
| LNDUR | 1 | | 1.064 | 1.064 | 46.79*** |
| TREE | 9 | | 2.527 | 0.281 | 12.35*** |
| Error | 966 | 21.971 | | 0.023 | $R^2$ = 0.913 |
| Total | 978 | 252.243 | | | |

***Significant at 0.001 level.

where $b_2$ is the fertilization/cultivation effect (0.0 for FERT = 2 and -0.321 for no fertilizer) and $b_4$ is the TREE effect (distributed lognormally with mean = 0.0 and variance = 0.00269). By far, the LNLEN term accounted for most of the predictive power of the equation. This is due to the high association between branch length and number of nodes on the branch (Figure 5.2). The negative sign of this exponent means that ln(node density) decreases as LNLEN increases; longer branches have a lower node density. This observation was verified in the analysis of node position given in the following section and will be discussed further at that point. This fact also correlates well with the observation made from P. White above. It may also be true that these longer branches (with their lower node density) hold leaves which are larger than average. The sign of both the fertilization/cultivation and soil moisture index parameters is positive, indicating that both fertilization/cultivation and increasing soil moisture availability increase node density. (The fertilization/cultivation term increases from no-fertilization/cultivation effect of -0.321 to a fertilization/cultivation effect of 0.0.) Presumably, under better growing conditions, the trees can have a higher leaf density. The significance of the TREE term indicates that individual trees differ in their node density; some trees produce nodes closer together than others. This trait may be genetically determined.

Node Position

As mentioned earlier in this chapter, many authors have measured shoot length or shoot growth rate through the growing

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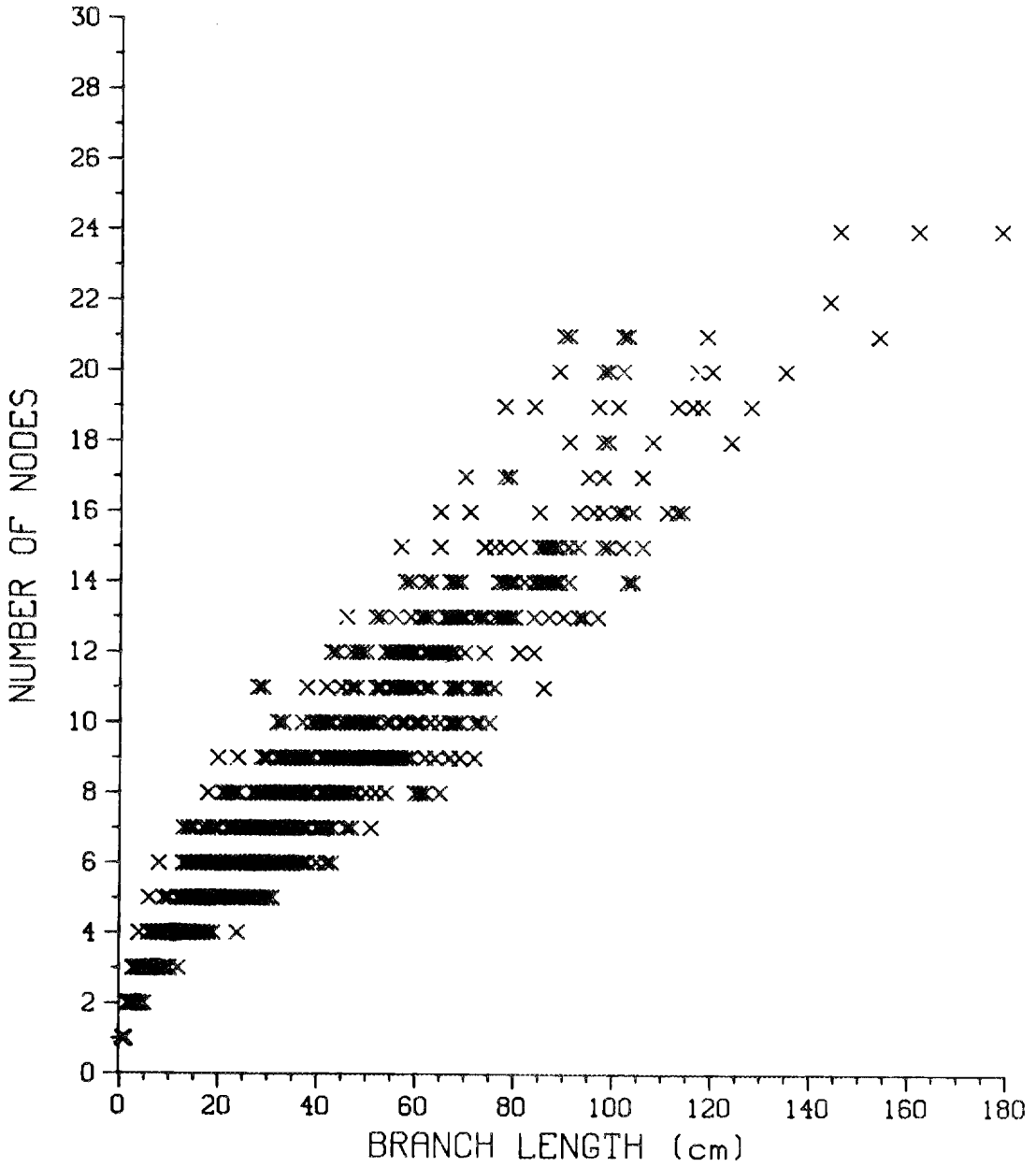


Figure 5.2. Relationship between branch section length and number of nodes on the branch section.

season. Although this is so, few studies give node positions along those branches. Early work is qualitative. Ward (1964) cites Busgen and Munch (1929) who wrote that it is "well known that on any given shoot the length of internodes tends to be relatively small near the apex, greater in the middle, and small near the base of the season's shoot." It must be kept in mind, however, that at this time growth was considered to follow a "grand period" curve. This is not true for all species. Fisher (1978) presented data showing that the length of the first internode in Terminalia catappa was greater than 25 cm, and that subsequent internodes were spaced less than 1 cm apart. Baxter and Cannell (1978) observed increasing internode length towards the stem apex in Sitka spruce (Picea sitchensis (Bong.) Carr.). Powell (1977) reported that the nodes were distributed uniformly on branches with four or more buds but became more concentrated near the apex. Critchfield (1971) observed that shoots of striped maple (Acer pensylvanicum L.) with more than seven nodes had two distinct peaks in internode length. He cited previous work of his which found this to be true for longer shoots of Populus trichocarpa (1960) and Ginkgo biloba (1970). Borchert (1976) developed a computer program to analyze shoot growth and gave examples of node positions, but in his example with pin oak, the length to the first internode after each growth flush really is the sum of two or three internodes. The purpose of this section is to examine node position on branches of various lengths in American sycamore.

Graphs were drawn to show node position for branches with 5, 8, 11, 14, and 17 nodes. On branches with only 5 nodes, internode distances increased with node number. The other curves appeared to be sigmoidal in shape. An early attempt was made to model this response by fitting linear, quadratic, and cubic curves through these data by the method of Grizzle and Allen (1969). This approach failed on two counts: a lack of fit was observed for several of the models (for all three curves for the data with 11 nodes), and the $Q_1^{-1}$ matrix was not positive definite for the class with 17 nodes, so no model could be fit for those data.

In a second attempt to model node position, the data for each node class were replotted as relative node position (node number /number of nodes) versus relative node distance (node distance /branch length) to determine if the curves followed a previously described general family of curves. The curves were "standardized" because the branches of any node class differed in length. In addition to these curves, the first differences (slopes) were also plotted (Figure 5.3). A subset of only approximately six curves are shown in each of these graphs.

At this point it should be noted that internode distance is a function of several variables. In species with preformed buds, the number of nodes is determined in one growing season, and weather of the second growing season influences internode distances. By contrast, in sycamore (and other species with free growth), both the number of nodes and internode distance are related to current weather. The distance between two nodes in these species is a

Figure 5.3. Relative node distance and slope plotted against relative node position for the node classes. The heavy lines are the mean responses for all observations on that node class. Lighter lines are a subsamples of branches. For node classes with few observations, all data are plotted.

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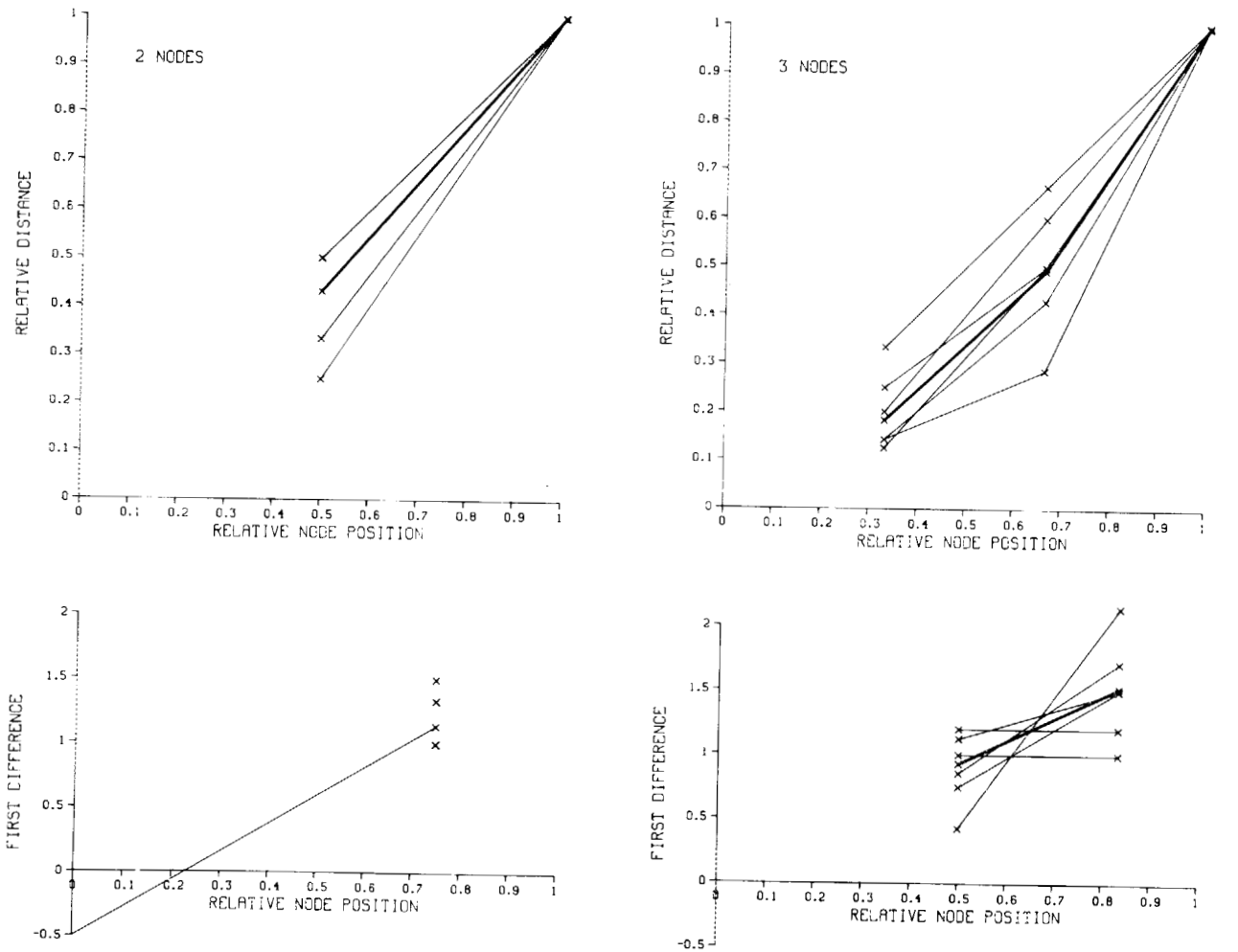


Figure 5.3

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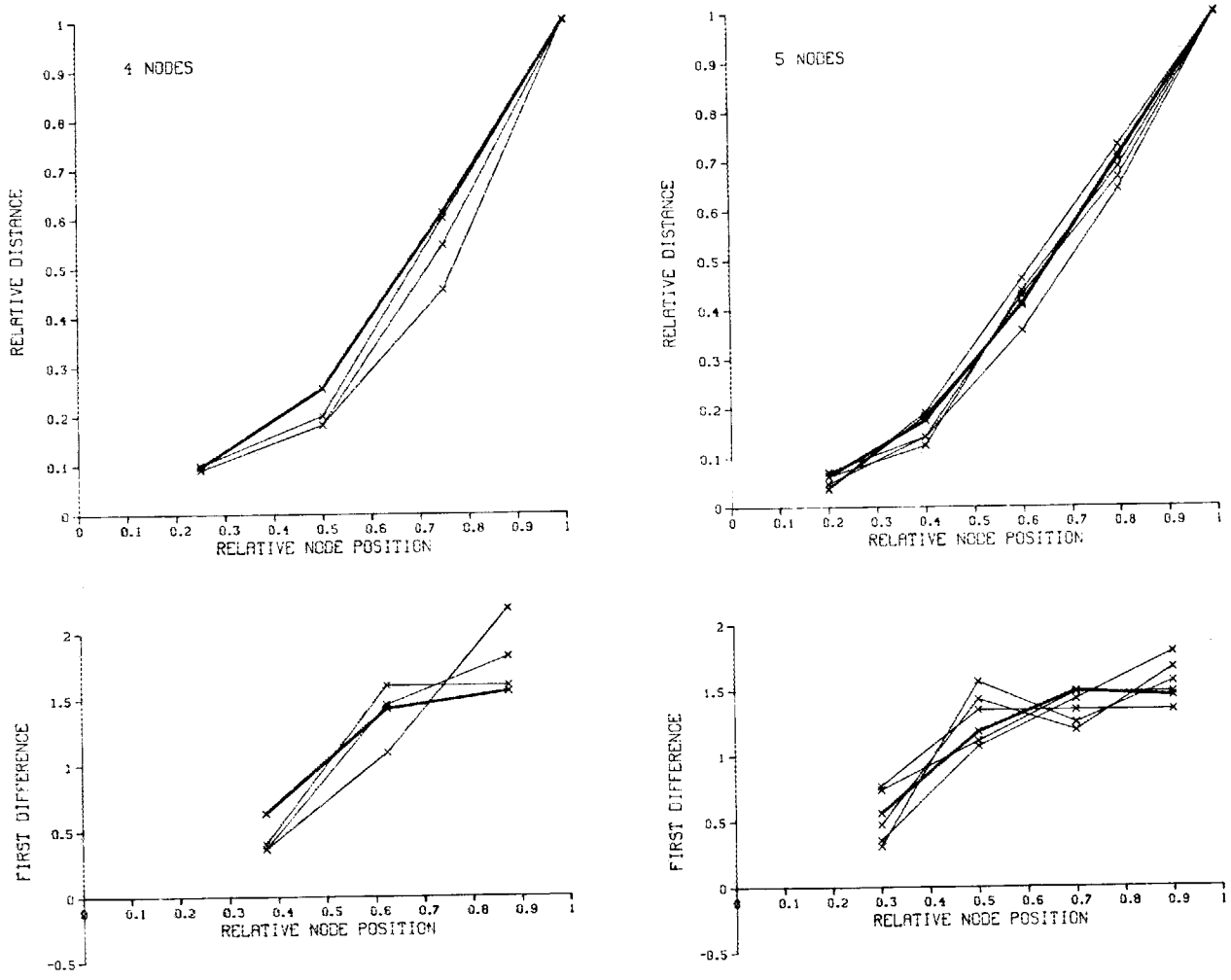


Figure 5.3 (continued)

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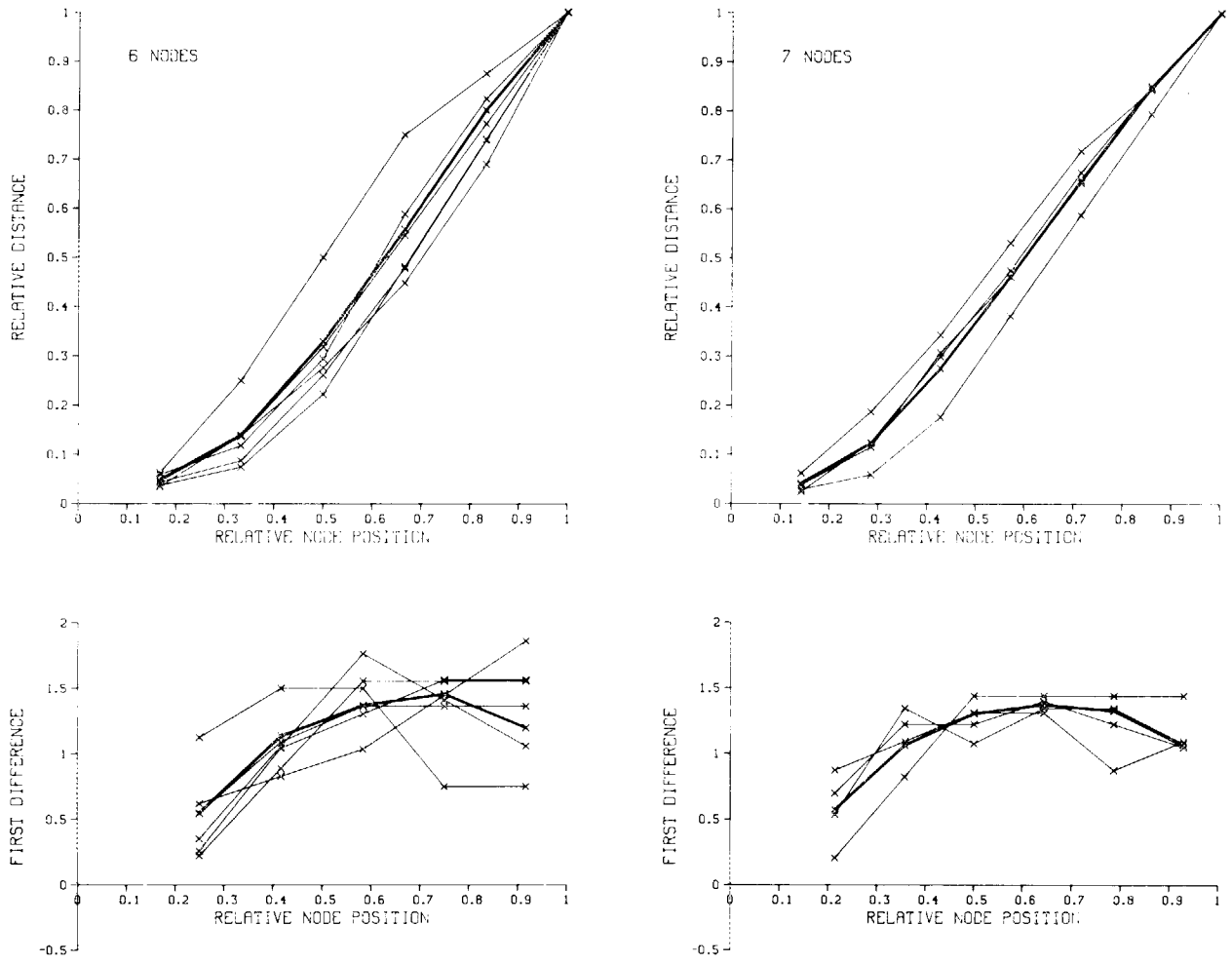


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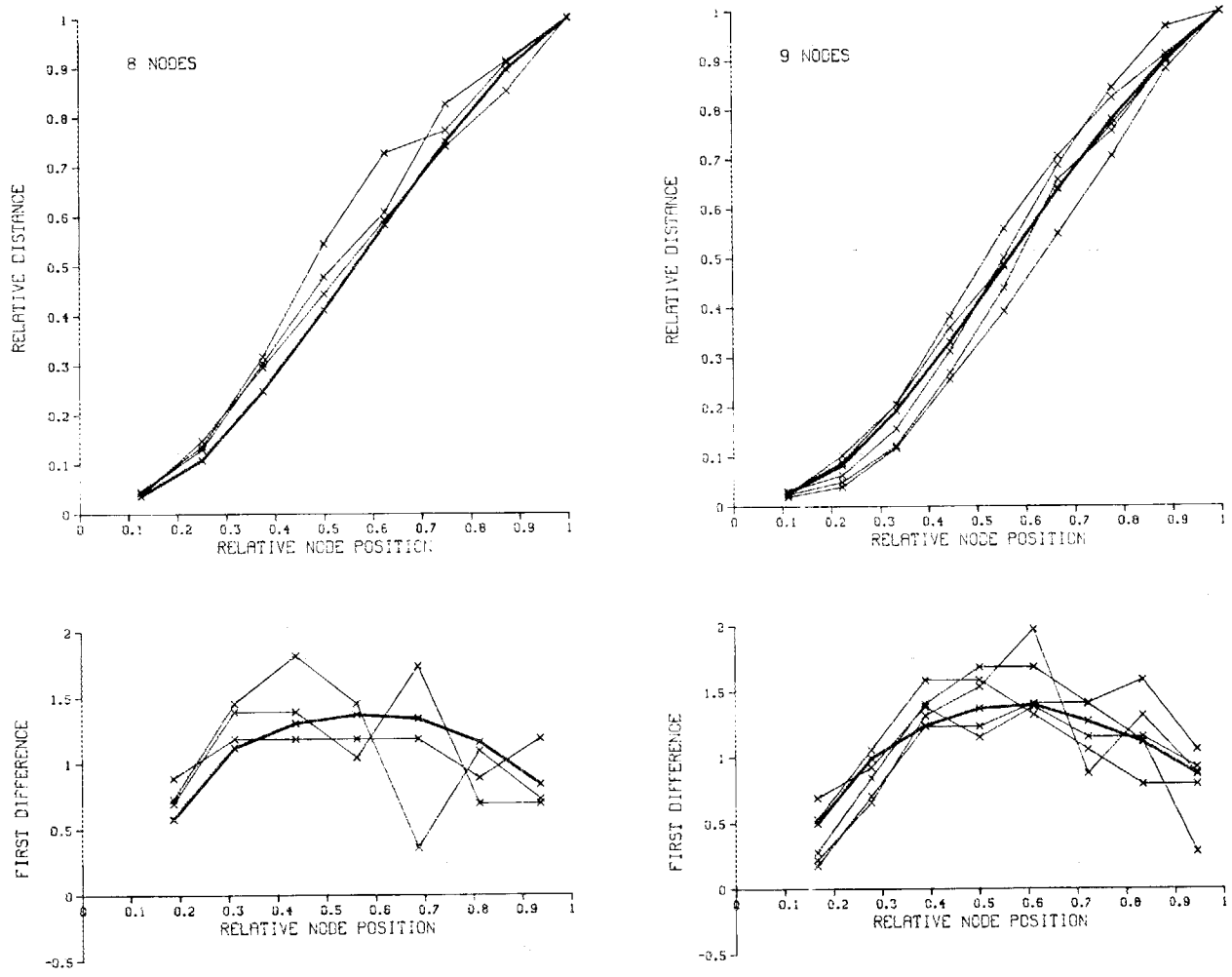


Figure 5.3 (continued)

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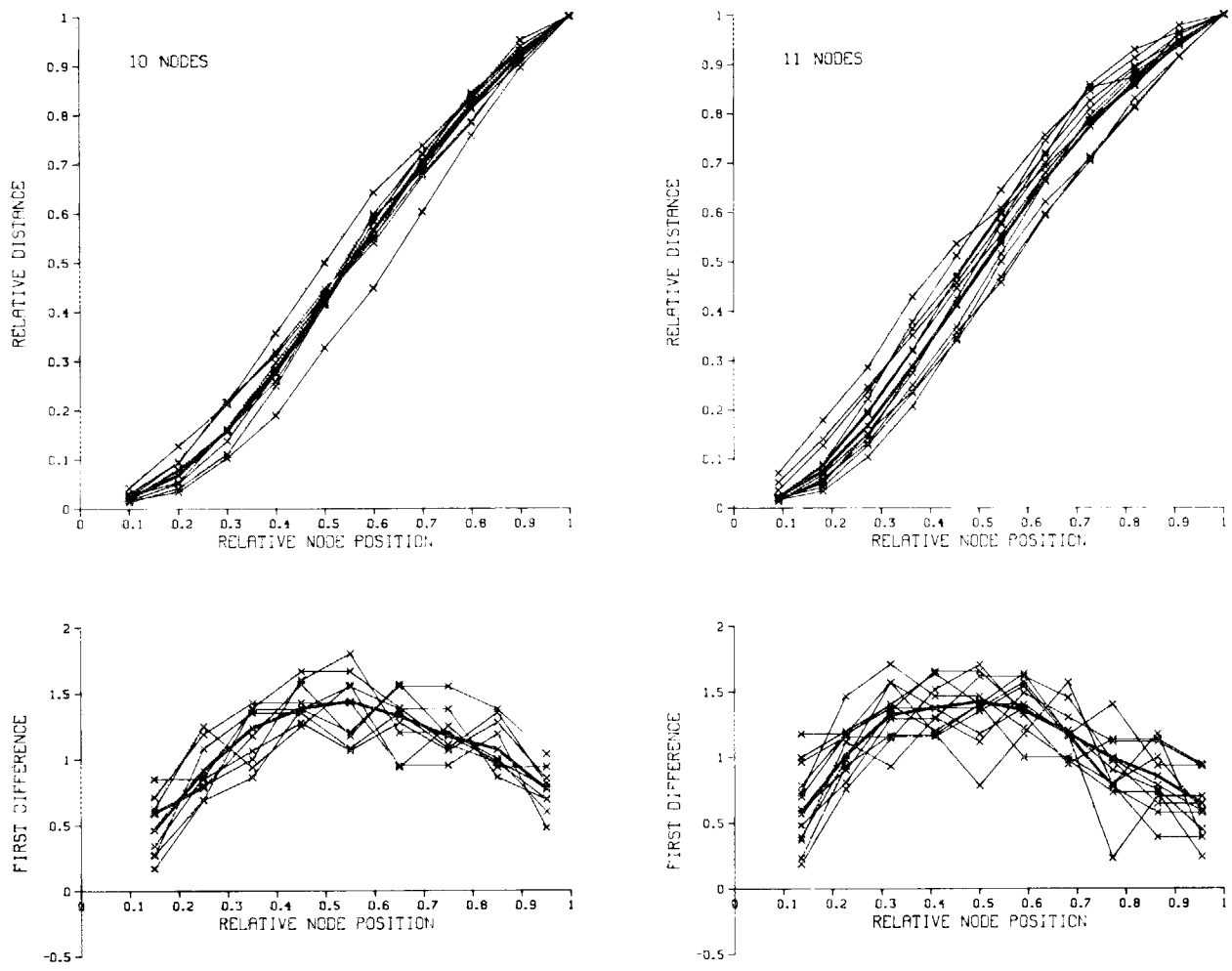


Figure 5.3 (continued)

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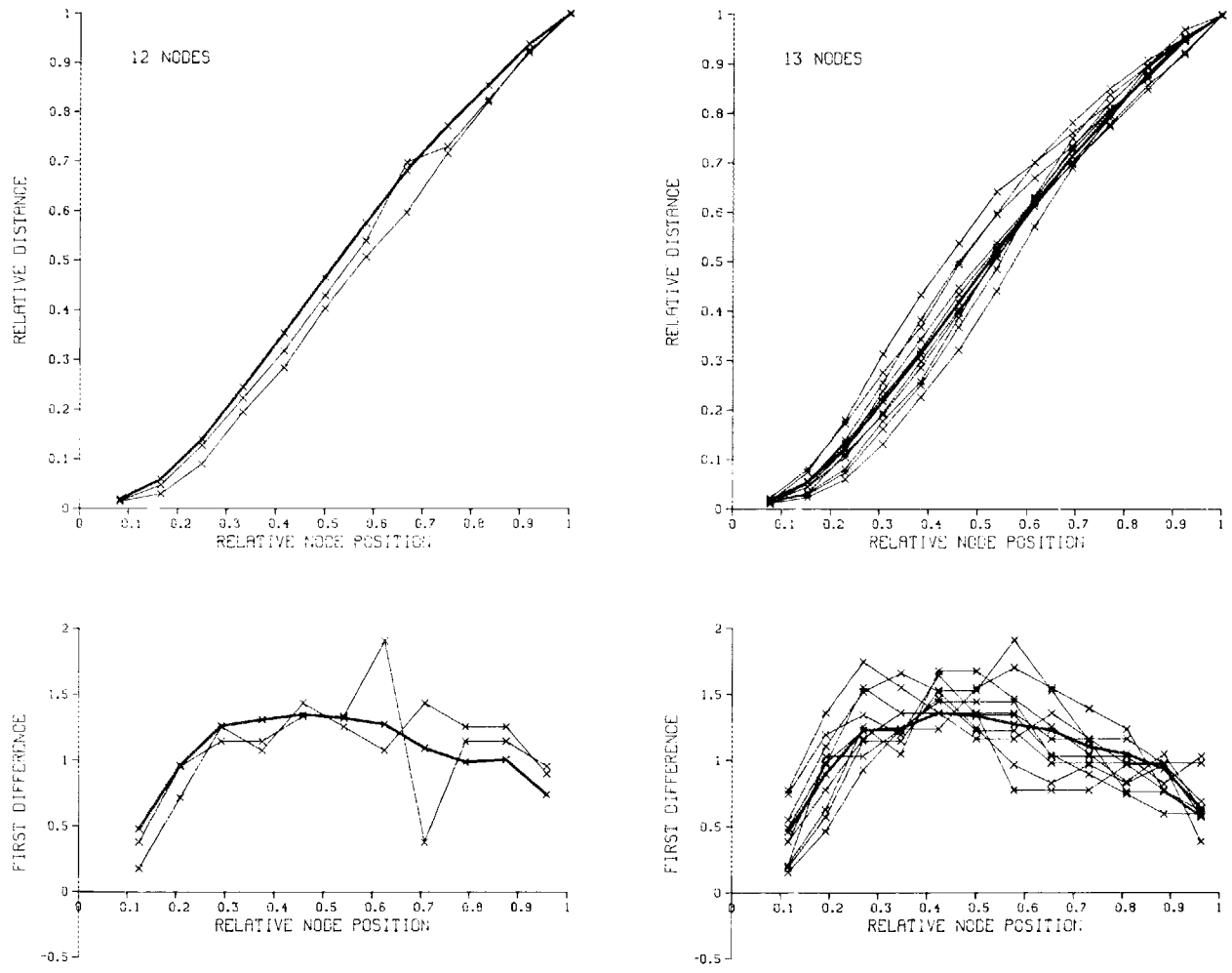


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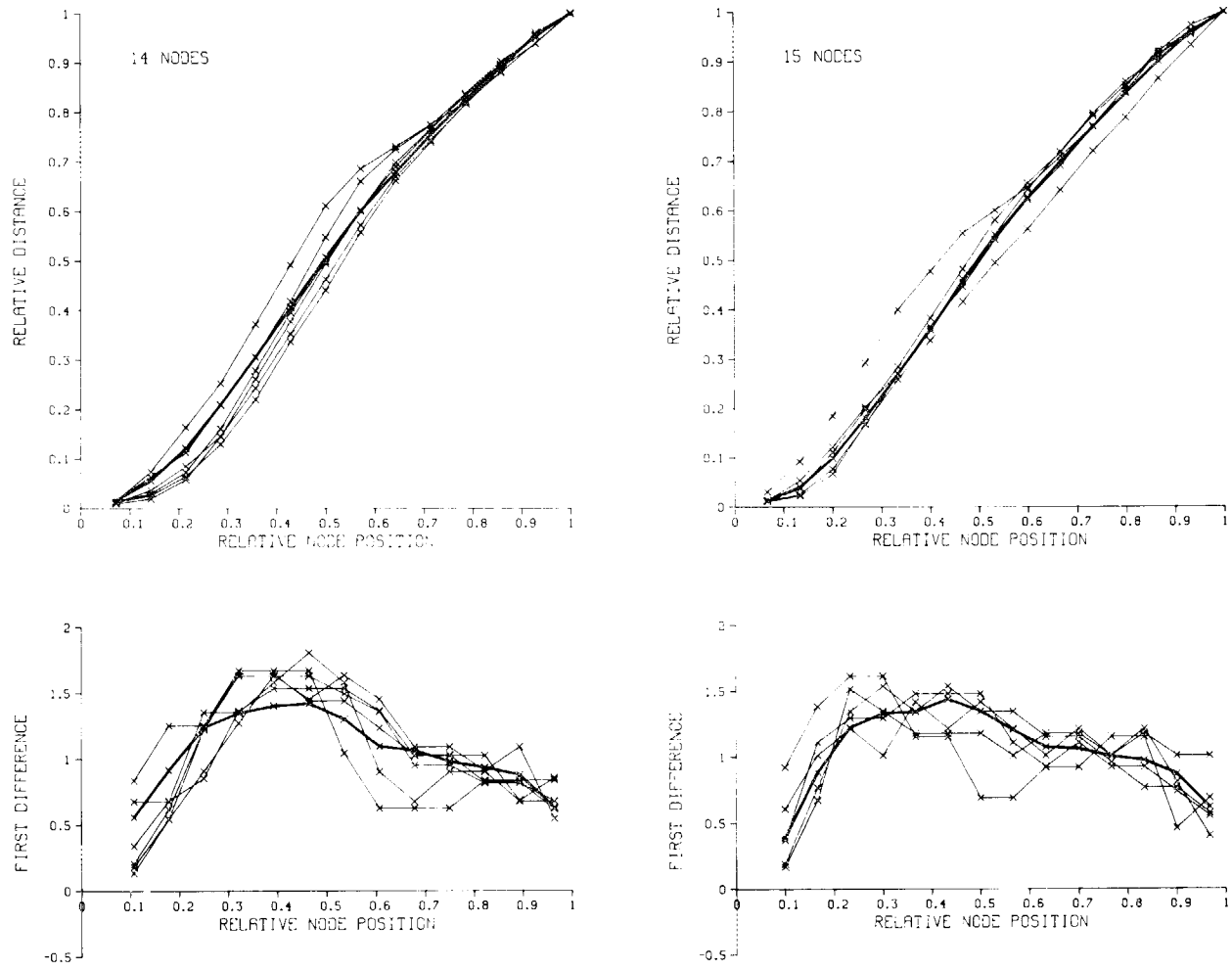


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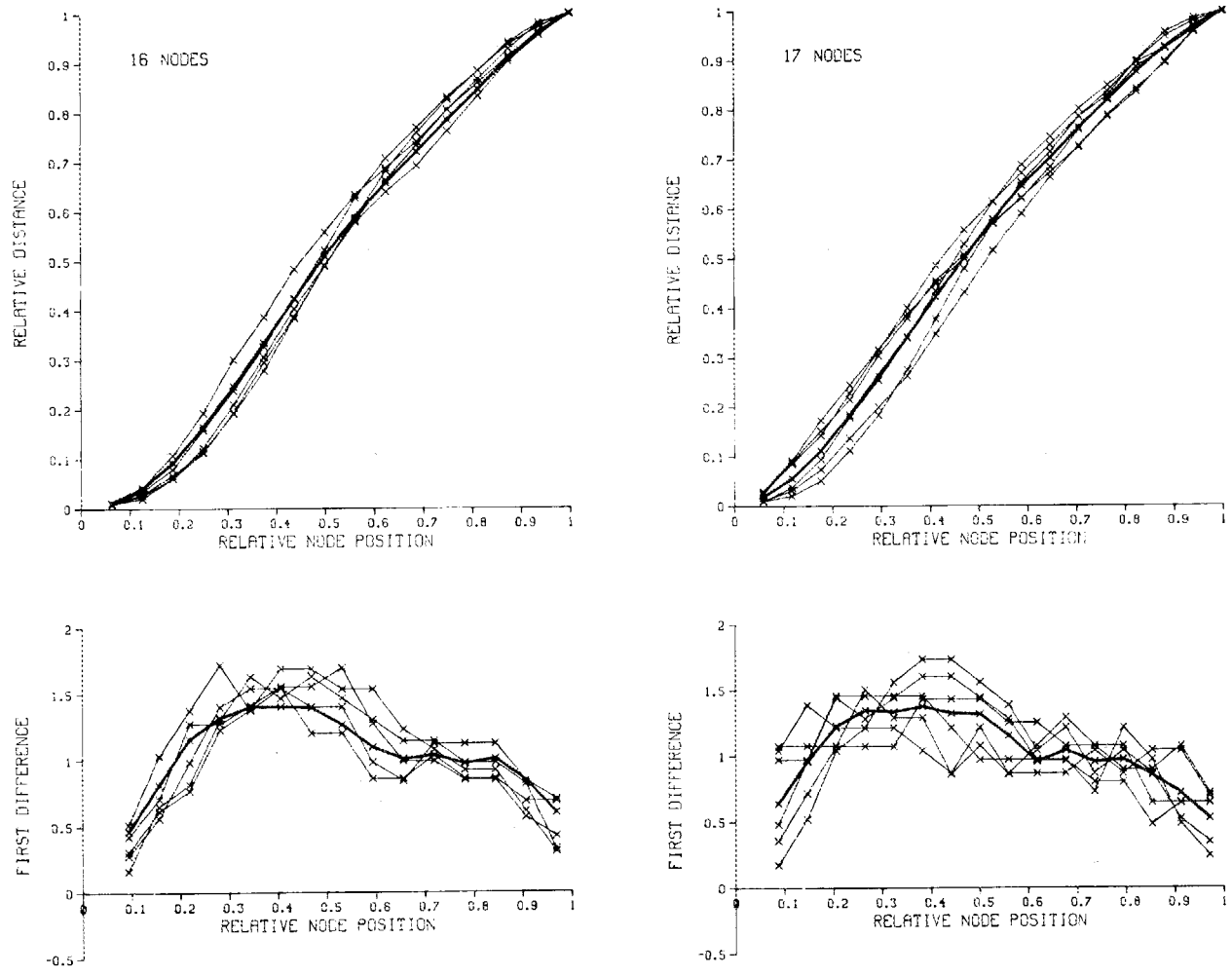


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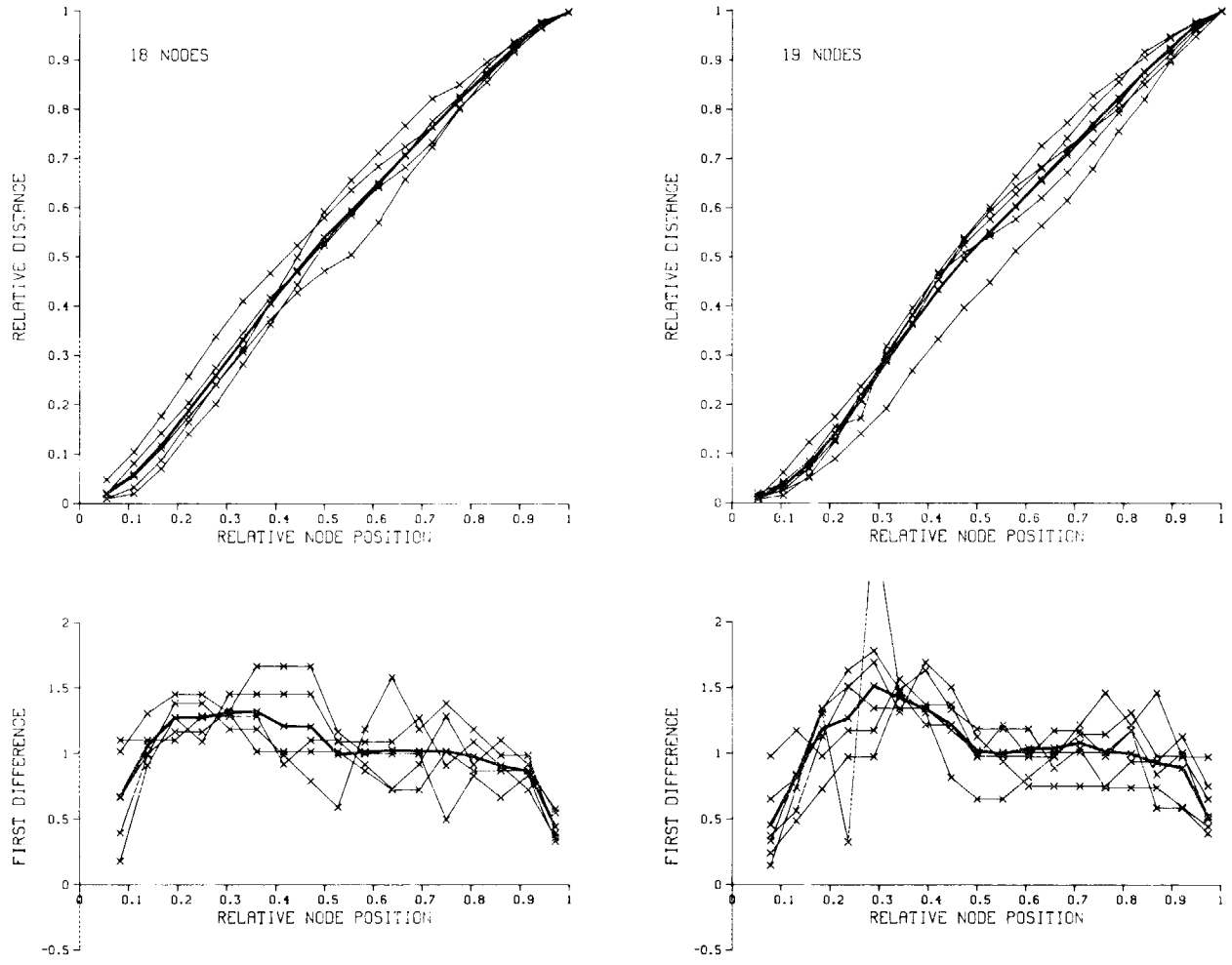


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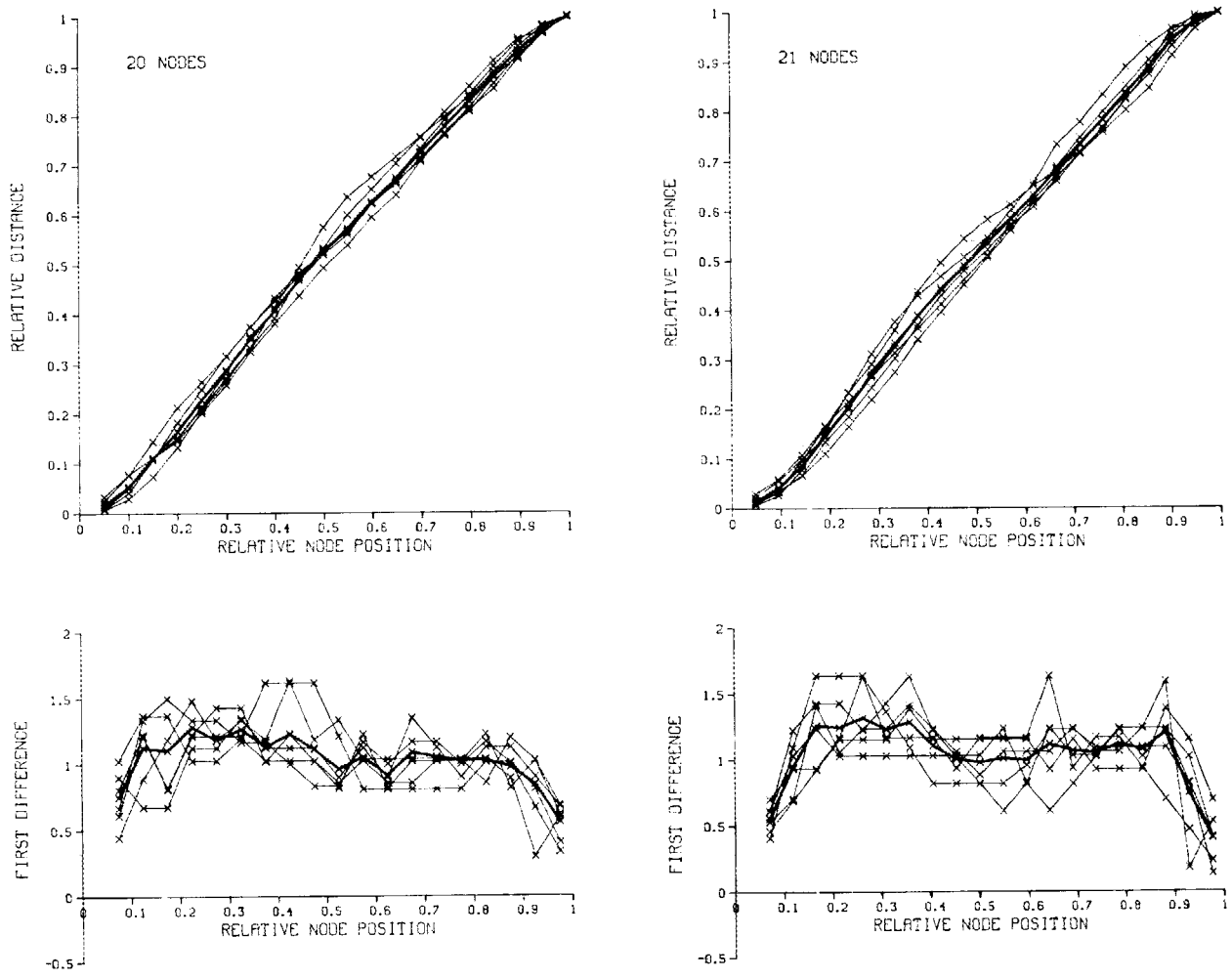


Figure 5.3 (continued)

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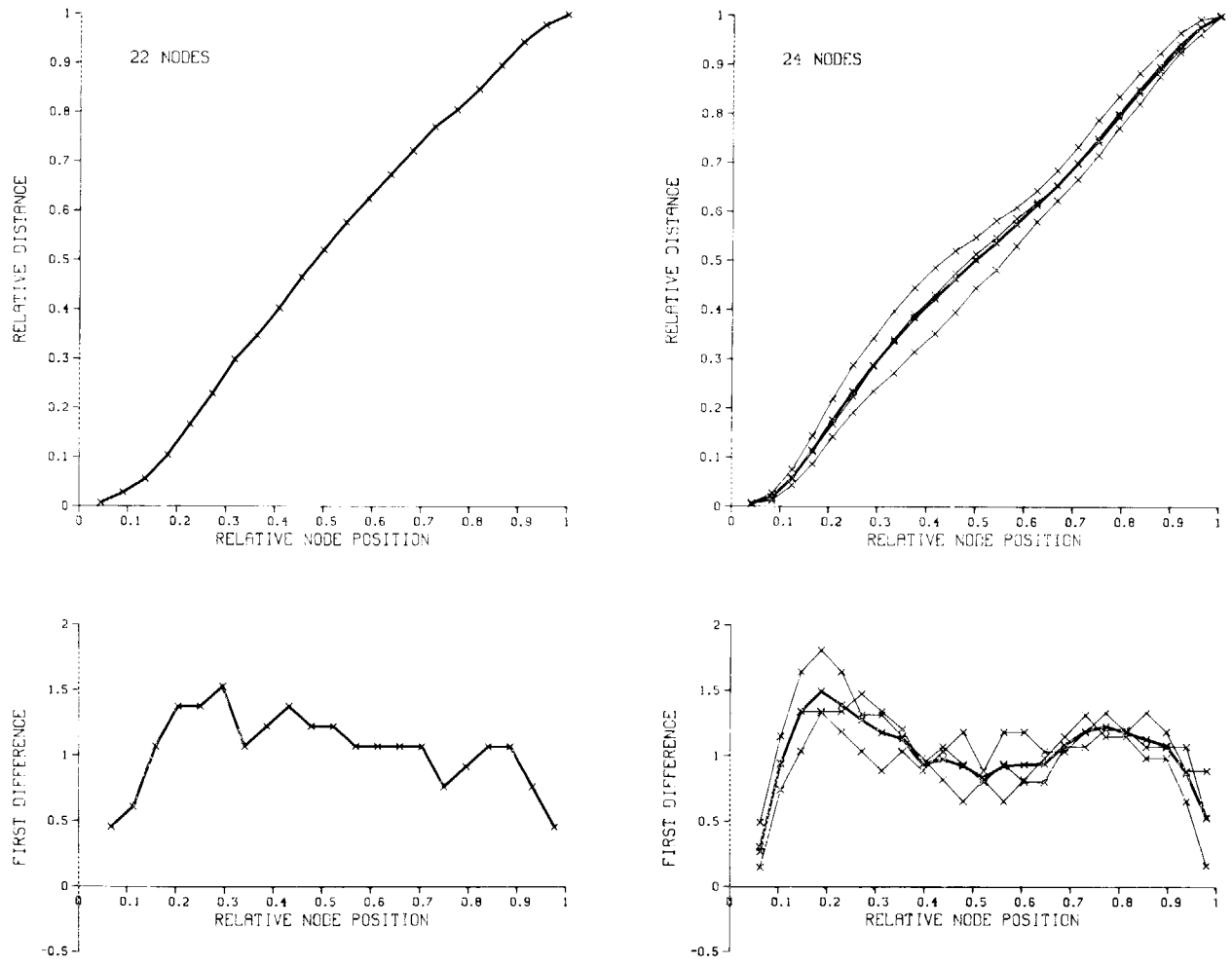



Figure 5.3 (continued)

function of the time that has elapsed between formation of the two nodes and the rate of elongation. In the following discussion, we will assume that the rates of these two processes are correlated.

In the plots of this figure, three distinct phases of branch growth can be identified: increasing internode distance; almost constant, but slightly declining internode distance; and rapidly declining internode distance. All three phases can be observed on the branches with the greatest number of nodes (i.e., the longest branches), and, as a result, these curves are sigmoid in shape. These three phases can also be observed on the plots of the first differences for the longer branches. The slopes increase to a maximum, follow a slightly declining plateau, and then decrease to zero. As the plots for shorter and shorter branches are examined, the middle phase of growth becomes less important until it disappears. The third phase also declines in importance on progressively shorter branches until it too disappears. The section given above on number of nodes demonstrated that node density decreases with increasing branch length. From the figures given in this section, it can be concluded that this occurs through an increase in the center phase of growth, where nodes are spaced further apart. The higher node density observed on the shorter branches is a result of the absence of this center phase and an increase in importance of the first and third phases of growth.

The growth of higher plants has been compared to accumulation of capital at continuous compound interest (Leopold and Kriedemann 1975). The embryo represents initial capital, and net productivity

is determined by the rate of growth. This analogy may be extended to include plant parts as well as whole plants. In this study, it can be applied to shoot elongation and node positions. All branches showed the first of the three phases: increasing internode length. Whether this pattern was regulated by internal or environmental factors is unknown. For the shorter branches, growth stopped at this point, perhaps as a result of crown expansion with its increased shading and competition for water and nutrients. These branches may die in subsequent years due to lowered light levels (Millington and Chaney 1973). Longer branches, once they had accumulated sufficient capital, produced nodes at a regular interval. This process continued until growth was limited by other factors, presumably related to the end of the growing season. Internode distance declined beyond this point.

If it is true that the rate of node formation and the rate of elongation are correlated, then growth in sycamore does appear to follow a "grand period" of growth. This statement, however, should be accepted only tentatively. A closer examination of the curves indicates that two, or perhaps more sigmoid shaped curves can be seen on the longer branches. The graphs of the first differences are not "smooth", indicating that node formation is affected by other factors (e.g., weather).

Phyllotaxis: The Trunk

Analysis of branch azimuths differs from analysis of other variables discussed to this point in that the measurements are on a circular scale instead of the more familiar linear one. For

example, consider two branches with azimuths of 5 and 355 degrees. The linear mean of these two observations is 180 degrees, exactly opposite the direction of the true circular mean of 0 degrees. Techniques have been developed to analyze data of this type (e.g., Batschelet 1981, Mardia 1972).

Primary branches were examined for a preferred orientation. This situation could result either from branches being formed at that azimuth or from selective branch death. Previous work (Schutt, unpub. man.) had suggested that branch death may be greatest along the row direction in plantation-grown sycamore trees. The technique to analyze circular data with means that are 180 degrees apart (axial data) is to double the angles and reduce them to modulo 360 degrees (Batschelet 1981). To test the hypothesis of a preferred branch orientation, both the azimuths and the doubled azimuths were analyzed. Data for the 10 study trees were pooled and examined by AGI. Type I branches were analyzed separately.

Table 5.3 gives the results for this analysis. Branch azimuths for several primary branch positions are shown in Figure 5.4. Results of the Rayleigh test show no preferred branching direction. In the test of the axial data, the direction of the Type I branches in only one trunk class was significant, and this result may be spurious due to small sample size. A second option is that Type I branches may have formed at a preferred azimuth, although this explanation does not find support from the other trunk AGI's.

Angles of divergence between consecutive leaves or branches were calculated by subtraction. Chapter 2 mentioned that it was not

Table 5.3. Rayleigh test for a preferred direction of primary branching for sections with more than 5 observations.

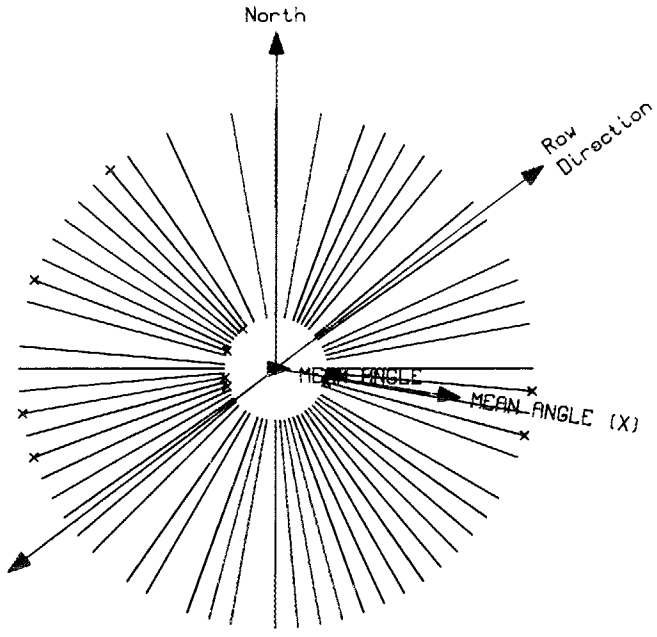
| Trunk Age | Proleptic Class | N | r | r (angles doubled) | Mean Angle | Circular Variance[1] |
|---|---|---|---|---|---|---|
| 2 | I | 118 | 0.025$^{ns}$ | 0.054$^{ns}$ | 43.9 | 80.0 |
| 2 | II | 6 | 0.261$^{ns}$ | 0.725* | 279.1 | 69.7 |
| 3 | I | 73 | 0.043$^{ns}$ | 0.110$^{ns}$ | 1.5 | 79.3 |
| 4 | I | 83 | 0.033$^{ns}$ | 0.063$^{ns}$ | 202.4 | 79.7 |
| 5 | I | 67 | 0.077$^{ns}$ | 0.034$^{ns}$ | 213.9 | 77.2 |
| 5 | II | 43 | 0.086$^{ns}$ | 0.145$^{ns}$ | 232.0 | 77.9 |
| 6 | I | 34 | 0.169$^{ns}$ | 0.222$^{ns}$ | 123.9 | 73.9 |
| 6 | II | 20 | 0.239$^{ns}$ | 0.072$^{ns}$ | 17.9 | 70.7 |

[1]NOTE: The maximum circular variance is 81.03 degrees.

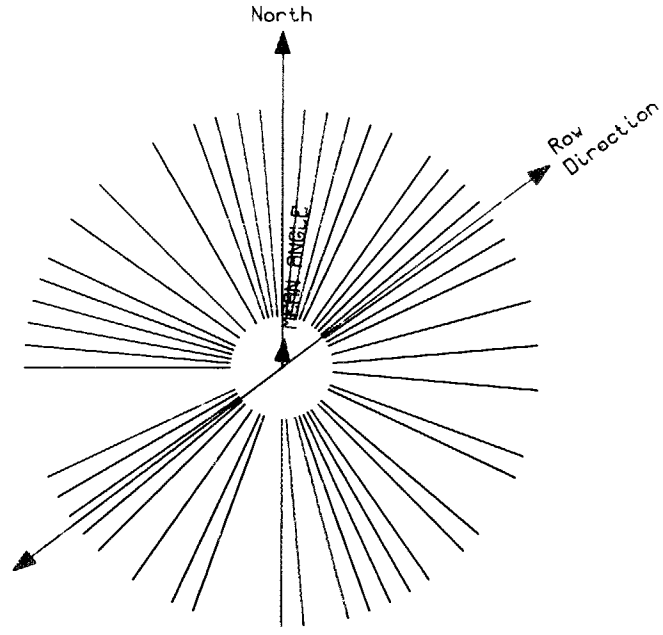
$^{ns}$Not significant.

*Significant at 0.05 level.

Figure 5.4. Azimuth of Type I and Type II proleptic primary branches at various canopy positions. Compass north (North), sample size (N), mean angles (ANGLES), circular variance (S), and length of the mean vector (R) are also shown. Since the mean angles are 180 degrees apart, only the first of each pair is plotted.




| BRANCH TYPE | N | ANGLES | | S | R |
|---|---|---|---|---|---|
| TYPE II | 118 | 90.82 | 270.82 | 39.41 | 0.05 |
| TYPE I (X) | 6 | 98.80 | 278.80 | 21.23 | 0.73* |



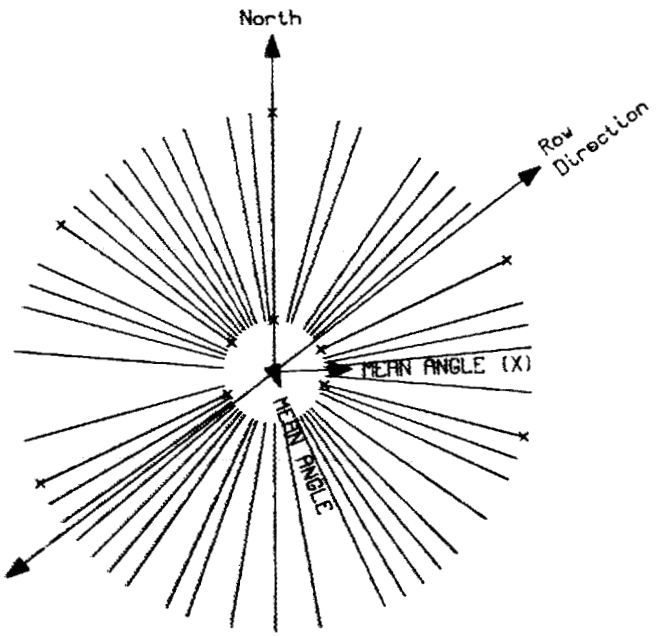

| BRANCH TYPE | N | ANGLES | | S | R |
|---|---|---|---|---|---|
| TYPE II | 73 | 5.09 | 185.09 | 38.21 | 0.11 |

Figure 5.4

ORNL-DWG 85-10929

DIRECTION OF
TYPE II AND TYPE I
BRANCHES

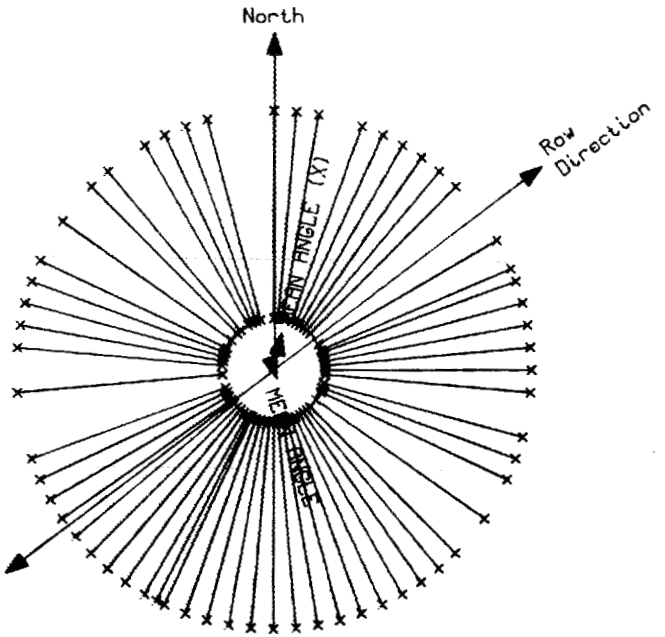
TA-4 01A-0 02A-0 03A-0 04A-0




| BRANCH TYPE | N | ANGLES | | S | R |
|---|---|---|---|---|---|
| TYPE II | 83 | 158.02 | 338.02 | 39.22 | 0.06 |
| TYPE I (X) | 5 | 88.23 | 268.23 | 33.91 | 0.30 |

DIRECTION OF
TYPE II AND TYPE I
BRANCHES

TA-5 01A-0 02A-0 03A-0 04A-0




| BRANCH TYPE | N | ANGLES | | S | R |
|---|---|---|---|---|---|
| TYPE II | 67 | 160.63 | 340.63 | 39.82 | 0.03 |
| TYPE I (X) | 43 | 12.09 | 192.08 | 37.47 | 0.14 |

Figure 5.4 (continued)

possible to determine node position on the lower two trunk sections (trunk age (TA) five and six) on several trees, so branches on these sections were not included in the analysis. These differences were examined to determine if they were normally distributed.

Results are shown in Table 5.4. The angle of divergence was normally distributed on TA1 for all 10 trees, for 6 of 10 trees on TA2, for 8 of 10 trees on TA3, and for 6 of 9 trees on TA4. This table also shows that the mean angle is greater than 180 degrees on three of the 10 trees for TA1, TA2, and TA3, and 2 of the 9 trees for TA4. This is probably due to a reversal of the direction of the ontogenetic spiral. On these sections the mean divergence angle is close to 220 degrees. If the reversal in the direction of the phyllotaxis is accounted for, this mean is approximately 140 degrees, a value close to the other means.

Next, the frequency of phyllotaxis reversal was examined to determine if it was higher on any tree or in any year of growth by a chi-square test (Sokal and Rohlf 1969). The calculated value of 4.455 for a tree effect was much less than the tabular value of 16.919 ($\alpha = 0.05$). Likewise, the year effect (0.27) was non significant (compared with a tabular value of 7.815, $\alpha = 0.05$). Therefore, phyllotaxis reversal appears to be spread across the population and may develop in any year. The mechanism causing this phenomenon is unknown as is its significance. No other works were found which described this phenomenon, so its occurrence in other species is also unknown.

Table 5.4. Results from the Shapiro-Wilk tests for normality of the angle of divergence between consecutive leaves (TA = 1) or branches (TA = 2, 3, or 4) for the different trunk ages (TA) on each tree.

| | TA = 1 | | | TA = 2 | | | TA = 3 | | | TA = 4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tree | N | Mean | W | N | Mean | W | N | Mean | W | N | Mean | W |
| 2 | 13 | 146.9 | 0.909$^{ns}$ | 11 | 209.5 | 0.751** | 6 | 153.3 | 0.956$^{ns}$ | 9 | 238.9 | 0.893$^{ns}$ |
| 4 | 13 | 138.1 | 0.946$^{ns}$ | 13 | 223.5 | 0.931$^{ns}$ | 5 | 217.0 | 0.938$^{ns}$ | 6 | 128.3 | 0.877$^{ns}$ |
| 5 | 19 | 143.4 | 0.978$^{ns}$ | 9 | 163.9 | 0.775** | 6 | 225.0 | 0.843$^{ns}$ | 4 | 160.0 | 0.826$^{ns}$ |
| 6 | 10 | 160.5 | 0.963$^{ns}$ | 14 | 143.6 | 0.918$^{ns}$ | 7 | 160.0 | 0.792* | 7 | 219.3 | 0.920$^{ns}$ |
| 7 | 18 | 136.4 | 0.918$^{ns}$ | 12 | 148.3 | 0.710** | 8 | 230.0 | 0.905$^{ns}$ | 8 | 134.4 | 0.956$^{ns}$ |
| 8 | 16 | 208.8 | 0.971$^{ns}$ | 8 | 141.3 | 0.903$^{ns}$ | 4 | 161.3 | 0.981$^{ns}$ | 5 | 133.0 | 0.752* |
| 9 | 13 | 220.4 | 0.924$^{ns}$ | 8 | 177.5 | 0.911$^{ns}$ | 6 | 149.2 | 0.689** | 2 | 147.5 | - |
| 10 | 15 | 221.3 | 0.969$^{ns}$ | 13 | 205.4 | 0.788** | 7 | 139.3 | 0.934$^{ns}$ | 7 | 142.1 | 0.795* |
| 11 | 11 | 175.9 | 0.932$^{ns}$ | 13 | 131.9 | 0.903$^{ns}$ | 8 | 136.3 | 0.916$^{ns}$ | 7 | 136.4 | 0.957$^{ns}$ |
| 12 | 16 | 164.4 | 0.936$^{ns}$ | 10 | 153.5 | 0.940$^{ns}$ | 5 | 177.0 | 0.893$^{ns}$ | 12 | 155.8 | 0.757** |

$^{ns}$Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

Observations for trunk sections which were not distributed normally were deleted, and the remaining observations were pooled to test for normality. These distributions were not normal for TA1 or TA2 but were for TA3 and TA4. The reason for this is unknown. The sample size decreased from TA1 to TA4 (N = 144, 66, 49, and 41), and SAS also used a different normality test for the latter two TA's. The effects of these factors are unknown. An ANOVA was performed to determine if differences in the angle of divergence could be explained by a tree effect and also by a trunk age effect within tree. These two variables were not significant ($p > 0.05$), and together they explained only 7.2% of the variation in the data. Obviously, other factors are involved in determining the difference between the mean and observed angles of divergence.

Phyllotaxis: Branches

Field observations suggested that second- and higher-order branches form oppositely along their mother branch at azimuths of 90 and 270 degrees. This hypothesis was tested by a V-test (Batschelet 1981). As mentioned above, analysis of axial data is preceeded by doubling the angles and reducing them to modulo 360.

Results are shown in Table 5.5 for branch positions with more than four branches. Figure 5.5 shows azimuths for several selected branch positions. Most of the statistics calculated are highly significant ($p \leq 0.001$) showing that the branches are distributed circular normal with means of 90 and 270 degrees.

Table 5.5. Results from the V-test for second- and higher-order branches to determine if branch azimuths are distributed circularly normal with means of 90 degrees and 270 degrees. Branch angles were doubled for the test. Results are presented for all positions with more than 4 observations.

| Trunk Age | Order 1 Age | Order 2 Age | Order 3 Age | Proleptic Class | N | u | Mean Angle[1] | Circular Variance |
|---|---|---|---|---|---|---|---|---|
| 2 | 2 | | | II | 7 | 3.59*** | 92.1 | 7.9 |
| 3 | 2 | | | I | 219 | 13.64*** | 89.7 | 23.9 |
| 4 | 2 | | | I | 202 | 11.42*** | 86.7 | 26.5 |
| 4 | 2 | | | II | 6 | 3.31*** | 88.4 | 8.4 |
| 4 | 3 | | | I | 92 | 9.29*** | 86.0 | 22.5 |
| 4 | 3 | 2 | | I | 80 | 9.85*** | 88.8 | 19.0 |
| 4 | 3 | 2 | | II | 6 | 2.62** | 108.3 | 9.8 |
| 5 | 2 | | | I | 148 | 9.86*** | 91.3 | 26.5 |
| 5 | 2 | | | II | 42 | 4.59*** | 90.3 | 28.6 |
| 5 | 3 | | | I | 93 | 4.41*** | 94.9 | 33.2 |
| 5 | 3 | | | II | 33 | 4.04*** | 81.5 | 28.1 |
| 5 | 3 | 2 | | I | 74 | 8.74*** | 85.9 | 21.2 |
| 5 | 3 | 2 | | II | 22 | 5.48*** | 87.1 | 16.7 |
| 5 | 4 | | | I | 91 | 3.96*** | 87.5 | 34.0 |
| 5 | 4 | | | II | 39 | 4.62*** | 95.4 | 27.7 |
| 5 | 4 | 2 | | I | 58 | 8.04*** | 85.4 | 20.0 |
| 5 | 4 | 2 | | II | 12 | 4.03*** | 86.2 | 16.7 |
| 5 | 4 | 3 | | I | 44 | 6.99*** | 85.3 | 20.1 |
| 5 | 4 | 3 | | II | 14 | 4.18*** | 86.5 | 18.3 |
| 5 | 4 | 3 | 2 | I | 19 | 5.10*** | 92.3 | 16.7 |
| 5 | 5 | | | II | 15 | 2.58** | 78.3 | 28.2 |
| 5 | 5 | 2 | | II | 7 | 2.55** | 79.7 | 21.1 |
| 5 | 5 | 3 | | II | 10 | 3.31*** | 94.5 | 20.3 |
| 5 | 5 | 4 | | II | 12 | 4.22*** | 86.3 | 14.6 |
| 6 | 2 | | | I | 38 | 6.33*** | 90.7 | 21.2 |
| 6 | 2 | | | II | 11 | 4.14*** | 90.5 | 13.9 |
| 6 | 3 | | | I | 39 | 3.08*** | 87.4 | 32.7 |
| 6 | 3 | | | II | 7 | 2.37** | 86.0 | 24.3 |
| 6 | 3 | 2 | | I | 29 | 5.05*** | 77.2 | 20.8 |
| 6 | 4 | | | I | 40 | 3.97*** | 80.8 | 29.5 |
| 6 | 4 | | | II | 10 | 0.76[ns] | 119.1 | 33.4 |
| 6 | 4 | 2 | | I | 9 | 3.24*** | 89.9 | 19.7 |
| 6 | 4 | 3 | | I | 15 | 4.63*** | 84.5 | 15.1 |
| 6 | 5 | | | I | 20 | 0.99[ns] | 112.7 | 35.7 |
| 6 | 5 | | | II | 7 | -0.42[ns] | 358.0 | 38.1 |
| 6 | 5 | 2 | | I | 13 | 3.04*** | 85.8 | 25.6 |
| 6 | 5 | 3 | | I | 9 | 2.86** | 96.4 | 22.5 |
| 6 | 5 | 4 | | I | 16 | 2.94** | 89.1 | 28.1 |
| 6 | 5 | 4 | | II | 6 | 2.84** | 81.2 | 15.2 |

[1]Only one mean angle is given. The second mean angle is equal to the first plus 180°.

[ns]Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

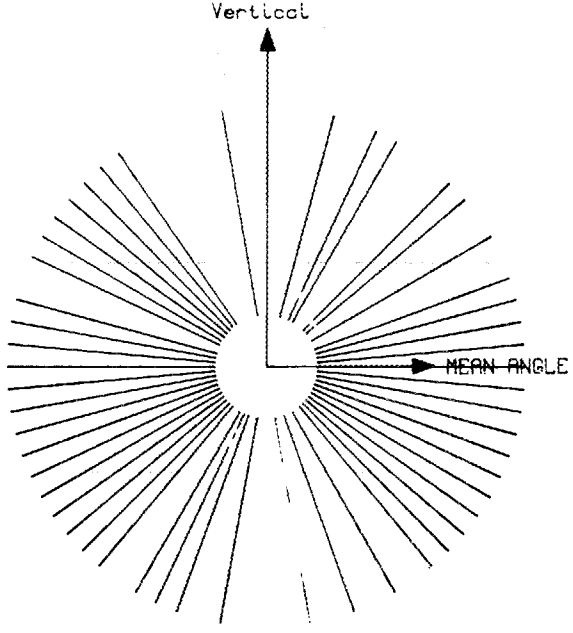
***Significant at 0.001 level.

Figure 5.5. Azimuth of second- and higher-order branches at various canopy positions. Relative north (Vertical), sample size (N), mean angles (ANGLES), circular variance (S), and length of the mean vector (R) are also shown. Since the mean angles are 180 degrees apart, only the first of each pair is plotted.

ORNL-DWG 85-10984

DIRECTION OF
TYPE II
BRANCHES

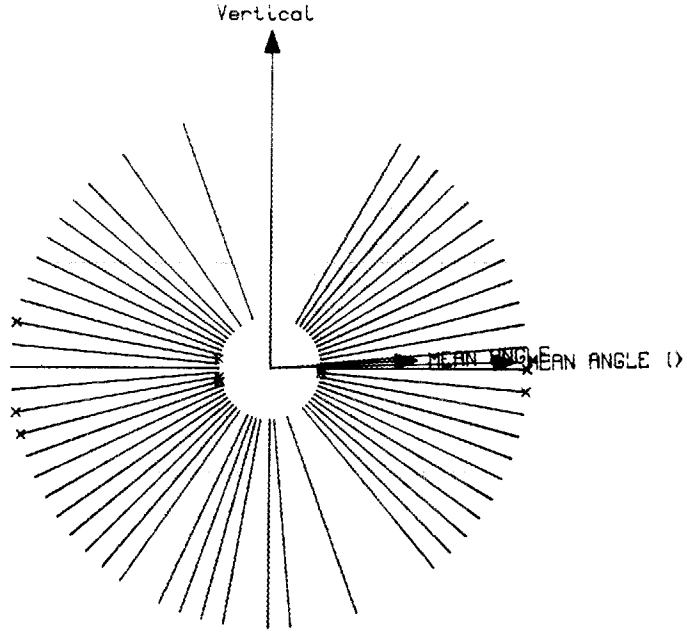
TA-3 01A-2 02A-0 03A-0 04A-0




| BRANCH TYPE | N | ANGLES | | S | R |
|---|---|---|---|---|---|
| TYPE II | 219 | 89.66 | 269.66 | 23.91 | 0.65*** |

DIRECTION OF
TYPE II AND TYPE I
BRANCHES

TA-4 01A-2 02A-0 03A-0 04A-0



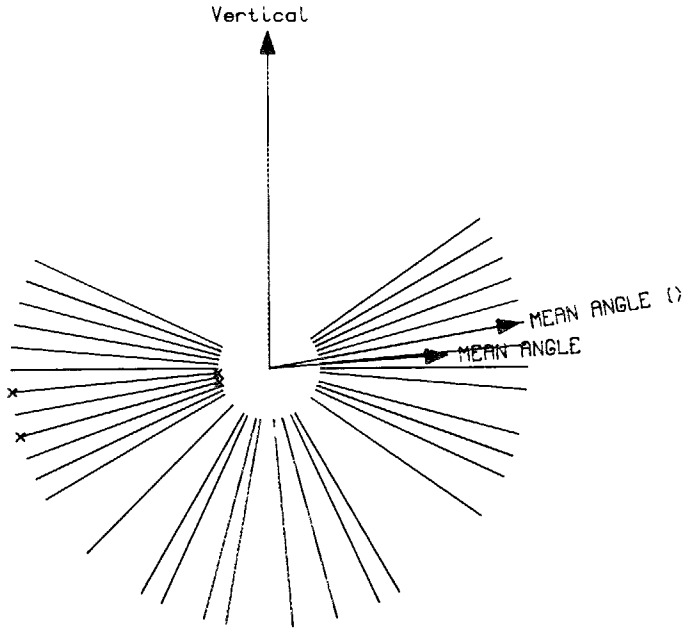

| BRANCH TYPE | N | ANGLES | | S | R |
|---|---|---|---|---|---|
| TYPE II | 202 | 86.68 | 266.68 | 26.50 | 0.57*** |
| TYPE I (X) | 6 | 88.37 | 268.37 | 8.44 | 0.96*** |

Figure 5.5

ORNL-DWG 85-10985

DIRECTION OF
TYPE II AND TYPE I
BRANCHES

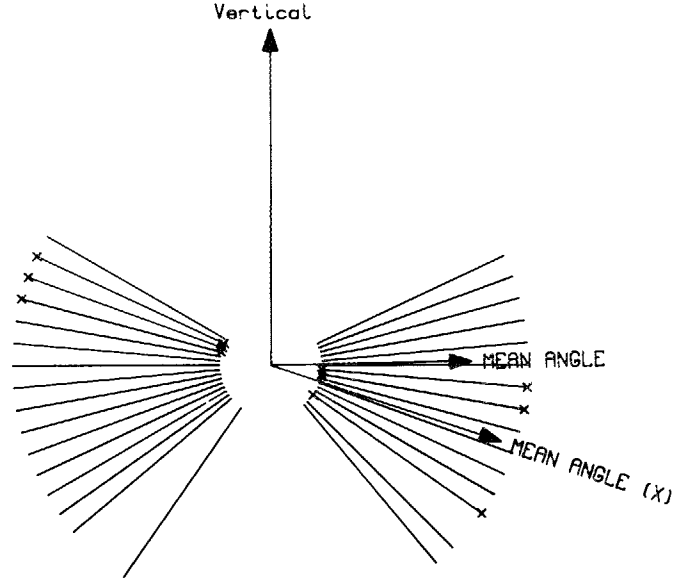
TA-4 01A-3 02A-0 03A-0 04A-0




| BRANCH TYPE | N | ANGLES | | S | R |
|---|---|---|---|---|---|
| TYPE II | 92 | 85.96 | 265.96 | 22.49 | 0.69*** |
| TYPE I (X) | 2 | 80.00 | 260.00 | 4.99 | 0.98 |

DIRECTION OF
TYPE II AND TYPE I
BRANCHES

TA-4 01A-3 02A-2 03A-0 04A-0




| BRANCH TYPE | N | ANGLES | | S | R |
|---|---|---|---|---|---|
| TYPE II | 80 | 88.84 | 268.84 | 19.02 | 0.78*** |
| TYPE I (X) | 6 | 108.26 | 288.26 | 9.76 | 0.94*** |

Figure 5.5 (continued)

Field observations also suggested that azimuths of daughter branches formed near the tip of a long mother branch were formed at all compass directions. To test for a change in branch phyllotaxis, all observations were pooled and subset by node number and node distance class. All positions with fewer than five branches were deleted from this analysis as were positions that were not distributed normally.

Results from the Rayleigh test by node distance are shown in Table 5.6 and results by distance class are shown in Table 5.7. Azimuth distributions become random at 13 nodes or at a distance greater than 90 cm. In the analysis for the bimodal distribution of branch azimuths, three branch positions were not significantly concentrated around the means of 90 and 270 degrees. These were on the 4- and 5-year-old sections of primary branches attached to TA6. The branches at these positions had probably undergone a lot of sub-branch mortality on the shorter, basal branches, and the surviving branches were probably the longer, apical branches formed by spiral phyllotaxis. This may be the reason the hypothesis of bimodal distribution was not rejected. It is clear from Table 5.7 that the significance level of the concentration parameter declines even before this distance. From these tables, it is also apparent that the angular deviation increases with increasing node number or node distance. These hypotheses were tested by regression analyses,

Table 5.6. Results from the Rayleigh test to determine the location where branch phyllotaxis changes: Results for node number. A bimodal distribution was assumed and the angles were doubled for the analysis.

| Node Number | N | r | Mean Angle[1] | Angular Deviation |
|---|---|---|---|---|
| 1 | 7 | 0.817** | 80.8 | 17.3 |
| 2 | 84 | 0.633*** | 87.2 | 24.5 |
| 3 | 245 | 0.669*** | 86.1 | 23.3 |
| 4 | 281 | 0.676*** | 88.1 | 23.1 |
| 5 | 248 | 0.667*** | 88.7 | 23.4 |
| 6 | 202 | 0.670*** | 89.9 | 23.3 |
| 7 | 167 | 0.574*** | 87.3 | 26.4 |
| 8 | 115 | 0.503*** | 89.4 | 28.6 |
| 9 | 67 | 0.418*** | 84.0 | 30.9 |
| 10 | 57 | 0.397*** | 82.1 | 31.5 |
| 11 | 39 | 0.463*** | 90.0 | 29.7 |
| 12 | 26 | 0.477** | 112.3 | 29.3 |
| 13 | 22 | 0.137[ns] | 91.4 | 37.6 |
| 14 | 7 | 0.491[ns] | 89.5 | 28.9 |

[1]Only one mean angle is given. The second mean angle is equal to the first plus 180°.

[ns]Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

Table 5.7. Results from the Rayleigh test to determine the location where branch phyllotaxis changes: Results for node distance. A bimodal distribution was assumed and the angles were doubled for the analysis.

| Node Distance | N | r | Mean Angle[1] | Angular Deviation |
|---|---|---|---|---|
| 0-10 cm | 301 | 0.643*** | 86.9 | 24.2 |
| 10-20 cm | 393 | 0.668*** | 87.9 | 23.3 |
| 20-30 cm | 285 | 0.655*** | 89.3 | 23.8 |
| 30-40 cm | 221 | 0.600*** | 87.1 | 25.6 |
| 40-50 cm | 142 | 0.593*** | 86.4 | 25.8 |
| 50-60 cm | 104 | 0.432*** | 94.0 | 30.5 |
| 60-70 cm | 62 | 0.357*** | 87.3 | 32.5 |
| 70-80 cm | 39 | 0.393** | 89.2 | 31.6 |
| 80-90 cm | 16 | 0.434* | 85.0 | 30.5 |
| 90-100 cm | 11 | 0.430[ns] | 89.3 | 30.6 |

[1]Only one mean angle is given. The second mean angle is equal to the first plus 180°.

[ns]Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

and Tables 5.8 and 5.9 show that both models are significant. The parameterized models are:

$$\text{Circular Variance} = 19.28 + 1.03(\text{Node Number})$$

and

$$\text{Circular Variance} = 22.15 + 0.120(\text{Node Distance}) \quad .$$

Frequency plots showing angle of divergence were generated for all node positions greater than 13 (N = 12) and for all lengths greater than 90 cm (N = 7). The plot for node position appeared to have a bimodal distribution with means near 150 and 230 degrees. This indicated that daughter branches on first- and higher-order branches may form in a clockwise or a counterclockwise direction as they do on the trunk. All observations greater than 180 degrees were changed so that the direction of phyllotaxis was in the opposite direction. The resulting distribution of differences did not differ from normal ($p > 0.05$) and the mean angle did not differ significantly ($p > 0.05$) from the "ideal" angle of 137.5 degrees.

In summary, the phyllotaxis of daughter branches that formed on first- and higher-order branches is opposite (distichous) with means of 90 and 270 degrees. With increasing node number/distance, the circular deviation around these means increases linearly to the thirteenth node or to a distance of 90 cm. After this point, the phyllotaxis is no longer opposite but spiral, and the mean angle of divergence does not differ significantly from 137.5 degrees. While the number of observations at this point is few, it appears that the phyllotaxis can be either clockwise or counterclockwise.

Table 5.8. ANOVA analysis for the regression predicting circular variance from node number.

| Source of Variation | df | SS | MS | F |
|---|---|---|---|---|
| Node number | 1 | 150.30 | 150.30 | 35.44*** |
| Error | 10 | 42.41 | 4.24 | $R^2$ = 0.780 |
| Total | 11 | 192.71 | | |

***Significant at 0.001 level.

Table 5.9. ANOVA analysis for the regression predicting circular variance from node distance.

| Source of Variation | df | SS | MS | F |
|---|---|---|---|---|
| Node distance | 1 | 86.31 | 86.31 | 28.62** |
| Error | 7 | 21.11 | 3.02 | $R^2$ = 0.804 |
| Total | 8 | 107.42 | | |

**Significant at 0.001 level.

The section on branch length stated that acrotony may be advantageous to sycamore. This is probably also true for branch azimuth. One study of leaf angles, areas, and canopy development (Duncan 1971) demonstrated that, for plant canopies with a leaf area index greater than 3.0, maximum photosynthesis was achieved when the upper elements were held vertically and lower elements were held horizontally. This prediction has been observed for some deciduous forest canopies (e.g., Miller 1969). McMillen and McClendon (1979) observed leaf inclination of ten species of woody deciduous dicots to be more horizontal in the shade than in the sun. These patterns appear to correlate with branch azimuth in sycamore in that the shorter, basal branches on each AGI are held horizontally. While branch inclination may differ from leaf inclination, this arrangement could result in greater light interception. By contrast, the longer, apical branches are formed at all azimuths. This arrangement is advantageous in that it increases the probability that one of these daughters may be able to survive and extend the crown.

Number of Daughters

The number of daughter branches that can potentially form on a mother branch is limited by the number of nodes on that branch, and this, in turn, is related to the mother branch length (see the section on "Number of Nodes"). Some trees can avoid this limit by forming more than one bud at a node (Chapter 4).

The number of daughter branches that actually forms on a mother branch has been related to mother branch length. Ward (1964) explained 57% of the variance in the number of daughters formed on red oak from mother shoot length. Cannell (1974) also found that the number of lateral branches in lodgepole pine (Pinus contorta Dougl.) and Sitka spruce was related to mother shoot length. This relationship varied with provenance. These two variables were also correlated on older Sitka spruce trees (Cochrane and Ford 1978), but not on younger trees. For sycamore, the correlation between the number of daughters and the number of nodes on the mother branch ($r = 0.948$, $p \leq 0.0001$) was slightly higher than the correlation with mother branch length ($r = 0.929$, $p \leq 0.0001$). A regression equation was then developed using the number of nodes on the mother branch section and a random class variable representing differences due to a tree effect.

The ANOVA table for this analysis is shown in Table 5.10. The parameterized model is:

$$\text{Number of Daughters} = -1.836 + 0.829(\text{Number of Nodes}) + \text{TREE} \quad .$$

Most of the variation in number of daughters produced can be explained by these two independent predictors. The type III sums of squares show that much of this predictive power comes from the strong relationship with number of nodes. The random TREE effect is assumed to be distributed normally with mean 0.0 and calculated variance of 0.1607. As in previous analyses, this TREE variable may

Table 5.10. ANOVA analysis for the regression predicting number of daughter branches formed from the number of nodes on the parent branch.

| Source of Variation | df | Sum of squares: Full model | Sum of squares: Type III | MS | F |
|---|---|---|---|---|---|
| Model | 10 | 2104.77 | | 210.48 | 364.08*** |
| Number of nodes | 1 | | 1882.66 | 1882.66 | 3095.63*** |
| Tree | 9 | | 47.60 | 5.29 | 8.70*** |
| Error | 287 | 174.54 | | 0.61 | $R^2 = 0.923$ |
| Total | 297 | 2279.32 | | | |

***Significant at 0.001 level.

represent a genetic effect. Several authors have found that the number of daughters formed is heritable. Faulkner's (1970) review included heritability estimates for the number of branches formed per whorl in conifers. Polk (1974) found that daughter production is heritable for jack pine (Pinus banksiana Lamb.). It is not unreasonable to assume that the same is true for sycamore.

In the section analyzing extension growth, the following principles were stated: (1) increasing module number results in decreasing module size, (2) branching rate must decline to avoid intra-crown competition, and (3) the number of branches on trees becomes asymptotic. Growth in which either the probability of branching or the number of branches formed per branching event changes with time is called nonstationary (Waller and Steingraeber, in press). The analysis of branch length given above demonstrated that branch annual extension growth declined exponentially with increasing branch age. The analysis in this section adds that the number of daughter branches formed along these branches also declined, showing that branching in sycamore is nonstationary. Therefore, sycamore follows the first two of these principles.

While it has been stated that branching rate must decline with time, the mechanism through which this occurs has not yet been elaborated. The current analysis indicates that it occurs through a decline in mother branch length and not as a decline in the branching rate (expressed as number of daughters per number of nodes or branch length). This can be deduced from the fact that the regression is

linear and that the intercept is near zero (although it does differ significantly from zero). This analysis was also run with mother branch length (MLEN) and TREE as independent variables. The regression was significant ($p \leq 0.0001$) and explained 89.0% of the variation in the data. This second regression is important because the intercept does not differ significantly from zero, and it lends even stronger evidence to the case that branching rate per unit mother length is constant. This relationship has been observed by other authors. It is implicit in Ward's (1964) regression predicting number of daughter branches formed on red oak. It was also explicitly stated by P. White (1984) who observed a correlation between decreasing branch length and branching rate in *Aralia spinosa*.

The relationship between number of daughter branches formed and parent length was developed for all crown positions, including the upper, exposed crown as well as lower, shaded crown. Therefore, it appears that the number of branches formed is independent of the amount of light received by the mother branch section. Because competition for light is the most important variable influencing branch survival (Millington and Chaney 1973), competition by neighboring trees would not be expected to influence this relationship. If competition does affect branching density, it would probably do so directly through its effect on extension growth and only indirectly through the number of daughters formed.

Mother/Daughter Branch Angles

The morphological processes governing the expression of branch angle were discussed earlier in this chapter. This section will analyze the angle of divergence between mother and daughter branches.

Field observations indicated that the angle of divergence between a mother and daughter branches increased with distance from the AGI tip. Correlations between distance ($r = -0.677$) or node numbers ($r = -0.658$) with branch inclination were significant ($p \leq 0.0001$) for 1-year-old primary branches. This relationship was also noted for higher-order branches. This observation was added to the regression predicting mother/daughter branch angle equations through the following variables: node number (NO), node distance (NODE), and relative node position (RELDIST = NODE/LENGTH). Epinasty was represented by either the number of nodes (NNODES) or the length (MLEN) of the mother branch section. Negative geotropism is probably related to both the vigor of the daughter branch (related to length, DLEN) and the number of daughter branches (NDAUT) formed. These variables were added to the equations. Since this mother/daughter branch angle may differ with branch order, a class variable representing order (ORDER) was also added. A term representing increasing parent age (PAGE) was nested inside the ORDER effect to determine if branch angles increased from tree tip to base. Finally, a random TREE variable was added to the model to account for any tree effect.

Results from these analyses are shown in Tables 5.11, 5.12, and 5.13. Overall, the three models explain a similar amount of the

Table 5.11. ANOVA analysis for the regression predicting mother/daughter branch angle: node number. This analysis differs from the following two in that it includes the daughter node number and the number of nodes on the parent branch. See text for an explanation of the symbols.

| Source of Variation | df | Sum of squares: Full model | Sum of squares: Type III | MS | F |
|---|---|---|---|---|---|
| Model | 24 | 113265.48 | | 4719.40 | 48.89*** |
| NO | 1 | | 14923.73 | 14923.73 | 154.60*** |
| NNODES | 1 | | 5847.82 | 5847.82 | 60.58*** |
| NDAUT | 1 | | 119.73 | 119.73 | 1.24$^{ns}$ |
| DLEN | 1 | | 7729.49 | 7729.49 | 80.07*** |
| ORDER | 3 | | 2880.83 | 960.28 | 9.95*** |
| PAGE (ORDER) | 8 | | 2103.98 | 263.00 | 2.72** |
| TREE | 9 | | 26007.00 | 2889.67 | 29.93*** |
| Error | 1803 | 174048.74 | | 96.53 | $R^2$ = 0.394 |
| Total | 1827 | 287314.22 | | | |

$^{ns}$Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

Table 5.12. ANOVA analysis for the regression predicting mother/daughter branch angle: node distance. This table is similar to Table 5.11 but substitutes node distance for node number and mother length for number of nodes on the mother.

| Source of Variation | df | Sum of squares: Full model | Sum of squares: Type III | MS | F |
|---|---|---|---|---|---|
| Model | 24 | 111660.95 | | 4652.54 | 47.76*** |
| NODE | 1 | | 12866.11 | 12866.11 | 132.06*** |
| MLEN | 1 | | 6545.47 | 6545.47 | 67.19*** |
| NDAUT | 1 | | 687.18 | 687.18 | 7.05** |
| DLEN | 1 | | 6083.71 | 6083.71 | 62.45*** |
| ORDER | 3 | | 3432.33 | 1144.11 | 11.74*** |
| PAGE (ORDER) | 8 | | 3342.04 | 417.75 | 4.29*** |
| TREE | 9 | | 23143.71 | 2571.52 | 26.40*** |
| Error | 1803 | 175653.27 | | 97.42 | $R^2$ = 0.389 |
| Total | 1827 | 287314.22 | | | |

[ns]Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

Table 5.13. ANOVA analysis for the regression predicting mother/daughter branch angle: relative node distance. This table is similar to Table 5.12 but substitutes relative daughter position (RELDIST) for node distance.

| Source of Variation | df | Sum of squares: Full model | Sum of squares: Type III | MS | F |
|---|---|---|---|---|---|
| Model | 24 | 108641.78 | | 4526.74 | 45.68*** |
| RELDIST | 1 | | 9846.94 | 9846.94 | 99.37*** |
| MLEN | 1 | | 919.29 | 919.29 | 9.28** |
| NDAUT | 1 | | 749.87 | 749.87 | 7.57** |
| DLEN | 1 | | 12601.21 | 12601.21 | 127.16*** |
| ORDER | 3 | | 2869.86 | 956.62 | 9.65*** |
| PAGE (ORDER) | 8 | | 3333.54 | 416.69 | 4.20*** |
| TREE | 9 | | 24410.52 | 2712.28 | 27.37*** |
| Error | 1803 | 178672.44 | | 99.10 | $R^2$ = 0.378 |
| Total | 1827 | 287314.22 | | | |

[ns]Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

variation in the mother/daughter branch angle. In the first two regressions, the variable representing branch position (node number or distance) added the most predictive power to the model. Mother/daughter branch angles widen with increasing distance from the branch tip. This confirms field observations. In both regressions, daughter length was the next most important variable; longer daughters form at a more acute angle than shorter ones. In the third regression, the order of importance of these two variables was reversed. Above, it was discussed that the basal, shorter, horizontally held branches may have an advantage for light interception. This analysis adds that these same branches are held at a greater angle from the mother than branches near the branch section tip. This would also be advantageous for light interception by minimizing the possibility of leaf overlap. These short branches also have a short life span. Therefore, they may perform a function similar to that of the rachis of compound leaves but differ from it in having a longer life span. In contrast to these branches, the longer, more acutely held branches near the tip would be favored to increase crown size if environmental conditions allow. This situation has been observed in the field.

In the first two regressions, the variable representing epinasty was next in importance. Long mother branches (which also have more nodes) have wider mother/daughter branch angles. This result agrees well with theory if mother length does accurately represent epinasty. In both of these regressions, the TREE effect was next in importance. As was stated in previously discussed

analyses, this term may represent a genetic effect. Polk (1974) found the angle of origin to be heritable in jack pine, and Faulkner's paper (1970) gives estimates of the heritability of this trait for several conifers. Brown (1971a) and Kramer and Kozlowski (1979) both state that branch angle in woody angiosperms is under genetic control. In the third regression, the order of importance of these last two variables was also reversed.

Significant differences were also found among branch orders, confirming that those branches differ in their geotropic action (Brown 1971a).

The effect of parent age within order was also significant. Others have observed that primary branch inclinations decrease basipetally. This was not observed in the present study. The reason for this is unknown, but a partial explanation may come from a consideration of the branch population dynamics. On the 2-year-old section of the trunk, all first-order branches are present and vary from the apical, longer, acutely held branches to the basal, shorter, horizontally held branches. Because branch death is concentrated on the basal, shorter branches, the mean inclination will increase merely due to branch death. This may be countered by the actual increase in branch angle with age. These two processes result in no apparent trend of increasing branch inclination with age. Because of this observation, the effect of parent age was assumed to be random instead of fixed. The expected mean for this effect is 0.0 and the calculated variance is 1.722. This same problem of the change in branch metapopulations was

encountered and discussed in the section on extension growth, and it deserves further attention.

In the first analysis, the effect of the number of daughters was not significant ($p > 0.05$), but it was in the other two regressions (although less significant than all other variables in the model).

Because of the slightly higher R-square value, the regression with node number and number of nodes on the mother was chosen for the branching model. The parameterized equation is:

$$\text{Parent angle} = 42.865 - 1.804(\text{NO}) + 1.737(\text{NNODES}) + 0.232(\text{NDAUT}) - 0.167(\text{DLEN}) + \text{ORDER} + \text{PAGE(ORDER)} + \text{TREE}$$

where ORDER is 4.210, 10.024, 1.457, and 0.0 for orders 1, 2, 3, and 4; PAGE(ORDER) is normally distributed with mean 0.0 and variance 1.722; and TREE is normally distributed with mean 0.0 and variance 17.169.

Branch Inclination

The epinastic effect exerted by the leader decreases with increasing distance from the growing tip (Brown 1971a). Therefore, the processes that determine branch inclination during the second and following years of growth differ from those of the first year. At the branch tip, negative geotropism continues to make the branch grow more vertically, although this effect declines with increasing crown age (Moorby and Wareing 1963). In addition, increasing branch

weight causes the branch to become horizontally oriented, and this force will be opposed by reaction wood formation and geo-epinasty (Jankiewicz and Stecki 1976). In the last section, the angles between a mother branch and 1-year-old daughter branches were analyzed. This section will examine inclination of subsequent branch growth.

Branch inclinations become more vertical with increasing section age for primary branches of all ages (Figure 5.6). A linear model was chosen to fit this relationship. Since the inclination of the first branch section relative to gravity is determined by its azimuth and inclination relative to its mother section, this first angle (FIRANG) was entered into the regression as an independent variable. The distance (DIST) to each branch section from the branch base was added to account for the change in inclination with increasing branch age. Because the distance to the first branch angle (DFIANG) differs with branch order (ORDER), these two variables were added to the model. DFIANG, FIRANG, and DIST were nested within order in the first iteration of this analysis to account for potential interactions. As in previous analyses, a random variable representing a tree effect (TREE) was added to account represent genetic differences.

Results of this regression are shown in Table 5.14. Both the DFIANG term and the DFIANG(ORDER) and FIRANG(ORDER) interaction terms were not significant ($p > 0.05$). Also, the parameters for the ORDER term were extremely high, and the intercept term was

Figure 5.6. Branch inclination of each annual growth increment for all primary branches. (a) Trunk age = 2 (TA2). (b) TA3. (c) TA4. (d) TA5. (e) TA6. Type I branches are marked with a boxed "X" and Type II branches are marked with an "X."

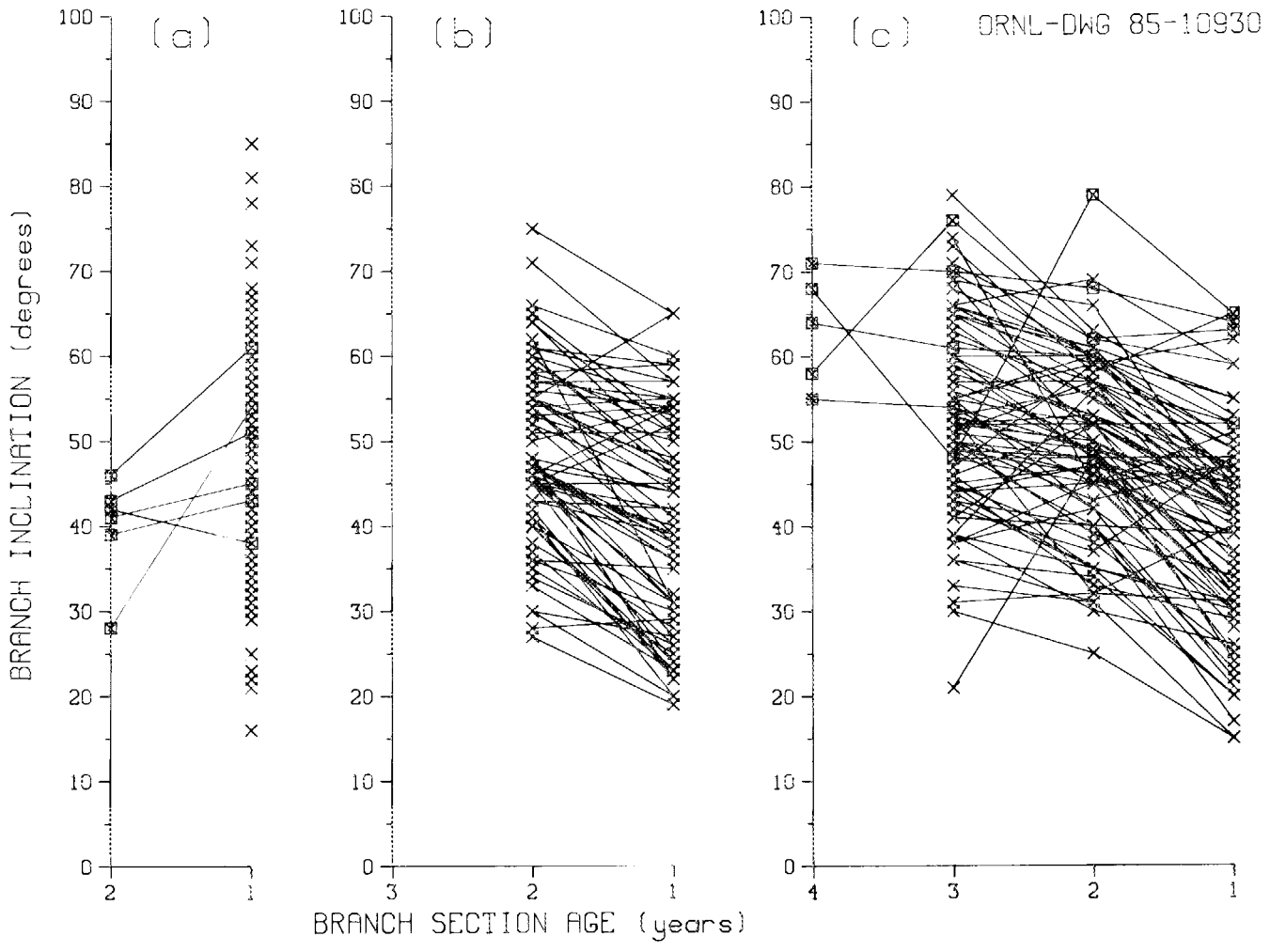

ORNL-DWG 85-10930
(a)
(b)
(c)
BRANCH INCLINATION (degrees)
BRANCH SECTION AGE (years)
0
10
20
30
40
50
60
70
80
90
100
1
2
3
4

Figure 5.6

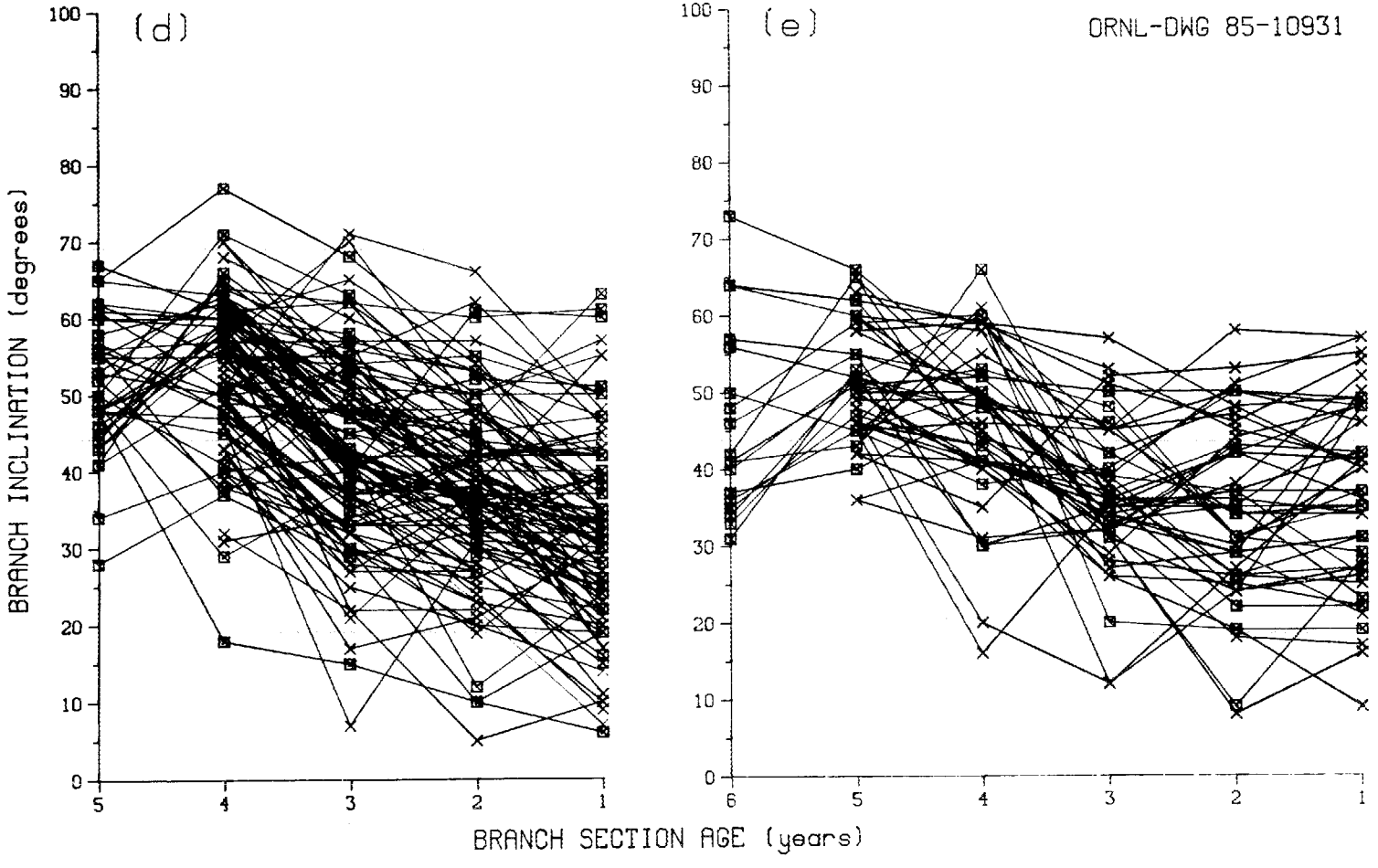



Figure 5.6 (continued)

Table 5.14. ANOVA table for the regression predicting branch inclination. For a description of the variables, see the text.

| Source of Variation | df | Sum of squares: Full model | Sum of squares: Type III | MS | F |
|---|---|---|---|---|---|
| Model | 22 | 182001.30 | | 8272.79 | 84.98*** |
| DFIANG | 1 | | 97.85 | 97.85 | 1.01$^{ns}$ |
| FIRANG | 1 | | 24705.34 | 24705.34 | 253.78*** |
| DIST | 1 | | 931.00 | 931.00 | 9.56** |
| ORDER | 2 | | 1072.20 | 536.10 | 5.51** |
| DFIANG (ORDER) | 1 | | 3.21 | 3.21 | 0.03$^{ns}$ |
| FIRANG (ORDER) | 2 | | 366.71 | 183.36 | 1.88$^{ns}$ |
| DIST (ORDER) | 2 | | 958.53 | 479.26 | 4.92** |
| TREE | 9 | | 23707.18 | 2634.13 | 27.06*** |
| Error | 1125 | 109519.95 | | 97.35 | $R^2$ = 0.624 |
| Total | 1147 | 291521.25 | | | |

$^{ns}$Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

extremely low. Because of these facts, the regression was rerun, and all variables that were nonsignificant in the first analysis were deleted. In this resulting regression, the distance term (DIST) was non significant, although it previously had been significant. The regression was run a third time without this term, and the results are shown in Table 5.15. The parameterized model is:

$$\text{Inclination} = (31.773 + \text{ORDER}) + 0.398(\text{FIRANG}) + (\text{DIST(ORDER)})(\text{DIST}) + \text{TREE}$$

where: ORDER is -6.614, -0.880, -5.533, and 0.0 for orders 1, 2, 3, and 4; DIST(ORDER) is -0.116, -0.191, -0.258, and 0.752 for orders 1, 2, 3, and 4; and TREE is distributed normally with mean 0.0 and variance 23.998. The first branch angle (FIRANG) was the best predictor of branch inclination in this model. This result is as expected. The branch angles are probably highly inter-correlated and, therefore, the first angle would be a good predictor of subsequent angles. The DFIANG(ORDER) term was also highly significant. While branch inclinations are probably correlated, the correlation between the first angle and subsequent angles probably declines with increasing distance from the first angle as later angles become more vertically oriented. The significance of the distance variable lends evidence to support this hypothesis. In the first regression, the parameters for the ORDER term were similar in magnitude, but opposite in sign from the variable representing the distance to the first angle (DFIANG). Omission of the DFIANG term in the current analysis made the magnitude of the ORDER term more

Table 5.15. ANOVA for the reduced model predicting branch inclination. See the text for a description of the variables.

| Source of Variation | df | Sum of squares: Full model | Sum of squares: Type III | MS | F |
|---|---|---|---|---|---|
| Model | 17 | 181085.37 | | 10652.08 | 109.09*** |
| FIRANG | 1 | | 32715.31 | 32715.31 | 335.04*** |
| ORDER | 3 | | 2333.99 | 778.00 | 7.97*** |
| DIST (ORDER) | 4 | | 23845.11 | 5961.28 | 61.05*** |
| TREE | 9 | | 24055.07 | 2672.79 | 27.37*** |
| Error | 1131 | 110437.44 | | 97.65 | $R^2 = 0.621$ |
| Total | 1148 | 291522.81 | | | |

***Significant at 0.001 level.

reasonable. Because of the observed interaction between these variables, the ORDER term in the third regression probably represented the increasing distance of each successive branch order from the bole. The TREE term was also significant. As mentioned above, several authors have found that branch angles are genetically inherited. These studies included angles other than the mother/1-year-old-daughter angles analyzed above. Polk's (1974) work on jack pine demonstrated that the angle of termination is inherited in that species. He also found that the maximum branch curvature (the greatest departure of a branch from a straight line extending from the point of origin to the branch tip) is heritable. Faulkner's work (1970) included heritability estimates for branch inclination, including observations for branches at several whorls; it is unknown if these values are for angles of origin, angles of termination, or another angle measurement. Nelson et al. (1981) observed significant differences between angles of origin and angles of termination for Populus clones. They also found that increasing density decreased branch angles of origin and increased angles of termination. In a later paper (Burk et al. 1983) they developed a model to simulate the geometry of first-order branches for that species.

# CHAPTER 6

# MODEL DEVELOPMENT AND VALIDATION

## Introduction

At some point in the development of any field of science, it becomes appropriate to synthesize current knowledge about a particular topic into a cogent whole. This may be done by developing a model which integrates both extant observations and theories about the processes producing those observations. This model then becomes a formal description of, and hypothesis about the phenomena.

Information about plant growth has reached the level where models are now being synthesized. These models may be classified by their scale of resolution; they may simulate growth of plant parts, whole plants, or entire populations. Plant models may also be categorized by their theoretical framework; some are purely descriptive, being empirically derived, and others are developed primarily from theory.

The work by Pietarinen et al. 1982 is an example of a theoretical model which simulates growth of plant parts. Their equations have accounted for 68% to 93% of the variance in daily shoot and needle growth and 50% to 60% of the variance in diameter growth in Scots pine. Another theoretical model for the growth of plant parts is the work of Jankiewicz (1972). This model was developed to explain increasing difference in size between two buds

or young shoots. A third example of this modeling approach is the work of Thornley (1977).

At the second level of resolution, whole-plant models consider individual plants as the object of study. A more detailed description of this type of model will follow later.

At the broadest modeling scale are models which simulate growth of communities. Shugart and West (1980) have reviewed forest models, identifying those which can be used to simulate succession. They have grouped these models into those which are based on individual trees, those based on gaps, and those based on stands. These models range in complexity from matrices which give probabilities of tree-by-tree replacement to complex models which include the tree's three-dimensional geometry.

Models of individual plants can be subclassified by the dimensions that they grow. Some keep a budget of carbon allocation within a plant (e.g., Ledig 1969, Promnitz 1975, Thornley 1972a,b). Others keep track of extension growth. This subclass can be further subdivided into two-dimensional (e.g., Bell et al. 1979) and three-dimensional models (e.g., Fisher and Honda 1977, Hofmann 1981). The three-dimensional models which simulate individual branches on trees are very detailed in that they must include branch azimuths and inclinations as well as extension growth. A third subclass of the individual plant models records both tree diameter and extension growth (e.g., Daniels and Burkhart 1975, Daniels et al. 1979, and Mitchell 1975). Models of this type are usually part of a

stand model. While they are three-dimensional, their degree of resolution is less than models which explicitly grow branches.

Whole-plant models can also be subclassified by their theoretical framework into empirical (statistical) models and pure theoretical models. It should, however, be understood that these two subclasses are not mutually exclusive. Empirical models are, indeed, built upon a theoretical framework, and theoretical models require an empirical base. Empirical models are highly data-dependent and are usually designed to simulate a specific situation. Examples are: Bell et al. 1979, Daniels and Burkhart 1975, Daniels et al. 1979, Fisher and Honda 1977, and Hofmann 1981. The pure theoretical models can be further subdivided into those which consider physiological processes and those which consider physical processes. Physiological models include the work of Ledig (1969), Promnitz (1975), and Thornley (1972a,b) and examples of theoretical models that examine physical phenomena are: Cohen (1967), Honda (1971), and McMahon and Kronauer (1976). Other theoretical models which examine some particular aspect of branching were discussed in Chapter 4. Both the empirical and the theoretical whole-plant models have their advantages and disadvantages and their uses. The strength of the physiologically based models is that they incorporate biological processes. These models usually consist of a set of differential equations which describe carbon allocation within the plant. Their shortcoming is that this allocation is limited to a course scale of resolution for the plant dimensions

that they model. For example, Promnitz's (1975) work includes allocation to four pools: stem elongation, stem thickening, roots, and leaf mass. Absent from this work is any explicit geometry of the plant. Empirical models have the advantage of considering the plant's geometry at either a course or fine scale of resolution, and they have been used for management purposes (Daniels and Burkhart 1975). The criticism of this modeling approach is that they lack "complete biologically-derived causal relationships for growth" (Promnitz 1975).

An "ideal" tree growth model would incorporate the effects of both genetic potential and environmental resources and conditions on cellular physiological processes. This model would then allocate cellular products to a geometrically-explicit routine for radial and extension growth. The limitation to developing this model is the lack of information on carbon allocation and the effects of genetics and environment on this process. For this reason, there has not been more hybridization between these two modeling approaches. This area of physiological research is just now burgeoning (e.g., Gifford and Evans 1981, Wardlaw 1976, and Wareing and Patrick 1975).

Three-dimensional, empirical tree models have another advantage which was mentioned in Chapter 1. Many studies of canopy physiological processes occur at the level of the individual branch (e.g., Dickmann and Gordon 1975) or at selected canopy positions (e.g., upper and lower canopy, McLaughlin and McConathy 1979). Other processes, such as light interception and branch death,

themselves depend, in part, upon canopy geometry. These models can be used to make inferences about canopy design (e.g., Honda and Fisher 1978, Honda and Fisher 1979).

The purpose of this chapter is to present a branching model for plantation-grown sycamore (*Platanus occidentalis* L.) trees. The model is similar to that of Honda (1971 and its second generation offspring; e.g., Fisher and Honda 1977) and Hofmann (1981) in that it examines the three-dimensional extension growth of a species. The equations developed in Chapters 3 and 5 were used to predict the various components of growth.

## Model Description

The model consists of a main program which, in turn, calls a series of subroutines. A flowchart of MAIN is given in Figure 6.1. A listing of the FORTRAN code for the entire model is given in Appendix A. Model input data are given in Appendix B. The model uses the following subroutines:

INPUT - inputs length of the run, number of trees, soil characteristics, site characteristics, monthly mean temperature and total precipitation, standard deviations for the climate variables, and the mean relative mode positions for each node class and their covariances.

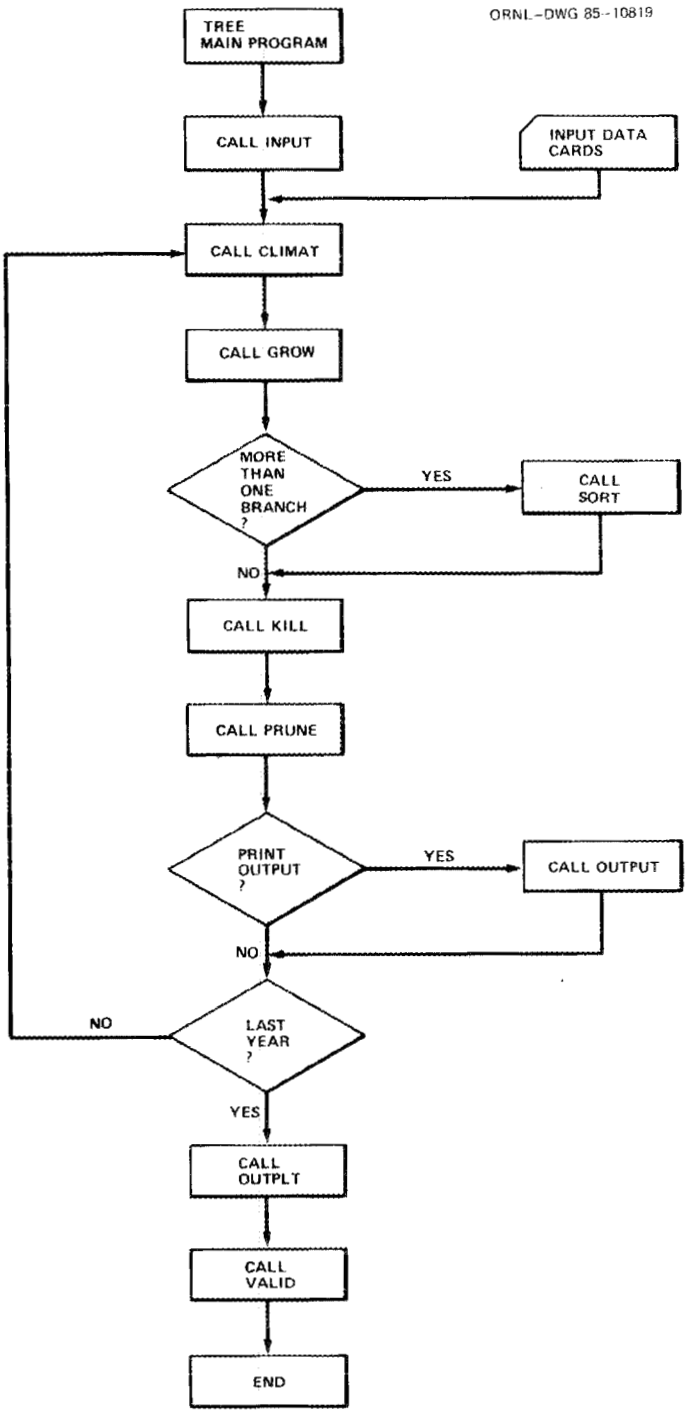



Figure 6.1. Flowchart for the main program in TREE. Each box containing the term CALL is a call to a subroutine.

CLIMAT - uses randomly generated monthly temperature and precipitation values to calculate the DUR soil moisture index developed in Chapter 3.

GROW - computes leader and branch extension growth. This subroutine is the workhorse of the model and will be discussed later in greater detail.

NODEAZ - calculates the number of nodes on a branch and their positions and azimuths.

KILL - determines trunk dieback, kills higher-order branches attached to a dead branch, and randomly kills living branches.

PRUNE - prunes dead branches from the storage arrays.

NEWID - generates ID for trunks and daughter branches.

COORD - determines branch coordinates as well as azimuth and inclination relative to gravity for 1-year-old branch sections.

SORT - sorts branches.

OUTPUT - outputs branch variables. It also has the facility to output node distances and azimuths.

OUTBR - a utility program used for debugging which outputs branch variables for one branch.

OUTPLT - outputs coordinates for plotting.

VALID - samples the model output to validate the model. This will be discussed below under the "Validation" section.

ERR - utility used to stop the program.

The storage arrays are designed to hold all the variables associated with one branch. At present, the program limits tree growth to six years, but this can be extended by expanding the dimension of the storage arrays, and by modifying the sort and output subroutines. Each branch is given an identification (ID) which accommodates up to a fifth-order branch. This ID includes the age (suffix "A") as well as the node number (suffix "N") of all ancestors of the branch. The method of branch identification is similar to that described in Chapter 2 but differs in that the node position for all branch orders becomes the node position for the next lower branch order. For example, a primary branch is designated by the age of the trunk to which it is attached (TA) and the node number on that trunk section (TN). Other branch variables in the model are: order (ORD), branch age (BAGE), inclination relative to the parent (PANG), azimuth relative to the parent (PAZ), mother length (GROM), mother node distance (NODE), "grandmother" node distance (NODEG), azimuth (AZ) and inclination (ANG) relative to gravity, length (LEN), number of nodes (NNODES), condition (COND), node/azimuth array pointer (NAPT), number of daughters (NDAUT), and x, y, and z coordinates (X, Y, and Z). Also associated with each branch are two 50 element arrays that store node distances (NODED) and azimuths (AZIM) for a maximum of 25 nodes for each of two years. A further description of several of the subroutines follows.

Subroutine CLIMAT

Chapter 3 discussed a program developed by Mann and Post (1980) to simulate soil moisture. That program was modified by Pastor and

Post to include their (1984) summary of Thornthwaite and Mather's actual evapotranspiration. Data for observed mean monthly temperatures and total monthly precipitation were added as input to the model, and three soil moisture indices were developed and used to analyze the effect of soil moisture deficits on extension growth. Subroutine CLIMAT is that same program, modified to generate random monthly soil moisture conditions. Input to this subroutine includes monthly mean temperature, total precipitation, and standard deviations for these variables calculated from 53 years of data. To determine if the monthly temperatures or amounts of precipitation are independent of one another, simple correlation coefficients were calculated. Of the 66 possible correlations for each set of variables, only 8 were significant ($p \leq 0.05$) for temperature and only 4 for precipitation. Therefore, the assumption was made that the monthly observations are independent. A normal random number generator was used to calculate monthly temperature and precipitation from these means and standard deviations.

Subroutine GROW

This subroutine is built around the variables defining a "complete description" of crown geometry that were listed at the beginning of Chapter 5. It also determines branch growth at all canopy positions and updates ID. A flowchart of the subroutine is given in Figure 6.2. The first year of growth, this subroutine calls NEWID to generate ID for the trunks and then calculates the random TREE effects for extension growth, number of daughters,

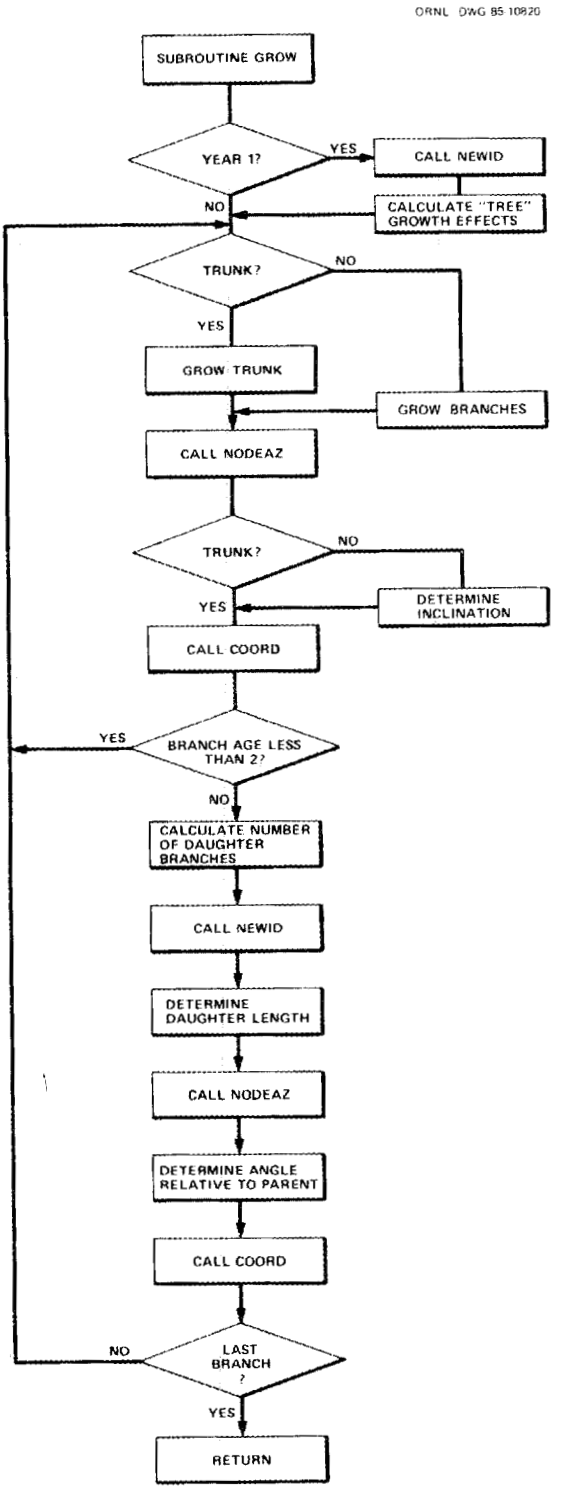



Figure 6.2. Flowchart for subroutine GROW. Each box with the term CALL is a call to a subroutine.

mother/daughter branch angle, and inclination. It then shifts values for LEN, ANG, NNODES, and NDAUT to the next array position (aging them) and increases the "age" variables in the ID. Since observed heights for first year growth are more a function of the depth of planting than of genetic or environmental factors, mean observed tree height (71.9 cm) and standard deviation (29.8 cm) are used in conjunction with a random number generator to determine first year growth. Height growth for other years is calculated from the equation developed in Chapter 3. For branches, extension growth is calculated using the equation developed in Chapter 5. The effects of environmental and genetic variables were included in that analysis by dividing branch AGI length by leader AGI length. The simulation includes these effects on branch extension growth by including their effect on leader extension growth. For example, a dry year will reduce extension growth throughout the crown through its effect on leader growth. For both leader and branches, NODEAZ is called to determine the distance to, and azimuth of each node. The inclination of the current branch growth is determined next. COORD is then called to determine the three-dimensional coordinates of the branch terminus. On 2-year-old branches, the number of daughters produced is calculated, NEWID is called to initialize the variables for these daughters, and variables obtained from the mother branch are stored. All daughter branches then follow a course of events which parallels that experienced by their mother

branch; their length is determined, NODEAZ is called to give node distance and azimuth, and COORD is called to calculate coordinates.

Subroutine NODEAZ

The purpose of this subroutine is to determine node distances and azimuths. These two variables are stored in each of two 50 element arrays. NODEAZ begins by calculating the number of nodes on a branch using the equation developed in Chapter 5. On branches older than two years, node positions on the 2-year-old section are temporarily stored in an array called NODEGT which is used to store NODEG for use in calculating branch extension growth. Node and azimuth measurements on the 1-year-old branch section are then moved to the 2-year-old position. Since a model could not be fit to the node distance data, mean vectors and covariance matrices were generated directly from the "normalized" node distance measurements. However, for several of the node classes, sample size was too small to accurately estimate these matrix elements. To circumvent this problem, branches of several node classes were pooled together, using piecewise linear interpolation. By this method, branches with 16, 17, and 18 nodes were pooled together, as were observations on branches with more than 19 nodes. NODEAZ then uses these covariance matrices and a multivariate normal random number generator to form a vector of deviates which is added to the mean vector. Back interpolation is performed where appropriate. Absolute node positions are calculated by multiplying relative node distances by branch lengths.

Primary branch azimuths are calculated from the observed mean angle of divergence (145.7 degrees), its standard deviation (43.0 degrees), and a random number generator. It was shown above (Chapter 5) that 27.5% of the annual growth increments (AGI's) had a reversed direction of phyllotaxis. A uniform number generator simulates this phenomenon in the model. On primary and higher-order branches, daughters form alternately at 90 and 270 degrees relative to the parent. Another uniform number is drawn to determine at which of these azimuths the first daughter branch forms. The azimuths then alternate between these two means with increasing variance up to a distance of 90 cm, at which point the phyllotaxis becomes spiral. A circular normal random number generator is used to predict the angular deviation for the opposite phyllotaxis. For the spiral phyllotaxis, the model uses a technique similar to that used for primary branches.

Subroutine KILL

This subroutine has three functions: to determine trunk dieback, to kill all higher-order branches attached to a dead branch, and to kill living branches. Field observations showed that 17.4% of the trees were one year younger than the plantation, and this was attributed to dieback. Of those that show dieback the first year, 12.5% also do so the second year. This is simulated by using a uniform number generator.

In subroutine GROW, a branch is marked for removal if its total extension growth is less than 0.5 cm in any year. Subroutine KILL marks for removal all higher-order branches attached to that branch.

KILL also kills living branches. Little is known about the demographic factors which produce final tree shape (J. White 1980). To obtain a thorough understanding of these processes would require making repeated observations on branch cohorts. This effort would lead to a statistical demography of branches, but would not elucidate the mechanisms behind the metapopulational changes. One current work on bud demography is Maillette's (1982a) paper on silver birch. She later (1982b) incorporated this information into a Leslie matrix which was used to examine population dynamics.

Little is known about the mechanisms involved in branch death. Millington and Chaney (1973) asserted that branch death is influenced by a number of factors and concluded that light intensity appears to be the most important of these. Other authors have attributed branch death to competition for light (and moisture and minerals; Harper 1977, Kramer and Kozlowski 1979, and J. White 1980). Putz et al. (1984) observed "crown shyness" in Costa Rican forests. They found two mechanisms proposed in the literature to explain this phenomenon: mutual shading and mechanical abrasion. Their field observations revealed broken twigs and few leaves on branches bordering crown shyness gaps. The sum of intercrown displacements during wind and crown separation distance in still air were examined, and the two were found to be significantly correlated.

They concluded that "crown shyness" in this forest was due to mechanical abrasion. With only few such exceptions, the literature on branch death is scant.

Lacking a strong theoretical base from which to determine branch death, empirical methods could be developed. For example, branches could be sorted by order, age, and number of nodes. At each node position in each of these subclasses, the branch survival probabilities could be calculated and used in the model. A second technique and the one used in this work is to infer changes in time from changes in space. The regression developed to predict the initial number of daughters present on 2-year-old branch sections (Chapter 5) was used to predict the initial number of daughters present on older branch sections. Survival was then calculated as the observed number of daughters on a branch divided by the predicted number of daughters. These mean survival rates were then modeled by a regression equation. It was assumed that mortality was concentrated on the short, basal branches. This assumption has an empirical basis (Schutt, unpub. man.). Table 5.10 shows that over 92% of the variation in number of daughters produced was explained from the number of nodes on the mother branch and a TREE effect. However, as mentioned in Chapter 2, the number of nodes could not be determined on several lower trunk sections, so this equation predicting number of daughters was reanalyzed using mother branch length and order.

Branch survival probabilities were predicted from parent branch order (PORDER), parent age nested within parent order (PARAGE(PORDER), and a random TREE class effect. Results are shown in Table 6.1. The parameterized model is:

$$SURVIV = 0.381 + PORDER + PARAGE(PORDER) + TREE$$

where PORDER is 0.894, 1.090, 0.939, and 0.000 for orders 0 (trunk), 1, 2, and 3; PARAGE(PORDER) is -0.089, -0.200, -0.158, and 0.308 for orders 0, 1, 2, and 3; and TREE is distributed normally with mean 0.0 and calculated variance 0.010. The number of branches surviving is equal to the predicted fraction multiplied by the initial number of daughters. Branches are flagged for deletion if their node number is less than the number of surviving daughters -1 (the minus 1 is added because no daughters form at the last node on a branch).

Subroutine COORD

This subroutine determines x, y, and z coordinates for all branch sections. Two points are calculated for the first year of branch growth, and in subsequent years only one is needed. When branches are formed, azimuth and inclination are calculated relative to the mother branch rather than relative to gravity. For primary branches, these azimuths and inclinations are the same and can be stored directly. For second- and higher-order branches, axis translation and rotation are needed to determine the coordinates of the branch AGI apex, and the equations for this orthogonal rotation were taken from Hofmann (1981). Once the coordinates for the first

Table 6.1. ANOVA for the regression predicting the probability of survival of daughter branches. Independent variables are the order of the parent branch (PORDER), parent age nested within order (PARAGE (PORDER)), and a random TREE effect.

| Source of Variation | df | Sum of squares: Full model | Sum of squares: Type III | MS | F |
|---|---|---|---|---|---|
| Model | 16 | 17.29 | | 1.08 | 16.18*** |
| PORDER | 3 | | 0.71 | 0.24 | 3.56* |
| PARAGE (PORDER) | 4 | | 11.42 | 2.86 | 42.76*** |
| TREE | 9 | | 5.56 | 0.62 | 9.25*** |
| Error | 535 | 35.73 | | 0.07 | |
| Total | 551 | 53.02 | | | $R^2$ = 0.326 |

[ns]Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

two points have been calculated, branch azimuth and inclination relative to gravity can be determined.

Subroutine SORT

Branches must be sorted by TREE, TA, TN, O1A, O1N, and so forth, for subroutines GROW and KILL to operate. A program written by Edwards (1976) at Oak Ridge National Laboratory was used to call the IBM Syncsort program from within the FORTRAN program. Since Edwards' program is system dependent, users wishing to execute the model on their computers will need to modify this section of the code.

## Model Validation

Following the development of a model is model evaluation; its performance must be evaluated. Shugart et al. (1980) have presented a variety of techniques used to verify and validate forest succession models. Modeling three-dimensional tree branching has not developed to this level of sophistication yet, and techniques are just now being developed to validate these models. This section proposes two such methods.

In the current work, mean branch growth at all canopy positions is predicted from regression equations and other analyses developed in Chapter 5. Random variation is entered into the model in several ways. One is through the TREE term used in many of these analyses. This random class variable (TREE) was used to account for potential data dependencies due to lack of independence, and the effect of this term was assumed to be normally distributed with mean 0.0.

However, estimation of fixed effects in an unbalanced mixed model is difficult, and it is the topic of current statistical research (e.g., Harvey 1982, Harville 1972). The approach taken in the present work was to treat the random TREE effect as fixed. This effect was then calculated and added back to the model. Since these tree effects were assumed to be due to genetics, the variables were prefixed with "GEN." These mean TREE effects are: GENEXT = 0.025, GENDAU = -0.379, GENANG = -0.222, GENINC = 4.995, GENNOD = 0.042, and GENSUR = -0.134. The variance for these effects was calculated from the analyses and added back to the branching program by multiplying its square root by a normal random deviate.

A second technique to add random variation to the model is through an error term. Regression analyses attempt to model all the variance present in a given data set. This tool assumes that the errors at any given value of the independent variable are normally distributed with common variance at each value of the independent variable. This common variance is the mean square error term in the regression ANOVA. This variance was added back to the model by using a random normal deviate generator.

Chapter 2 discussed a data set containing measurements of annual tree height for 36 trees. To validate tree extension growth, the model was modified to grow 36 stems. Values of the DUR soil moisture index for the six years of tree growth were input into the model for direct comparison between the two data sets. Tree heights were compared by t-tests. Table 6.2 shows that the model generated

Table 6.2. Results of the model validation for tree height.

| | N | | Mean height | | Standard deviation | | |
|---|---|---|---|---|---|---|---|
| Year | Observed | Model | Observed | Model | Observed | Model | t |
| 1982 | 36 | 36 | 535.1 cm | 493.4 cm | 114.6 cm | 108.5 cm | $1.583^{ns}$ |
| 1981 | 36 | 36 | 409.9 | 399.7 | 99.7 | 103.6 | $0.426^{ns}$ |
| 1980 | 36 | 36 | 321.3 | 316.4 | 86.4 | 100.9 | $0.223^{ns}$ |
| 1979 | 36 | 36 | 271.6 | 262.9 | 82.1 | 94.0 | $0.417^{ns}$ |
| 1978 | 35 | 36 | 195.6 | 165.9 | 77.3 | 81.0 | $1.578^{ns}$ |
| 1977 | 30 | 27 | 74.1 | 66.5 | 26.1 | 22.7 | $1.168^{ns}$ |

$^{ns}$Not significant.

trees are slightly smaller then the observed trees but that this difference is not significant for any year of growth. It was concluded that the model accurately predicts leader extension growth.

To validate the model's ability to produce branches, a data set was needed which contained observations measured by a technique different from that used to develop the model. This was done by measuring branches within a given area of the crown relative to gravity. A 0.25 $m^3$ cube was constructed with dowels for this task. Ten trees were chosen by the same selection criteria discussed in Chapter 2. Observation were made on each tree at each of several canopy positions, one near the tree top and one at each of four azimuths in the middle of the canopy. The cube at the tree top was placed so that: (1) the plane at the base of the cube was at 75% maximum tree height, (2) the trunk axis was in a second cube plane, and (3) a plane passing through the trunk axis and the cube center was at an azimuth of 165 degrees. This azimuth was chosen because it was perpendicular to the row direction (in an attempt to reduce competitive effects) and it was on the south side of the tree. Cube position for the tree's middle canopy was determined by finding the maximum branch reach (perpendicular distance) from the trunk. At these four positions, the cube was placed so that: (1) the plane at the base of the cube was at 50% maximum tree height, (2) a plumb line lowered from the center of the cube was at an azimuth of either 75, 165, 255, or 345 degrees (positions 2, 3, 4, or 5), and (3) a plane passing through both the tree trunk and

the center of the cube was parallel to two sides of the cube (i.e., the azimuths of the sides were at 75/255 and 165/345 degrees).

All branch AGI's falling within the volume of the cube were sampled. For each segment, the following were measured:

1. Primary branch age (or age of the primary branch to which the sample branch is connected,
2. branch section age for the branch and all its lower-order ancestors,
3. length of the branch AGI falling inside the cube,
4. azimuth relative to north, and
5. inclination relative to gravity.

Subroutine VALID examines every branch section generated by the model to determine if part of that branch lies within any of the validation positions. If not, the next branch section is examined. If it does, the same measurements made on the actual trees are taken from the branch.

Two models were compared to this data set. Both models include all the random branching effects described above; they differ in that model 1 does not include random branch mortality while model 2 does. Sample plots for these two models are shown in Figure 6.3.

Tables 6.3 and 6.4 give the results for the comparisons of these models with the validation data set. The mean number of branches produced by model 1 does not differ significantly from the observed data for any of the five cubes. In cube 1, this mean is slightly lower than the observed mean, yet for all other cases it is higher (almost twice as high in cube (3), although not significantly so.

Figure 6.3. Sample plots for trees generated by the model. Plots a-f are from model 1 and plots g-l are from model 2. Both of these models include all random effects. They differ in that model 2 includes random branch mortality and model 1 does not.

ORNL-DWG 85-10986

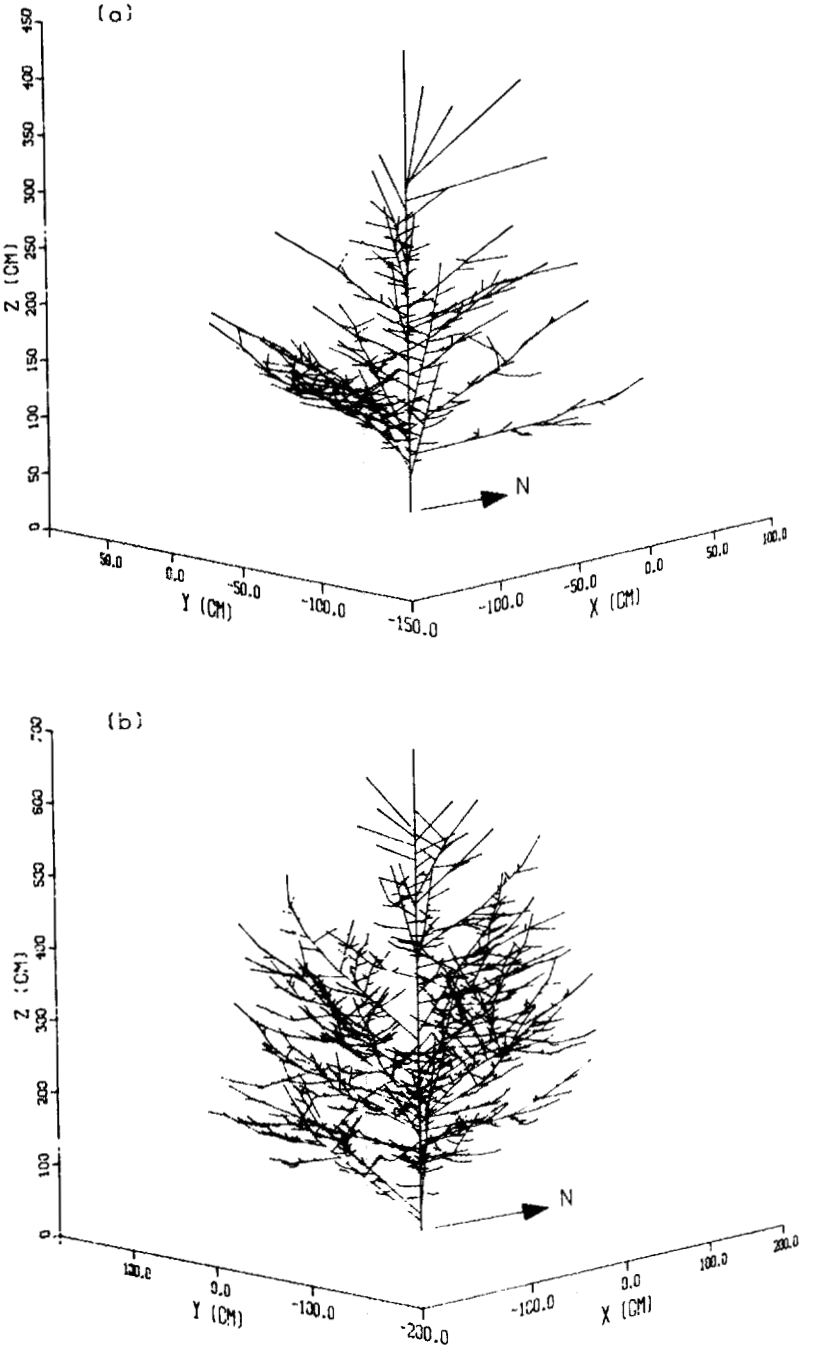



Figure 6.3

ORNL-DWG 85-10987

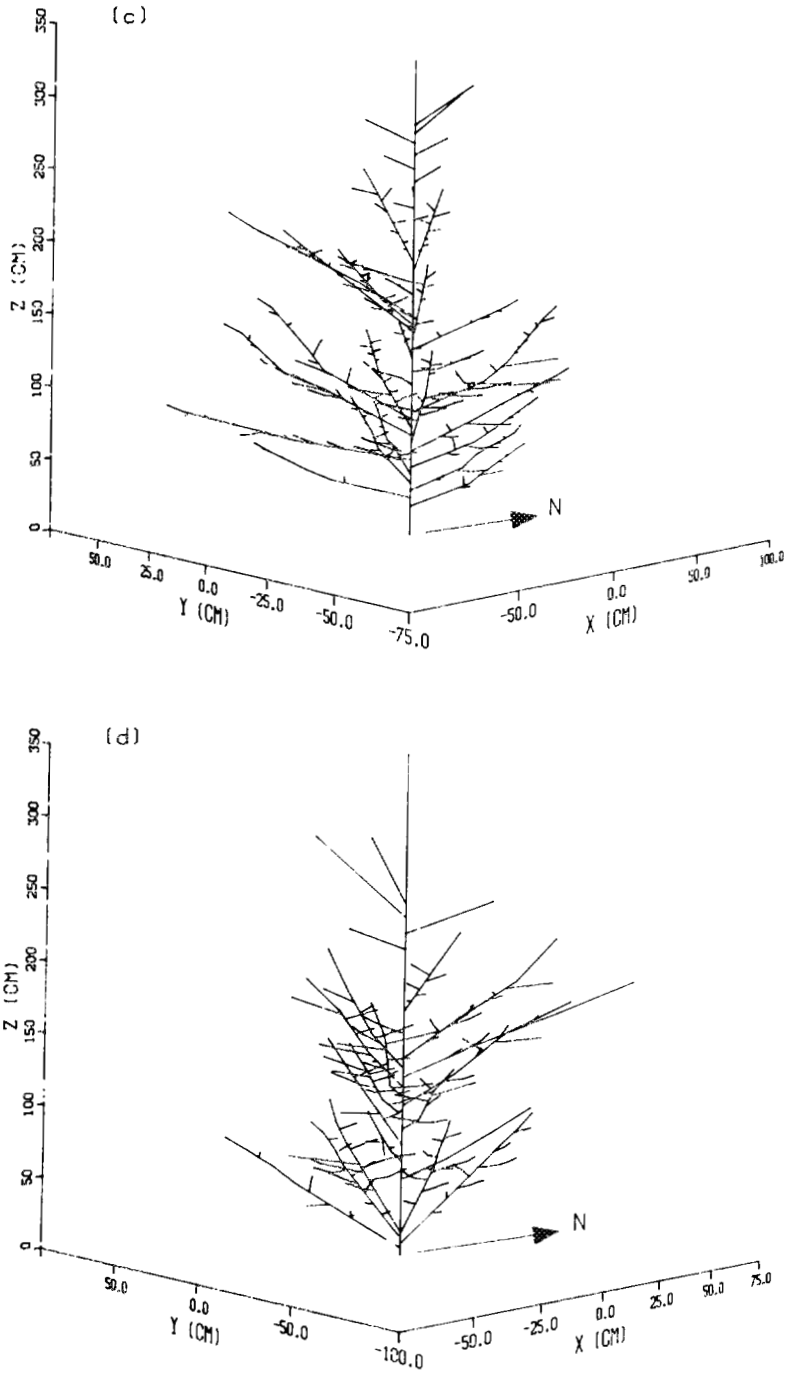



Figure 6.3 (continued)

ORNL-DWG 85-10988

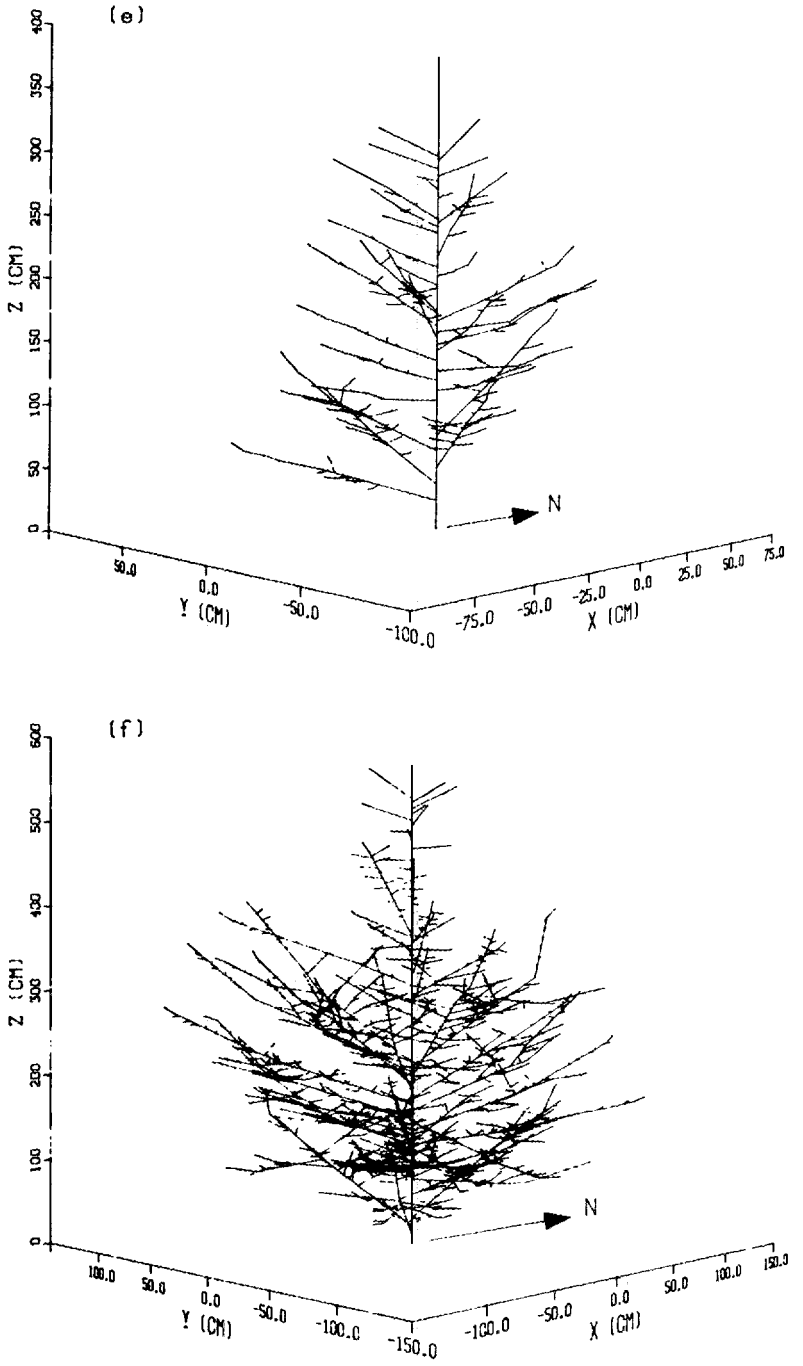



Figure 6.3 (continued)

ORNL-DWG 85-10989

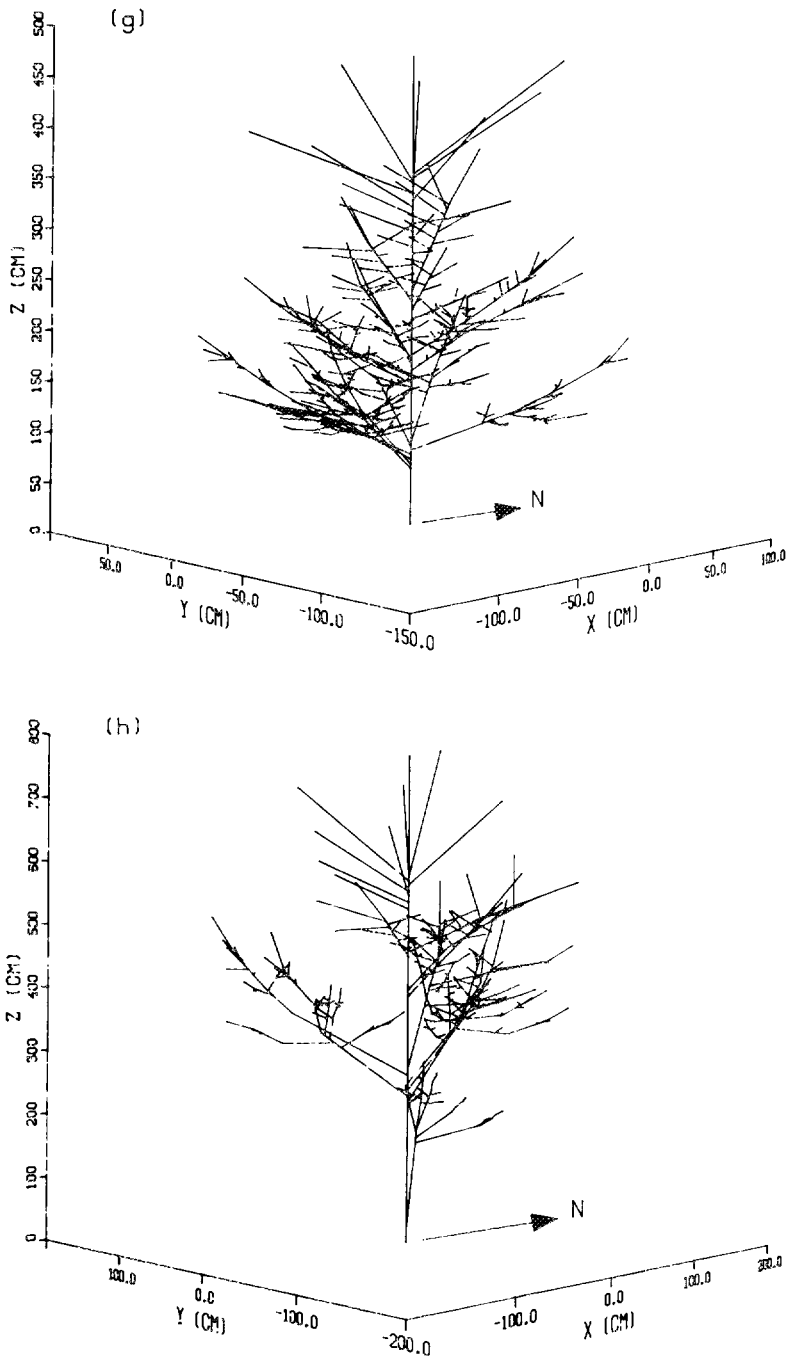
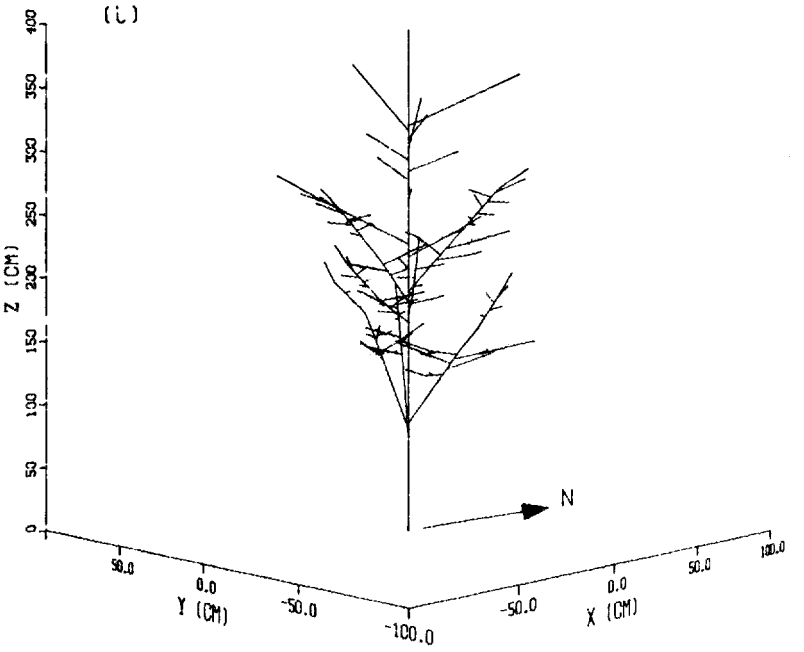



Figure 6.3 (continued)

ORNL-DWG 85-10990



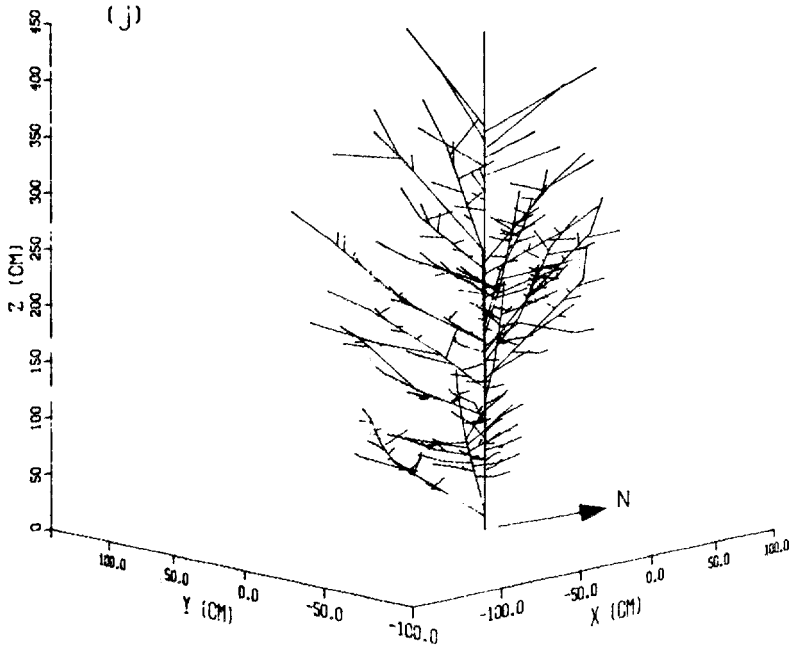
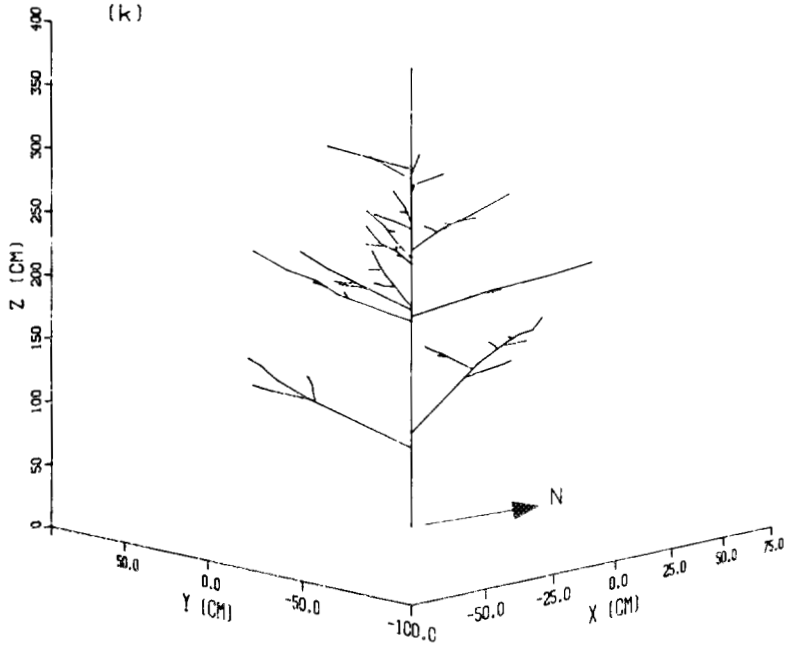




Figure 6.3 (continued)

ORNL-DWG 85-10991



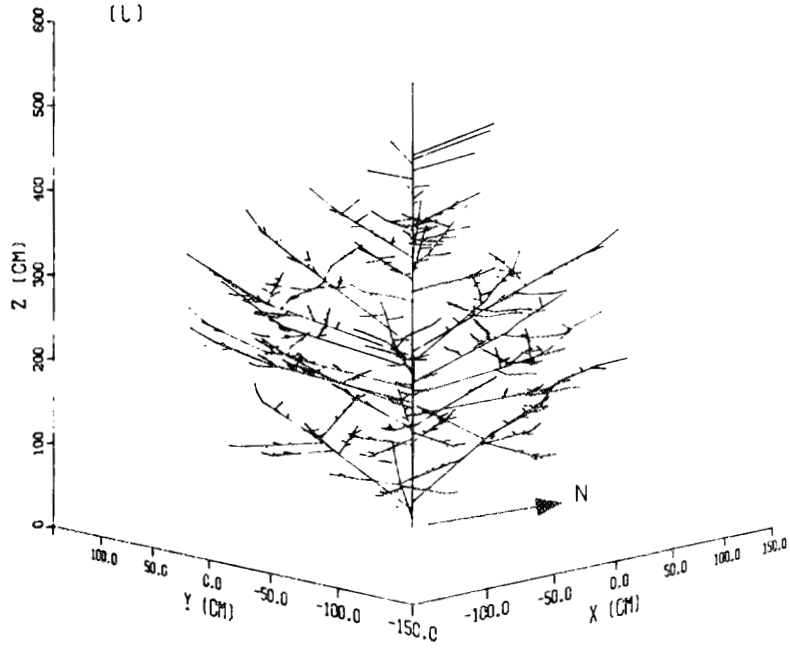




Figure 6.3 (continued)

Table 6.3. T-test comparisons for Models 1 and 2 with field observations on four branching variables. Model 1 does not include random branch mortality while Model 2 does include this effect. The mean values of the variables and the t statistics are shown.

| Variable | 1 | | 2 | | 3 | | 4 | | 5 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | t | $\bar{x}$ | t | $\bar{x}$ | t | $\bar{x}$ | t | $\bar{x}$ | t |
| Observed Cube | | | | | | | | | | |
| Number of Branches | 8.70 | | 19.10 | | 21.00 | | 19.80 | | 20.30 | |
| Primary Branch Age | 1.60 | | 3.31 | | 3.47 | | 3.36 | | 3.38 | |
| Mean Branch Section Length (cm) | 30.41 | | 11.70 | | 11.18 | | 13.70 | | 12.30 | |
| Mean Inclination (degrees) | 46.45 | | 61.19 | | 61.32 | | 57.75 | | 57.64 | |
| Model 1 Cube | | | | | | | | | | |
| Number of Branches | 7.00 | $0.60^{ns}$ | 27.00 | $-0.43^{ns}$ | 42.33 | $-2.04^{ns}$ | 29.00 | $1.30^{ns}$ | 26.00 | $-0.95^{ns}$ |
| Primary Branch Age | 1.43 | $1.03^{ns}$ | 3.74 | $-5.28^{***}$ | 3.72 | $-3.15^{**}$ | 3.79 | $-5.58^{***}$ | 3.62 | $-2.56^{*}$ |
| Mean Branch Section Length (cm) | 33.33 | $-0.59^{ns}$ | 11.52 | $0.12^{ns}$ | 11.98 | $-0.62^{ns}$ | 13.31 | $0.22^{ns}$ | 20.58 | $-4.50^{***}$ |
| Mean Inclination (degrees) | 52.66 | $-1.66^{ns}$ | 63.50 | $-0.79^{ns}$ | 57.43 | $1.65^{ns}$ | 55.54 | $1.06^{ns}$ | 54.68 | $1.05^{ns}$ |
| Model 2 Cube | | | | | | | | | | |
| Number of Branches | 3.83 | $2.62^{*}$ | 10.80 | $1.54^{ns}$ | 15.83 | $0.78^{ns}$ | 8.17 | $2.56^{*}$ | 10.83 | $2.03^{ns}$ |
| Primary Branch Age | 1.17 | $3.87^{***}$ | 3.56 | $-2.46^{*}$ | 3.42 | $0.51^{ns}$ | 3.43 | $-0.51^{ns}$ | 3.38 | $0.89^{ns}$ |
| Mean Branch Section Length (cm) | 49.39 | $-3.81^{***}$ | 13.63 | $-1.06^{ns}$ | 14.64 | $-2.57^{*}$ | 14.57 | $-0.40^{ns}$ | 20.58 | $-3.68^{***}$ |
| Mean Inclination (degrees) | 40.17 | $1.87^{ns}$ | 61.07 | $0.03^{ns}$ | 59.39 | $0.83^{ns}$ | 50.57 | $2.64^{**}$ | 54.68 | $1.05^{ns}$ |

$^{ns}$Not significant.

*Significant at 0.05 level.

**Significant at 0.01 level.

***Significant at 0.001 level.

Table 6.4. Chi-square tests to determine if the frequencies of branches in each order for Models 1 and 2 differ significantly from field observations.

| Sample position | Observed Order | | | | | Model 1 Order | | | | | | Model 2 Order | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Total | 1 | 2 | 3 | 4 | Total | $X^2$ | 1 | 2 | 3 | 4 | Total | $X^2$ |
| Cube 1 | 61 | 25 | | | 86 | 17 | 4 | | | 21 | $1.02^{ns}$ | 21 | 2 | | | 23 | 4.63* |
| Cube 2 | 40 | 100 | 49 | 2 | 191 | 14 | 26 | 26 | 0 | 66 | $7.67^{ns}$ | 11 | 31 | 12 | 0 | 54 | $1.09^{ns}$ |
| Cube 3 | 46 | 103 | 56 | 5 | 210 | 27 | 62 | 38 | 0 | 127 | $3.55^{ns}$ | 17 | 55 | 23 | 0 | 95 | $4.69^{ns}$ |
| Cube 4 | 52 | 99 | 44 | 3 | 198 | 21 | 41 | 25 | 0 | 87 | $3.27^{ns}$ | 13 | 23 | 12 | 1 | 49 | $0.30^{ns}$ |
| Cube 5 | 44 | 111 | 48 | | 203 | 30 | 35 | 13 | | 78 | 13.12** | 24 | 27 | 14 | | 65 | 9.15* |

$^{ns}$Not significant.

*Significant at 0.05 level.

After a period of time, the theoretical number of branches produced by trees is higher than the observed number (Borchert and Slade 1981, J. White 1980) and this difference increases as the tree ages. Because of this, branch mortality must be included in any model that predicts crown growth. The high variance of the data is probably the reason these means are not significantly different. However, some mortality does occur in model 1 in that subroutine GROW kills any branch whose annual extension growth is less than 0.5 cm in any given year. Without this aspect of the model, the number of branches produced would be even greater. Results for model 2 demonstrate that samples from this model have fewer branches than the validation data set (in some cases less than 1/2 than the observed number), although these differences are significant in only two of the five cubes. As shown in the section for subroutine KILL above, the regression used to predict branch survival described only 32.6% of the variation in this data set. Part of this may be due to the method used to estimate survival (in some cases it may be over 100%) and part can be attributed to the general lack of knowledge about the factors determining branch mortality. As a result, it appears that this regression overestimates mortality. Resolution of this problem will depend on the development of an empirical and theoretical basis for predicting branch mortality.

Results for the chi-square tests comparing frequencies of branches of each order are shown in Table 6.4. For model 1, the frequencies differ only for cube 5. Results for model 2 show that

cubes 1 and 5 differ significantly. In all three of these cases, the number of primary branches sampled is too high. Since the size of the cube is constant, sampling small trees results in including more young primary branches than would be included in a sample of a larger tree. This may be the case in this study. Overall, it appears that the distribution of branch orders produced by these two models well represents that of the actual trees.

Table 6.3 shows the comparison for branch lengths. The branches in cube 5 of model 1 are much longer than the measured trees. For all other canopy positions, the lengths are strikingly similar. Results for model 2 are more complicated. These lengths do not differ significantly from the field observations for cubes 2 and 4 yet do for cubes 1, 3, and 5 (cubes 1 and 5 at $p \leq 0.001$). Comparisons of the mean number of branches in both models showed that model 1 has more branches than average and model 2 has fewer (although only two of the ten comparisons are significant). It was also shown that the distribution of orders differed significantly for only three of the ten positions. Since this is so, it can be deduced that this difference is not due to selective mortality on second- and higher-order branches (shorter branches), but is evenly distributed across the shortest branches of all orders. When the methodology for determining branch mortality was being determined, it was assumed (based on a previous study) that the branches near the base of the parent AGI were killed. This assumption deserves further attention. The observation that primary branches are more

numerous than anticipated for three of the 10 study cubes is evidence against this theory. Another alternative explanation for this phenomenon is that the equation used to determine elongation growth needs further work. This may be the reason that no fourth-order branches were sampled.

For both models, only one of the comparisons for inclination was significant. The agreement with the data set is remarkable.

These analyses show that branch extension growth and branch mortality may be the most sensitive branching variables and the processes governing these phenomana deserve further attention. The analyses for the validation of model branching demonstrate that the model does a good job of simulating the crown geometry of sycamore.

# CHAPTER 7

## CONCLUSIONS AND IMPLICATIONS

The quotation given at the beginning of Chapter 1 stated that plant growth is a function of its genetic potential as modified by environmental factors. This work has been an attempt to quantify and model the processes involved in tree growth and to evaluate environmental effects on those processes.

Chapter 3 demonstrated that bole extension growth in plantation-grown sycamore (*Platanus occidentalis* L.) trees is a function of soil moisture, fertilization/cultivation, and tree genetics. The soil moisture tension used to define "extension growth stress" (-3 bars) worked well as both late-season soil moisture values and each of three soil moisture indices were able to predict extension growth. The analysis demonstrated that Union Camp's policy of early-rotation fertilization/cultivation and mid-rotation fertilization does increase height growth in this species at this site. The significance of the TREE effect also has management implications. One possibility is that this factor simply represents random events which affected individual trees (e.g., insect damage, shading, or micro-site effects). A second, and perhaps more viable option is that genetic differences exist among trees in their potential ability to elongate. This indicates that

selection could be done to choose superior genotypes which would increase biomass yield from these plantations.

Analysis of Type I proleptic branching (Chapter 4) showed that trees differ in their potential to produce Type I branches at given ages. Those that do produce Type I branches were examined, and it was found that the probability of a tree forming Type I branches in even years was associated with its probability of forming Type I branches in odd years. It was concluded that Type I proleptic branch formation has a genetic basis. Data were not available to determine if the effect of "age" on Type I branch formation was truly due to physiological age, or due to climate change over the study period, to fertilizer effects, or to interactions among any of these factors. The number of Type I proleptic branches was also found to be associated with the amount of leader extension growth.

Type I proleptic branching appears to be a mechanism through which a species can develop its photosynthetic area near the tree leader, and species with this mechanism available to them would have a selective advantage with respect to light interception. This also has management implications. Since weed competition is costly to a plantation manager, selection for trees with Type I branching may be a way to decrease this competition and, thereby, reduce costs. Since this trait is observed more frequently on trees with greater extension growth, concurrent selection for greater extension growth and Type I proleptic branch formation may have economic advantages.

Type I proleptic branches form along the lower trunk annual growth increment (AGI), form at a slightly more acute angle than

Type II proleptic branches, and, after the first year of growth, do not differ in elongation growth from Type II branches located at the same position.

Analyses were performed to quantify all variables needed for the "complete description" of canopy geometry discussed in Chapter 5.

An equation was developed to predict extension growth for all canopy positions from branch order, parent age, branch age, "ancestor" (e.g., mother, grandmother, and so forth) node distance (acrotony), and ancestor length.

Node density (number of nodes /branch length) was predicted from branch length, fertilization/cultivation, soil moisture, and a TREE effect. Both increased fertilization/cultivation and increased soil moisture availability increased node density. Longer branches have a lower node density, a fact observed by others.

The figure for node position demonstrated that there are three identifiable phases in branch growth. In the first, branch internode distance increases. This is followed by a period of almost constant, but slightly declining, internode distance. In the third phase, internode distance decreases. All three phases are identifiable on longer branches (those with more nodes). With decreasing branch length, the middle phase becomes less important and finally disappears. On shorter branches, the third phase also disappears. On the shortest branches, the first phase becomes less evident.

Phyllotaxis of branches of all orders was examined. Primary branches show no preferred direction of orientation. The mean angle of divergence between leaves or branches was 145.7 degrees with a

standard deviation of 43.0 degrees. The direction of this spiral was clockwise, but on 27.5% of the trunk sections it was reversed. This reversal of the direction of the ontogenetic spiral was spread across the population; it was not concentrated at any tree age or on any tree.

Second- and higher-order branches form at mean angles of 90 and 270 degrees relative to their mother branch. The circular variance about these means increases with increasing node number or distance on a branch AGI. At a point beyond 13 nodes or 90 cm, the phyllotaxis becomes spiral. While the number of observations beyond this point is few, it appears that here, as well as for the primary branches, the direction of the spiral can be either clockwise or counterclockwise.

Most of the variation in the number of daughter branches formed on a mother branch was predicted from the number of nodes on the mother (or mother length) and a TREE effect. This relationship was used in Chapter 6 to develop a regression equation to predict branch mortality.

The angle of divergence between a mother and daughter branch was determined from daughter node number, number of nodes on the parent, number of daughters, daughter length, branch order, parent age within order, and a TREE effect. In this analysis, the number of nodes was used to represent epinasty, and the number of daughters and daughter length were used to represent the daughter branches' ability to resist this effect. All variables were significant.

Branch inclination was predicted from branch order, the first angle of the branch, the distance to that first angle (which also includes an effect due to order), and a TREE term. With increasing branch age, branch tips become oriented more vertically.

The relationships developed for the branching variables were synthesized into a FORTRAN model to simulate the three-dimensional crown geometry of sycamore. Output for leader extension growth by the model agrees well with observed data on extension growth as does output describing model branching.

The statistical analyses developed in this work demonstrate a varying degree of "success" in explaining the variation in the data. Some of the models explain over 90% (e.g., those predicting node density or number of daughter branches) and others explain less (e.g., trunk extension growth $R^2$ = 0.549, branch extension growth $R^2$ = 0.792, degree of Type I proleptic branching $R^2$ = 0.112, and branch survival $R^2$ = 0.326). The degree of success of the fit of a statistical model is a result of one of several factors. One such factor is the skill with which the model to be fit is chosen (e.g., the correct curve shape and the correct variables). Another problem which results in poorly fit models is a lack of understanding of the mechanisms governing the process being modeled. This results in attempting to guess at those mechanisms and then including them in the model. This problem is compounded in situations where a number of variables are involved, a situation often encountered in the present work. Even where some theoretical information is known (e.g., parent/daughter branch angle is affected by epinasty and

negative geotropism) it was still necessary to select a variable which would best represent this effect. Even in this example, where a theoretical basis of the phenomenon was somewhat known, only 39.4% of the variance was accounted for.

This lack of fit of the equations to the data indicate areas of branch growth that deserve further attention. For example, little is known about the control of the degree of Type I branching. The control of branch death is, likewise, little understood. In this second example, the analysis is so complicated (involving tree genetics, cellular physiology, tree crown morphology, abiotic environment, etc.,) that an approach using a three-dimensional branching model to examine the effect of crown morphology may be the most viable alternative.

There are many other processes that a spatially-explicit branching model may be used to study. Chapter 1 mentioned light interception as one potential area. Data on crown display have already been collected (Chapter 2), and this is the next logical place for future model work. This new light model, which would include light interception, could be used as the basis of other investigations. For example, it could be used for management purposes to simulate plantation geometry and to examine the effects of spacing or tree genetic variation on light interception. The place to add spacing effects has already been designated in subroutine NEWID. For this application, the effects of spacing on branch characteristics would need to be added. This was the topic of a related study (Schutt, unpub. man.).

The light interception model could also be used to study canopy energy allocation. The relationship between the total amount of light intercepted by a branch and the amount of extension growth could be explored. This may also lead to an understanding of the processes controlling branch death. It may also be possible to use this model to examine the effect of crown geometry on physiological processes. If these techniques lead to further elucidation of the mechanisms governing crown architecture, then those mechanisms could be added to the model's theoretical framework model for the next generation of models.

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# APPENDIX A

# FORTRAN PROGRAM

```
C*****************************************************************************
C
C  THIS PROGRAM GENERATES THREE DIMENSIONAL SYCAMORE TREES
C
C*****************************************************************************
C THE CODE TO THE COMMENT CARDS IS AS FOLLOWS:
C C -COMMENT TO DOCUMENT THE MODEL
C CB -LINES USED TO GROW ONLY THE BOLE
C CC- DEBUGGING TOOL
C CE -"ERROR" RANDOM EFFECTS
C CC -WORK TO BE COMPLETED IN THE MODEL
C CP -LINES USED TO CALL SUBROUTINE KILL JUST TO PRUNE HIGHER ORDER BRANCHES
C CR - RANDOM NUMBER GENERATOR INITIALIZATION
C CS -TO CHANGE THE SIZE OF THE STORAGE USED BY THE MODEL, CHANGE ALL
C CT -"TREE" RANDOM EFFECTS
C CV -LINES TO BE COMMENTED TO VALIDATE THE MODEL
C CW -RANDOM CLIMATE
C      SIZE OF ALL TREE ID ARRAYS AS WELL AS THE STATEMENTS MARKED
C      WITH THIS COMMENT STATEMENT
       COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),O2N(3000),O3A(3000),O3N(3000),O4A(3000),O4N(3000),
     & ORD(3000),BAGE(3000),PANG(3000),PAZ(3000),GROW(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
       INTEGER*2 TREE,TA,TN,O1A,O1N,O2A,O2N,O3A,O3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
       REAL LEN
       LOGICAL*1 COND
       COMMON /CLDATA/ MT(12), TSD(12), MPPTN(12), PPTNSD(12), FC, FCMM,
     & DRY3, BGS, EGS, PLAT
       REAL MT, MPPTN
       COMMON /DUR/ DURLN
CO       COMMON /LEAFID/ PANGL(3000),PAZL(3000),PL(3000),LL(3000),WL(3000),
CO      & AZL(3000),ANGL(3000)
       COMMON /NOBR/ NOBRT,NOBROT,NOTREE
       INTEGER*2 NOBRT,NOBROT,NOTREE
       COMMON /NO/ NYEARS,NTREES,NOYR
       INTEGER*2 NYEARS,NTREES
       LOGICAL*1 FLAG
CE
CV
       DIMENSION DURVAL(6)
       DATA DURVAL /-0.71335,-0.24080,0.00000,-0.90387,-0.26657,0.00000/
C RSTART(I,J): I AND J ARE "ANY INTEGERS"
CR
       CALL RSTART(395879,76)
       NOBRT =0
       NOBRCT =0
       KPRT =1
       CALL INPUT
       DO 20 I=1,NYEARS
         NOYR =I
CE
CV
CV        CALL CLIMAT
         DURLN =DURVAL(I)
         WRITE(6,1) I,DURVAL(I)
     1   FORMAT(' YEAR=',I2,'  LNDUR =',F9.5)
         NOBROT =NOBRT
         CALL GROW
CE
         IF (NOBRT .GT. 1) CALL SORT
```

```
        FLAG =.FALSE.
        IF (MOD(I, KPRT) .EQ. 0) CALL OUTPUT(FLAG)
        CALL KILL
        FLAG =.TRUE.
CC
CC        IF (MOD(I, KPRT) .EQ. 0) CALL OUTPUT(FLAG)
CE
        CALL PRUNE
CC
CC        IF (MOD(I, KPRT) .EQ. 0) CALL OUTPUT(FLAG)
        IF (NOYR .LT. NYEARS) GO TO 20
CE
        CALL OUTPLT
        CALL VALID
        WRITE(6,10) I
   10   FORMAT(' END OF YEAR ',I1)
   20 CONTINUE
      WRITE(6,25) NOBRT
   25 FORMAT(' TOTAL NUMBER OF BRANCHES =',I5)
      STOP
      END
C***********************************************************************
C
C      THIS SUBROUTINE INPUTS DATA
C
C***********************************************************************
      SUBROUTINE INPUT
      COMMON /CLDATA/ MT(12), TSD(12), MPPTN(12), PPTNSD(12), FC, FCMM,
     & DRY3, BGS, EGS, PLAT
      REAL MT, MPPTN
      COMMON /NO/ NYEARS,NTREES,NOYR
      INTEGER*2 NYEARS,NTREES
      COMMON /MSMVN/ IPOINT(2,17),OMEAN(141),OSIGMA(906)
      INTEGER*2 IPOINT
C  DATA THAT IS REQUIRED FOR THE OPERATION OF THIS ROUTINE IN THE
C  ORDER OF INPUT:
C  CARD: VARIABLE:                                              FORMAT:
C     1  NYEARS = NUMBER OF YEARS IN THE SIMULATION              I5
C    1B  NTREES = NUMBER OF TREES IN THE SIMULATION              I5
C     2  FC = CENTIMETERS OF WATER THE SOIL CAN HOLD
C             AT FIELD CAPACITY                                F8.4,1X
C     2  DRY3 = CENTIMETERS OF WATER BELOW WHICH TREE GROWTH
C              STOPS (3 BARS)                                 F8.4,1X
C     2  DRY15 = PERMANENT WILTING POINT FOR PLANTS (15 BARS) F8.4,1X
C     3  BGS = YEAR DAY ON WHICH THE GROWING SEASON BEGINS (4/15) F5.1,1X
C     3  EGS = YEAR DAY ON WHICH THE GROWING SEASON ENDS (10/15) F5.1,1X
C     3  PLAT = LATITUDE OF PLOT (DEGREES NORTH)               F5.2
C     4  T = MEAN TEMPERATURES (JAN-DEC)  CENTIGRADE           12F6.2
C     5  TSD =TEMPERATURE STANDARD DEVIATION                   12F6.3
C     6  MPPTN = MEAN PRECIPITATION (JAN-DEC) CENTIMETERS      12F6.3
C     7  PPTNSD = PRECIPITATION ST.DEV. (JAN-DEC) CENTIMETERS  12F6.3
C        XMCNTH = THE ARRAY WHICH STORES THE MONTHLY BEGINNING WATER
C                 VALUES. TO GET THE VALUE FOR ANY GIVEN MONTH, USE THE
C                 VALUE FOR MONTH (I +1), THE END-OF-MONTH VALUE.
C     8  K = THE SIZE OF THE NODE POSITION ARRAYS                I2
C     9  OMEAN = THE OBSERVED MEAN RELATIVE NODE POSITION        F9.7
C    10  OSIGMA = THE OBSERVED COVARIANCE MATRIX                 E12.6
C
C
C  INPUT LENGTH OF RUN
C
      READ(5,5,END=1000) NYEARS
    5 FORMAT(I5)
```

```
      WRITE(6,10) NYEARS
   10 FORMAT('0NUMBER OF YEARS =',I5)
C
C  INPUT NUMBER OF TREES
C
      READ(5,5,END=1000) NTREES
      WRITE(6,11) NTREES
   11 FORMAT ('0NUMBER OF TREES =',I5)
C
C  INPUT SOIL CHARACTERISTICS
C
      READ(5,15,END=1000) FC, DRY3, DRY15
   15 FORMAT(3(F7.4,1X))
C
C  PASTOR AND POST'S AET REQUIRE FC  TO BE IN MM
C
      FCMM =FC *10.
      WRITE(6,20) FC, DRY3, DRY15
   20 FORMAT('0FIELD CAPACITY =',F8.4,2X,'3 BAR TENSION =',F8.4,2X,'15
     &BAR TENSION  =',F8.4)
C
C  INPUT SITE CHARACTERISTICS
C
      READ(5,25,END=1000) BGS, EGS, PLAT
   25 FORMAT (2(F5.1,1X),F5.2)
      WRITE(6,30) BGS, EGS, PLAT
   30 FORMAT ('0GROWING SEASON: BEGINNING DAY =',F5.1,2X,'END DAY =',
     & F5.1,2X,'LATITUDE =',F5.2)
C
C  INPUT MEAN MONTHLY TEMPERATURES AND STANDARD DEVIATIONS, AND CONVERT
C  FROM ENGLISH UNITS TO SI UNITS
C
      READ(5,40,END=1000) (MT(I),I=1,12)
   40 FORMAT(12F6.2)
      READ(5,50,END=1000) (TSD(I),I=1,12)
   50 FORMAT(12F6.3)
      DO 45 I=1,12
      MT(I)=(MT(I) -32)/1.8
      TSD(I) =TSD(I) /1.8
   45 CONTINUE
C
C  INPUT PRECIPITATION DATA AND CONVERT FROM ENGLISH UNITS TO SI UNITS
C
      READ(5,50,END=1000) (MPPTN(I),I=1,12)
      READ(5,50,END=1000) (PPTNSD(I),I=1,12)
      DO 55 I=1,12
      MPPTN(I)=MPPTN(I) *2.54
      PPTNSD(I) =PPTNSD(I) *2.54
   55 CONTINUE
C
C  WRITE OUT INPUT DATA
C
      WRITE(6,60)
   60 FORMAT('0MEAN TEMPERATURES (C)')
      WRITE(6,65)
   65 FORMAT(4X,'JAN',6X,'FEB',6X,'MAR',6X,'APR',6X,'MAY',
     >6X,'JUN',6X,'JUL',6X,'AUG',6X,'SEP',6X,'OCT',6X,'NOV',6X,'DEC')
      WRITE(6,70) (MT(I),I=1,12)
   70 FORMAT(' ',12(F7.2,2X))
      WRITE(6,75)
   75 FORMAT('0TEMPERATURE STANDARD DEVIATIONS (C)')
      WRITE(6,65)
      WRITE(6,80) (TSD(I),I=1,12)
```

```
   80 FORMAT(' ',12(F7.3,2X))
      WRITE(6,85)
   85 FORMAT('0MEAN PRECIPITATION (CM)')
      WRITE(6,65)
      WRITE(6,80)(MPPTN(I),I=1,12)
      WRITE(6,90)
   90 FORMAT('0PRECIPITATION STANDARD DEVIATIONS (C)')
      WRITE(6,65)
      WRITE(6,80)(PPTNSD(I),I=1,12)
C
C INPUT THE MEAN VECTORS FOR NODE POSITIONS AND THEIR COVARIANCE.
C THE VARIABLE K GIVES THE SIZE OF THE ARRAY. NNODES 16-18 WERE
C TREATED AS 17; NNODES 19+ WERE TREATED AS 21. BECAUSE THE LAST
C DISTANCE WAS ALWAYS =1.0, THE VECTORS ARE ALWAYS OF LENGTH
C NNODES -1.
      DO 125 NPT=1,16
CC
CC       WRITE(6,95) NPT
CC   95 FORMAT(' NPT =',I2)
         READ(5,100,END=1000) K
  100    FORMAT(I2)
         MBEG =IPOINT(1,NPT)
         MEND =MBEG +K -1
CC
CC         WRITE(6,105) K,MBEG,MEND
CC  105    FORMAT(' ',7X,I2,2(5X,I3))
         READ(5,110,END=1000) (OMEAN(I), I=MBEG,MEND)
  110    FORMAT(8F9.7)
         ISBEG =IPOINT(2,NPT)
         DO 125 I=1,K
           ISEND =ISBEG +I -1
CC
CC         WRITE(6,115) ISBEG,ISEND
CC  115      FORMAT(' ',30X,I4,5X,I4)
           READ(5,120,END=1000) (OSIGMA(J),J=ISBEG,ISEND)
  120      FORMAT(6E12.5)
           ISBEG =ISEND +1
  125 CONTINUE
CC
CC     WRITE(6,130) (CMEAN(I),I=1,141)
CC  130 FORMAT(' ',12F11.7)
CC     WRITE(6,135) (CSIGMA(I),I=1,906)
CC  135 FORMAT(' ',11E12.5)
      RETURN
 1000 WRITE(6,1001)
 1001 FORMAT(' INPUT ERROR!!!!!')
      RETURN
      END
C*********************************************************************
C
C       INITIALIZE COMMON BLOCKS
C
C*********************************************************************
      BLOCK DATA
      COMMON /DUR/ DURLN
      DATA DURLN /0.0/
      COMMON /MSMVN/ IPOINT(2,17),OMEAN(141),OSIGMA(906)
      INTEGER*2 IPOINT
      DATA IPOINT /1,1,2,2,4,5,7,11,11,21,16,36,22,57,29,85,37,121,
     &        46,166,56,221,67,287,79,365,92,456,106,561,122,697,142,907/
      COMMON /NODAZM/ NODED(3000,50),AZIM(3000,50)
      INTEGER*2 NODED
CS DIMENSION THIS STATEMENT TO (ARRAY SIZE) *50
```

```
      DATA NODED /150000*999/,AZIM /150000*999./
      COMMON /NODEGT/ NODEGT(25,4)
      INTEGER*2 NODEGT
      DATA NODEGT /100*999/
      COMMON /NOER/ NOBRT,NOBROT,NOTREE
      INTEGER*2 NOERT,NOBRCT,NOTREE
      DATA NOTREE /0/
      END
C*********************************************************************
C
C       THIS SUBROUTINE CALCULATES THE SOIL MOISTURE INDEX
C
C*********************************************************************
      SUBROUTINE CLIMAT
      COMMON /CLDATA/ MT(12), TSD(12), MPPTN(12), PPTNSD(12), FC, FCMM,
     & DRY3, EGS, EGS, PLAT
      REAL MT, MPPTN
      COMMON /DUR/ DURLN
      COMMON /NO/ NYEARS,NTREES,NOYR
      INTEGER*2 NYEARS,NTREES
C
C  PROGRAM FOR CALCULATING THE FRACTION OF THE
C  GROWING SEASON WITH FAVORABLE SOIL MOISTURE FOR GROWTH
C
      DIMENSION DDI3(12),C(12,26),D(12,6),DAYS(12),RT(12),RPPTN(12)
      DIMENSION XMONTH(13),U(12),AET(12)
      LOGICAL*1 FLAG /.FALSE./
      EQUIVALENCE (C(1,21),D(1,1))
C
C  MONTHLY CORRECTION FACTORS FOR 25-50 DEGREES LATITUDE NORTH
C  IN UNITS OF 12-HOUR 30-DAY PERIODS
C  ADJUSTED FOR VARYING DAY AND MONTH LENGTHS
C
      DATA C/.93,.89,1.03,1.06,1.15,1.14,1.17,1.12,1.02,.99,.91,.91,
     6       .92,.88,1.03,1.06,1.15,1.15,1.17,1.12,1.02,.99,.91,.91,
     7       .92,.88,1.03,1.07,1.16,1.15,1.18,1.13,1.02,.99,.90,.90,
     8       .91,.88,1.03,1.07,1.16,1.16,1.18,1.13,1.02,.98,.90,.90,
     9       .91,.87,1.03,1.07,1.17,1.16,1.19,1.13,1.03,.98,.90,.89,
     *       .90,.87,1.03,1.08,1.18,1.17,1.20,1.14,1.03,.98,.89,.88,
     1       .90,.87,1.03,1.08,1.18,1.18,1.20,1.14,1.03,.98,.89,.88,
     2       .89,.86,1.03,1.08,1.19,1.19,1.21,1.15,1.03,.98,.88,.87,
     3       .88,.86,1.03,1.09,1.19,1.20,1.22,1.15,1.03,.97,.88,.86,
     4       .88,.85,1.03,1.09,1.20,1.20,1.22,1.16,1.03,.97,.87,.86,
     5       .87,.85,1.03,1.09,1.21,1.21,1.23,1.16,1.03,.97,.86,.85,
     6       .87,.85,1.03,1.10,1.21,1.22,1.24,1.16,1.03,.97,.86,.84,
     7       .86,.84,1.03,1.10,1.22,1.23,1.25,1.17,1.03,.97,.85,.83,
     8       .85,.84,1.03,1.10,1.23,1.24,1.25,1.17,1.04,.96,.84,.83,
     9       .85,.84,1.03,1.11,1.23,1.24,1.26,1.18,1.04,.96,.84,.82,
     *       .84,.83,1.03,1.11,1.24,1.25,1.27,1.18,1.04,.96,.83,.81,
     1       .83,.83,1.03,1.11,1.25,1.26,1.27,1.19,1.04,.96,.82,.80,
     2       .82,.83,1.03,1.12,1.26,1.27,1.28,1.19,1.04,.95,.82,.79,
     3       .81,.82,1.02,1.12,1.26,1.28,1.29,1.20,1.04,.95,.81,.77,
     4 .81,.82,1.02,1.13,1.27,1.29,1.30,1.20,1.04,.95,.80,.76,72*0./
      DATA D/.80,.81,1.02,1.13,1.28,1.29,1.31,1.21,1.04,.94,.79,.75,
     6       .79,.81,1.02,1.13,1.29,1.31,1.32,1.22,1.04,.94,.79,.74,
     7       .77,.80,1.02,1.14,1.30,1.32,1.32,1.22,1.04,.93,.78,.73,
     8       .76,.80,1.02,1.14,1.31,1.33,1.34,1.23,1.05,.93,.77,.72,
     9       .75,.79,1.02,1.14,1.32,1.34,1.35,1.24,1.05,.93,.76,.71,
     *       .74,.78,1.02,1.15,1.33,1.36,1.37,1.25,1.06,.92,.76,.70/
C
C  DAYS(J) = NUMBER OF DAYS BETWEEN MID-MONTH I-1 AND I
C
      DATA DAYS/31.,28.,31.,30.,31.,30.,31.,31.,30.,31.,30.,31./
```

```
C
C  INITIALIZE VALUES THE FIRST YEAR
C
      IF (FLAG) GO TO 10
      DO 5 J=1,12
      U(J)=0.0
      AET(J)=0.0
      XMONTH(J)=0.0
    5 CONTINUE
      XMONTH(13) =0.0
      ACCPWL =0
      GSL=EGS -BGS
C
C  INITIALIZE WATER CONTENT OF SOIL IN JANUARY OF THE
C  INITIAL YEAR OF SIMULATION AT FIELD CAPACITY (FC)
C
      WATER = FC
      WATIMM =FCMM
C
C  ADJUST LATITUDE POINTER
C
      LAT=(PLAT+.5)-24
      IF(LAT.GE.26) LAT = 26
   10 CONTINUE
C
C INITIALIZE THE DDI3 ARRAY
C
      DO 15 J=1,12
        DDI3(J) =0.0
   15 CONTINUE
C
C  INITIALIZE TEMPERATURE EFFECIENCY (TE), AND CURRENT DAY (CDAY).
C
      TE = 0.0
      CDAY=0.
      DO 30 J=1,12
C
C  GENERATE TEMPERATURE DATA
C
CW
      RT(J) =MT(J) +TSD(J) *RNOR(0)
CW      RT(J) =MT(J)
      IF(RT(J) .GE. 0.0) GO TO 30
      WRITE (6,25) NCYR, J, RT(J)
   25 FORMAT('0TEMPERATURE SET TO ZERO'/
     *' YEAR   MONTH   TEMPERATURE'/1X,I4,4X,I2,8X,F5.1)
      RT(J)=0.0
   30 TE=TE+(.2*RT(J))**1.514
      A=.675*TE**3-77.1*TE**2+17920.0*TE+492390.0
      A=.000001*A
C
C  ENTER MONTHLY LOOP FOR WATER CALCULATIONS
C
      DO 75 J=1,12
C
C  GENERATE PRECIPITATION DATA
C
CW
      RPPTN(J) =MPPTN(J) +PPTNSD(J) *RNOR(0)
CW     RPPTN(J) =MPPTN(J)
      IF (RPPTN(J) .LT. 0.) RPPTN(J) =0.
C
C  STORE MONTHLY BEGINNING WATER VALUES AND TOTAL YEARLY WATER
```

```
C
      XMONTH(J)=WATER
C
C  COMPUTE EVAPOTRANSPIRATION (U)
C
      IF(RT(J).LE.0.0) GO TO 45
      U(J)=1.6*((10.0*RT(J)/TE)**A)*C(J,LAT)
      GO TO 50
   45 U(J) = 0.0
C
C  UPDATE WATER BALANCE, CURRENT DAY OF YEAR
C  COMPUTE ACTUAL EVAPOTRANSPIRATION FROM PASTOR AND POST 1984
C  PWL =POTENTIAL WATER LOSS
C  ACCPWL =ACCUMULATED WATER LOSS
C  CSM =CURRENT DEFICIT
C  AET =ACTUAL EVAPOTRANSPIRATION
C
   50 OWATER=WATER
      RPPTN(J) = AMAX1(0.0,RPPTN(J))
      PWL =RPPTN(J) -U(J)
      IF (PWL .GE. 0.0) GO TO 55
      PWLMM =PWL *10.
      ACCPWL = ACCPWL +PWLMM
      WATERM =WATIMM *(EXP((.000461 -1.10559 /FCMM) *(-1. *ACCPWL)))
      WATER =WATERM /10.
      WATER=AMAX1(0.0,WATER)
      CSM =WATER - OWATER
      AET(J) =AET(J) +(RPPTN(J) -CSM)
      GO TO 60
   55 WATER =OWATER +PWL
      WATER =AMIN1(FC, WATER)
      ACCPWL =0.
      WATIMM =WATER *10.
      CSM =WATER -OWATER
      AET(J) =AET(J) +U(J)
   60 CONTINUE
      IF (J .EQ. 12) XMONTH(13) =WATER
C
C  CALCULATE THE NUMBER OF DRY DAYS (3 BAR)
C
      OCDAY=CDAY
      CDAY=CDAY+DAYS(J)
      IF(CDAY .LE. BGS) GO TO 75
      IF(OCDAY .GE. EGS) GO TO 75
C
C  INCREMENT THE NUMBER OF DRY (3 BAR) DAYS, INTERPOLATING
C  IF NECESSARY, TRUNCATE AT ENDS OF GROWING SEASON
C
      IF(OWATER .GE. DRY3 .AND. WATER .GE. DRY3) GO TO 75
      IF(OWATER .GT. DRY3 .AND. WATER .LT. DRY3) GO TO 65
      IF(OWATER .LT. DRY3 .AND. WATER .GT. DRY3) GO TO 70
      DDI3(J)=DAYS(J)
      IF(OCDAY .LT. BGS .AND. CDAY .GT. BGS) DDI3(J)=CDAY-BGS
      IF(OCDAY .LT. EGS .AND. CDAY .GT. EGS) DDI3(J)=EGS-OCDAY
      GO TO 75
   65 DDI3(J)=DAYS(J)*(DRY3-WATER)/(OWATER-WATER)
      IF(OCDAY .LT. BGS .AND. CDAY .GT. BGS)
     *      DDI3(J)=AMIN1(DDI3(J),CDAY-BGS)
      IF(OCDAY .LT. EGS .AND. CDAY .GT. EGS)
     &  DDI3(J)=EGS-CDAY+DDI3(J)
      IF(DDI3(J) .LT. 0.0) DDI3(J)=0.0
      GO TO 75
   70 DDI3(J)=DAYS(J)*(DRY3-OWATER)/(WATER-OWATER)
```

```
      IF(OCDAY .LT. EGS .AND. CDAY .GT. EGS)
     & DDI3(J)=OCDAY+DDI3(J)-BGS
      IF(DDI3(J) .LT. 0.0) DDI3(J)=0.0
      IF(OCDAY .LT. EGS .AND. CDAY .GT. EGS)
     *       DDI3(J)=AMIN1(DDI3(J),EGS-OCDAY)
   75 CONTINUE
      WRITE(6,80)
   80 FORMAT(////'0MONTHLY TEMPERATURES (C)')
      WRITE(6,85)
   85 FORMAT(3X,'YEAR',6X,'JAN',6X,'FEB',6X,'MAR',6X,'APR',6X,'MAY',
     >6X,'JUN',6X,'JUL',6X,'AUG',6X,'SEP',6X,'OCT',6X,'NOV',6X,'DEC')
      WRITE(6,90)NOYR,(RT(J),J=1,12)
   90 FORMAT(' ',I5,4X,12(1X,F6.2,2X))
      WRITE(6,95)
   95 FORMAT('0MONTHLY PRECIPITATION (CM)')
      WRITE(6,85)
      WRITE(6,90)NOYR,(RPPTN(J),J=1,12)
      WRITE(6,100)
  100 FORMAT('0MONTHLY BEGINNING WATER VALUES AND DECEMBER''S END (CM)')
      WRITE(6,85)
  105 WRITE(6,110)NOYR,(XMONTH(J),J=1,13)
  110 FORMAT(' ',I5,4X,13(1X,F6.2,2X))
C
C  CALCULATE THE YEARLY NO. OF DRY DAYS AND THE FRACTION OF THE GROWING
C  SEASON AVAILABLE FOR GROWTH
C
      YDD3 =0.0
      DO 115 J=1,12
        YDD3= YDD3 +DDI3(J)
  115 CONTINUE
      WRITE (6,120)
  120 FORMAT('0FRACTION OF THE GROWING SEASON AVAILABLE FOR EXTENSION',
     &       ' GROWTH')
      DUR=1.0 -YDD3 /GSL
      WRITE(6,125)DUR
  125 FORMAT(1X,F10.4)
CC
CC       WRITE(6,125)DUR,YDD3,GSL
CC  125 FORMAT(1X,F10.4/' YDD3 =',F10.4/' GSL =',F5.1)
      DURLN =ALOG(DUR)
      FLAG =.TRUE.
CC
CC       WRITE(6,2002)
CC 2002 FORMAT(' END OF CLIMAT')
      RETURN
      END
C*****************************************************************************
C
C     THIS SUBROUTINE COMPUTES TREE EXTENSION GROWTH:
C     THE FIRST SECTION GROWS EXISTING BRANCHES AND THE SECOND SECTION
C     CREATES 'DAUGHTER' BRANCHES
C
C*****************************************************************************
      SUBROUTINE GROW
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),C2N(3000),O3A(3000),O3N(3000),O4A(3000),C4N(3000),
     & ORD(3000),BAGE(3000),PANG(3000),PAZ(3000),GROW(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,C1N,O2A,C2N,O3A,O3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
```

```
      LOGICAL*1 COND
      COMMON /DUR/ DURLN
      COMMON /NO/ NYEARS,NTREES,NOYR
      INTEGER*2 NYEARS,NTREES
      COMMON /NOBR/ NOBRT,NOBROT,NOTREE
      INTEGER*2 NOBRT,NOBROT,NOTREE
      COMMON /NODAZM/ NODED(3000,50),AZIM(3000,50)
      INTEGER*2 NODED
      COMMON /NODEGT/ NODEGT(25,4)
      INTEGER*2 NODEGT, ICPT, IGNO
      DIMENSION C(4), AMLO(4), AMNO(4), GNO(4), BAO(4),
     &          PAO(4,5), AMLPAO(4,5), AMNPAO(4,5), BAPAO(4,5)
      DATA O /3.781, -.493, -.397, 0./,
     &     AMLO /-.792, -.111, -.928, .358/,
     &     AMNO /1.466, 1.272, .844, .079/,
     &     GNO /0., .232, .802, .325/,
     &     BAO /-.511, -.556, -.145, -.177/,
     &     PAO /2.052, 1.836, 1.165, 1.843, 1.067, 4.721, -.612, 0.,
     &         1.776, 3.999, 2*0., 1.303, 3*0., 4*0./,
     &     AMLPAO /.779, -.402, .261, -.825, .821, -1.124, .325, 0.,
     &             -.139, -1.166, 2*0., -.208, 3*0., 4*0./,
     &     AMNPAO /-1.280, .183, -.106, .143, -1.124, .102, .009, 0.,
     &             -.194, .181, 2*0., -.036, 3*0., 4*0./,
     &     BAPAO /.086, -.298, -.512, 0., .137, -.220, 2*0.,
     &             .004, 3*0., 4*0., 4*0./
      DIMENSION OI(4), DO(4)
      DATA OI /-6.614, -0.880, -5.533, 0.0/,
     &     DO /-0.1161, -0.1909, -0.2582, 0.7519/
      INTEGER*2 TEASAV,OLEN
      INTEGER*2 NOBR, NODAUT
      DIMENSION OPANG(3)
      DATA OPANG /4.210396, 10.023550, 1.457318/
CE
      DIMENSION GENEXT(10), GENDAU(10), GENANG(10), GENINC(10)
CE      DIMENSION GENEXT(36), GENDAU(10), GENANG(10), GENINC(10)
      DATA GENEXT /10*999./, GENDAU /10*999./, GENANG /10*999./,
     &     GENINC /10*999./
CE      DATA GENEXT /36*999./
      INTEGER*2 IODEAD
      LOGICAL*1 FLAG
      IF (NOYR .NE. 1) GO TO 5
      CALL NEWID(NTREES)
      NOBROT =NOBRT
      DO 1 I=1,NTREES
CT
CE
        GENEXT(I) =0.025451473 +SQRT(0.021946795) *RNOR(0)
        GENDAU(I) =-0.379261322 +SQRT(0.160703831) *RNOR(0)
        GENANG(I) =-0.2218096100 +SQRT(17.16945369) *RNOR(0)
        GENINC(I) =4.995001855 +SQRT(23.99845355) *RNOR(0)
CT        GENEXT(I) =0.025451473
CT        GENDAU(I) =-0.379261322
CT        GENANG(I) =-0.2218096100
CT        GENINC(I) =4.995001855
    1 CONTINUE
    5 IODEAD =99
      DO 999 NOBR=1,NOBROT
        IF (.NOT. COND(NOBR)) GO TO 999
C
C SKIP BRANCHES WHERE THE PARENT BRANCH HAS DIED
C
      IF (ORD(NOBR) .GT. IODEAD) GO TO 999
      IODEAD =999
```

```
C
C FIND THE POINTER FOR THE GENETIC EFFECT ARRAYS
C
        NOTREE =TREE(NOBR)
        IF (ORD(NOBR) .EQ. 0) NOTR =NOBR
C
C MOVE THE LENGTHS AND INCLINATIONS
C
      IF (BAGE(NOBR) .EQ. 0) GO TO 10
C
C SHIFT THE LENGTHS, INCLINATIONS, NNODES, AND NDAUT
C
      IEND =BAGE(NOBR)
      J =IEND +1
      DO 8 I=1,IEND
        K =J
        J =J -1
        LEN(NOBR,K) =LEN(NOBR,J)
        ANG(NOBR,K) =ANG(NOBR,J)
        NNODES(NOBR,K) =NNODES(NOBR,J)
    8 CONTINUE
      IF (BAGE(NOBR) .EQ. 1) GO TO 10
      IEND =IEND -1
      J =IEND +1
      DO 9 I=1,IEND
        K =J
        J =J -1
        NDAUT(NOBR,K) =NDAUT(NOBR,J)
    9 CONTINUE
C
C AGE THE BRANCH
C
   10   BAGE(NOBR) =BAGE(NOBR) +1
C
C INCREASE THE AGE OF THE ID FOR HIGHER ORDER PARENTS
C NOTE THAT THIS POINT IN THE PROGRAM CAN ONLY BE REACHED IF THE BRANCH
C IS ALIVE
C NOTE ALSO THAT IN SUBROUTINE "KILL", IF A PARENT BRANCH DIES, ALL
C DAUGHTER BRANCHES DIE TOO
C
        IF (ORD(NOBR) -1) 20,19,11
   11   IF (ORD(NOBR) -3) 18,17,12
   12   IF (ORD(NOBR) -5) 16,15,13
   13   WRITE(6,14) NOBR
   14   FORMAT(' THE ORDER FOR BRANCH #',I5,' IS GREATER THAN 5!!!!!!')
   15   O4A(NOBR) =O4A(NOBR) +1
   16   O3A(NOBR) =O3A(NOBR) +1
   17   O2A(NOBR) =O2A(NOBR) +1
   18   O1A(NOBR) =O1A(NOBR) +1
   19   TA(NOBR) =TA(NOBR) +1
        GO TO 55
C*************************************
C  THIS SECTION DETERMINES LEADER GROWTH
C*************************************
   20   IF (NOYR.NE.1 .AND. (NOYR.NE.2 .OR. BAGE(NOBR).GT.1)) GO TO 30
CE
   25   LEN(NOBR,1) =71.93 +29.79 *RNOR(0)
CE   25   LEN(NOBR,1) =71.93
        IF (LEN(NOBR,1) -0.5) 25,25,100
C
C SAVE THE TRUNK AGE FOR USE IN CALCULATING IPA FOR BRANCH GROWTH
C
   30   TBASAV =BAGE(NOBR)
```

```
C
C  CALCULATE TRUNK HEIGHT GROWTH
C
CE
   35   ERROR =0.356425 *RNCR(0)
CE   35   ERROR =0.
   40   IF (NOYR .NE. 2) GO TO 45
C  YEAR 2 FERTILIZER EFFECT
        LEN(NOBR,1) =EXP(4.80918 +0.760937*DURLN +0.082655
     &  +GENEXT(NOTREE) +ERROR)
        IF (LEN(NOBR,1) -0.5) 35,35,100
   45   IF (NOYR .NE. 7) GO TO 50
C  YEAR 7 FERTILIZER EFFECT
        LEN(NOBR,1)=EXP(4.80918+0.760937*DURLN+GENEXT(NOTREE)
     &  +ERROR)
        IF (LEN(NOBR,1) -0.5) 35,35,100
C NO FERTILIZER EFFECT
   50   LEN(NOBR,1) =EXP(4.80918 +0.760937*DURLN -0.358011
     &  +GENEXT(NOTREE) +ERROR)
        IF (LEN(NOBR,1) -0.5) 35,35,100
C*************************************
C  THIS SECTION GROWS EXISTING BRANCHES
C*************************************
C
C  CALCULATE EXTENSION GROWTH OF EXISTING BRANCHES
C
C
C DETERMINE IPA FOR EXISTING BRANCHES
C
   55 IF (ORD(NOBR) -2) 57,60,56
   56 IF (ORD(NOBR) -4) 65,70,75
C ORDER 1
   57 OLEN =1
      IPA =TBASAV -TA(NOBR) +1
      GO TO 90
C ORDER 2
   60 OLEN =2
      IPA =TA(NOBR) -O1A(NOBR)
      GO TO 90
C ORDER 3
   65 OLEN =3
      IPA =O1A(NOBR) -O2A(NOBR)
      GO TO 90
C ORDER 4
   70 OLEN =4
      IPA =O2A(NOBR) -O3A(NOBR)
      GO TO 90
   75 IF (ORD(NOBR) .GT. 5) GO TO 80
         OLEN =4
         IPA =O3A(NOBR) -O4A(NOBR)
         GO TO 90
   80 WRITE(6,85) ORD(NOBR)
   85 FORMAT(' ORDER =',I3,' WHILE SETTING IPA FOR EXTENSION GROWTH')
   90 IF (IPA .GT. 5) IPA =5
CE
CE       ERROR =0.6868971 *RNCR(0)
      ERROR =0.
      IF (GROM(NOBR).GT.0 .AND. NODE(NOBR).GT.0 .AND. NODEG(NOBR).GT.0)
     & GO TO 96
        WRITE(6,95) NOBR,GROM(NOBR),NODE(NOBR),NODEG(NOBR)
   95 FORMAT(' BASE=0; NOBR=',I5,' GROM=',F5.1,' NODE=',I3,' NODEG=',I3)
      CALL OUTBR(NOBR)
   96 LEN(NOBR,1) =EXP(-6.436+O(OLEN)+PAC(OLEN,IPA))
```

```
     & *GRCM(NOBR)**(AMLO(OLEN)+AMLPAO(OLEN,IPA))
     & *NODE(NOBR)**(AMNO(OLEN)+AMNPAO(OLEN,IPA))
     & *NODEG(NOBR)**GNO(OLEN)* EXP(BAGE(NOBR)
     & *(BAO(OLEN)+BAPAO(OLEN,IPA)))
     & *EXP(ERROR)
     & *LEN(NOTR,1)
CC       WRITE(6,97)OLEN,IPA,O(OLEN),PAO(OLEN,IPA),GROM(NOBR),AMLO(OLEN),
CC      & AMLPAO(OLEN,IPA),NODE(NOBR),AMNO(OLEN),AMNPAO(OLEN,IPA),
CC      & NODEG(NOBR),GNO(OLEN),BAGE(NOBR),BAO(OLEN),BAPAO(OLEN,IPA),
CC      & LEN(NOTR,1),LEN(NOBR),NAPT(NOBR)
CC   98 FORMAT(' OLEN=',I1,' IPA=',I2,' O(OLEN)=',F6.3,' PAO(OLEN)=',F6.3,
CC      & ' GRCM(NOBR)=',F4.0,' AMLO(OLEN)=',F5.3,
CC      & ' AMLPAO(OLEN,IPA)=',F6.3,' NODE(NOBR)=',I3/' AMNO(OLEN)=',F5.3,
CC      & ' AMNPAO(OLEN,IPA)=',F5.3,
CC      & ' NODEG(NOBR)=',I3,' GNO(OLEN)=',F4.3,' BAGE(NOBR)=',I1,
CC      & ' BAO(OLEN)=',F5.3,' BAPAO(OLEN,IPA)=',F5.3/
CC      & ' LEN(NOTR,1)=',F4.0,' LEN(NOBR,1)=',F4.0,' NAPT=',I4,'*****')
C
C IF THE BRANCH GROWS LESS THAN 1 CM, IT DIES
C
      IF (LEN(NOBR,1) .GE. 0.5) GO TO 100
      ICDEAD =ORD(NOBR)
      COND(NOBR) =.FALSE.
      GO TO 999
C
C  DETERMINE NODE POSITIONS AND AZIMUTHS
C
CB
  100   CALL NODEAZ(NOBR)
CB  100   CONTINUE
C
C DETERMINE BRANCH INCLINATION RELATIVE TO GRAVITY
C
      IF (ORD(NOBR) .EQ. 0) GO TO 102
      DIST =0.
      IEND =BAGE(NOBR)
      DO 101 I=2,IEND
        DIST =DIST +LEN(NOBR,I)
  101 CONTINUE
CB
      ERROR =9.881590572 *ENOR(0)
CB      ERROR =0.
      ANG(NOBR,1) =(31.773 +OI(ORD(NOBR)))
     &              +0.3979 *(ANG(NOBR,BAGE(NOBR)))
     &              +(DO(ORD(NOBR)) *DIST) +GENINC(NOTREE) +ERROR
      IF (ANG(NOBR,1) .LT. 0.) ANG(NOBR,1) =0.
C
C DETERMINE BRANCH COORDINATES
C
  102 FLAG =.FALSE.
      CALL COORD(NOBR,NODAUT,FLAG)
C
C ADD LEAVES TO THE BRANCH
C
CC         IF (    ) CALL LEAF(NOBR)
C*************************************
C  THIS SECTION PRODUCES "DAUGHTER" BRANCHES
C*************************************
         IF (BAGE(NOBR) .LT. 2) GO TO 999
CB
CB SKIP THE DAUGHTER SECTION
CB
CB         IF (O1N(NOBR) .LE. 0) GO TO 999
```

```
C
C SKIP THIS SECTION FOR BRANCHES WITH ONLY ONE NODE
C
        IF (NNODES(NCBR,2) .LE. 1) GO TO 999
C
C  CALCULATE THE NUMBER OF DAUGHTERS
C
CE
      ERROR =0.7798520 *BNOR(0)
CE      ERROR =0.
      NDAUT(NOBR,1) =HFIX(-1.83575020 +0.82928330 *NNODES(NCBR,2)
     &        +GENDAU(NOTBEF) +ERROR +.5)
      IF (NDAUT(NCBR,1) .GE. 1) GO TO 104
      NDAUT(NCBR,1) =0
      GO TO 999
  104 IF (NDAUT(NOBR,1) .GE. NNODES(NOBR,2))
     &                NDAUT(NOBR,1) =NNODES(NOBR,2) -1
C
C  DETERMINE ID FOR NEW BRANCHES
C
      CALL NEWID(NCBR)
C
C DETERMINE THE NODE NUMBERS FOR THE DAUGHTER BRANCHES. I ASSUME THAT THE
C BRANCHES ARE ON CONSECUTIVE NODES AND ARE ALL CLUSTERED AT THE END OF
C THE BRANCH
C
      NODENO =NNODES(NOBR,2) -NDAUT(NOBR,1) -1
      NNDAUT =NDAUT(NCBR,1)
      DO 300 J=1,NNDAUT
        NODAUT =NCERT -NNDAUT +J
        NODENO =NODENO +1
C
C  STORE DAUGHTER VARIABLES
C
        NODE(NODAUT) =NODED(NAPT(NOBR),NODENO +25)
        PAZ(NODAUT) =AZIM(NAPT(NCBR),NODENO +25)
        GRCM(NODAUT) =LEN(NCBR,2)
      IF (CRD(NODAUT) -2) 106,108,105
  105 IF (CRD(NODAUT) -4) 110,115,120
C ORDER 1
  106   TN(NODAUT) =NODENO
        OLEN =1
        IPA =IBASAV -TA(NODAUT) +1
        GO TO 128
C ORDER 2
  108   IGNO =TN(NODAUT)
        O1N(NODAUT) =NODENO
        OLEN =2
        IPA =TA(NODAUT) -O1A(NODAUT)
        GO TO 125
C ORDER3
  110   IGNO =O1N(NODAUT)
        O2N(NODAUT) =NODENO
        OLEN =3
        IPA =O1A(NODAUT) -O2A(NODAUT)
        GO TO 125
C ORDER 4
  115   IGNO =O2N(NODAUT)
        O3N(NODAUT) =NODENO
        OLEN =4
        IPA =O2A(NODAUT) -O3A(NODAUT)
        GO TO 125
C ORDER 5
```

```
  120    IGNO =O3N(NODAUT)
         O4N(NODAUT) =NODENO
         OLEN =4
         IPA =O3A(NODAUT) -O4A(NODAUT)
  125    IORT =ORD(NODAUT) -1
         NODEG(NODAUT) =NODEGT(IGNO,ICPT)
C
C  CALCULATE DAUGHTER LENGTHS
C
  128    IF (IPA .GT. 5) IPA =5
CE
CE         ERROR =0.6868971 *ENOR(0)
         ERROR =0.
CC
CC         WRITE(6,130) NODAUT,OLEN,IPA,GROM(NODAUT),NODE(NODAUT),
CC      &                NODEG(NODAUT),BAGE(NODAUT),ERROR,NOTR
CC  130    FORMAT(' NODAUT =',I3/' OLEN =',I2/' IPA =',I2/' GROM =',F5.0/
CC      &          ' NODE =',I3/' NODEG =',I3/' BAGE =',I2/' ERROR =',F10.7/
CC      &          ' NOTR =',I2)
       IF (GROM(NODAUT).GT.0 .AND. NODE(NODAUT).GT.0
      & .AND. NODEG(NODAUT).GT.0) GO TO 132
       WRITE(6,131) NODAUT,GROM(NODAUT),NODE(NODAUT),NODEG(NODAUT)
  131 FORMAT(' BASE=0; NODAUT=',I5,' GROM=',F5.1,' NODE=',I3,' NODEG=',
      & I3)
       CALL OUTBR(NOBR)
       CALL OUTBR(NODAUT)
  132    LEN(NODAUT,1) =EXP(-6.436+O(OLEN) +PAO(OLEN,IPA))
      &    *GROM(NODAUT)**(AMLO(OLEN)+AMLPAO(OLEN,IPA))
      &    *NODE(NODAUT)**(AMNO(OLEN)+AMNPAO(OLEN,IPA))
      &    *NODEG(NODAUT)**GNO(OLEN)* EXP(BAGE(NODAUT)
      &    *(BAO(OLEN) +BAPAO(OLEN,IPA)))
      &    *EXP(ERROR)
      &    *LEN(NOTR,1)
CC       WRITE(6,1132)OLEN,IPA,O(OLEN),PAO(OLEN,IPA),GROM(NODAUT),
CC      & AMLO(OLEN),AMLPAO(OLEN,IPA),NODE(NODAUT),AMNO(OLEN),
CC      & AMNPAO(OLEN,IPA),NODEG(NODAUT),GNO(OLEN),BAGE(NODAUT),BAO(OLEN),
CC      & BAPAO(OLEN,IPA),LEN(NOTR,1),LEN(NODAUT),NAPT(NODAUT)
CC   98 FORMAT(' OLEN=',I1,' IPA=',I2,' O(OLEN)=',F6.3,' PAO(OLEN)=',F6.3,
CC      & ' GROM(NODAUT)=',F4.0,' AMLO(OLEN)=',F5.3,
CC      &' AMLPAO(OLEN,IPA)=',F6.3,' NODE(NODAUT)=',I3/' AMNO(OLEN)=',F5.3,
CC      & ' AMNPAO(OLEN,IPA)=',F5.3,
CC      & ' NODEG(NODAUT)=',I3,' GNO(OLEN)=',F4.3,' BAGE(NODAUT)=',I1,
CC      & ' BAO(OLEN)=',F5.3,' BAPAO(OLEN,IPA)=',F5.3/
CC      & ' LEN(NOTR,1)=',F4.0,' LEN(NOBR,1)=',F4.0,' NAPT=',I4,'*****')
C
C IF THE DAUGHTER GROWS LESS THAN 1 CM, IT DIES
C
       IF (LEN(NODAUT,1) .GE. 0.5) GO TO 134
       NDAUT(NOBR,1) =NDAUT(NOBR,1) -1
       NOBRT =NOBRT -1
       GO TO 300
CC
CC         WRITE(6,133) NODAUT,LEN(NODAUT,1)
CC  133    FORMAT(' NODAUT =',I2/' LEN(NODAUT,1) =',F5.1)
C
C  DETERMINE NODE POSITIONS AND AZIMUTHS
C
  134      CALL NODEAZ(NODAUT)
C
C  CALCULATE BRANCH ANGLES RELATIVE TO THE PARENT
C
         IF (ORD(NODAUT) .LE. 3) ORDER =CFANG(ORD(NODAUT))
         IF (ORD(NODAUT) .GT. 3) ORDER =0.000
```

```
CC
        NNN =0
CE
  135   ERROR =9.825113 *RNCB(0)
        ERRORT =1.312261 *RNOR(0)
CE  135   ERRCR =0.
CE        ERRCRT =0.
        PANG(NODAUT) =42.86466 -1.803771 *NODENO
     &       +1.736657 *NNCDES(NOBR,2) +0.2315104 *NDAUT(NOBR,1)
     &       -0.1666276 *LEN(NODAUT,1) +CRDER +ERRORT
     &       +GENANG(NOTREE) +ERROR
        IF (PANG(NODAUT) .GT. 0.) GO TO 138
        WRITE(6,136) NAPT(NODAUT),PANG(NCDAUT)
  136   FORMAT(' PANG RESET CN BRANCH NAPT =',I5,' OLD VALUE =',F6.1)
        CAIL CUTBR(NCBR)
        CAIL CUTBR(NCDAUT)
        WRITE(6,137) NCDENO,CRDER,ERRORT,NOTREE,GENANG(NOTREE),ERROR
  137   FORMAT(' NCDENO=',I3,' CRDER=',F8.4,' ERRORT=',F6.2,'NOTREE=',
     &  I2,' GENANG(NOTREE)=',F7.2,' ERRCR=',F6.2)
        NNN =NNN +1
        IF (NNN .GE. 20) STCP
        GO TO 135
  138   IF (PANG(NCDAUT) .IT. 99.) GC TC 139
        WRITE(6,136) NAPT(NCDAUT),PANG(NCDAUT)
        PANG(NODAUT) =98.
  139   CONTINUE
C
C DETERMINE DAUGHTER CCORDINATES
C
      FLAG =.TRUE.
      CALL CCORD(NCBR,NCDAUT,FLAG)
C
C ADD LEAVES TO THE BRANCHES
C
C
CO          IF (   ) CALL LEAF(NODAUT)
C
  300   CONTINUE
  999 CONTINUE
CC
CC      WRITE(6,2002)
CC 2002 FORMAT(' END CF GROW')
      RETURN
      END
C*********************************************************************
C
C     THIS SUBROUTINE CAICULATES NODE POSITIONS AND AZIMUTHS
C
C*********************************************************************
      SUBRCUTINE NCDEAZ(NC)
      INTEGER*2 NO
      COMMCN /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),O2N(3000),O3A(3000),O3N(3000),O4A(3000),C4N(3000),
     & ORD(3000),BAGE(3000),BANG(3000),BAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,C1N,O2A,C2N,O3A,O3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
      LOGICAL*1 COND
      COMMCN /DUR/ DURLN
      COMMCN /NOBR/ NCBRT,NCBROT,NOTREE
```

```
      INTEGER*2 NCERT,NCERCT,NOTREE
      COMMCN /NO/ NYEARS,NTREES,NOYR
      INTEGER*2 NYEARS,NTREES
      COMMCN /MSMVN/ IPOINT(2,17),OMEAN(141),OSIGMA(906)
      INTEGER*2 IPCINT
      COMMCN /NODAZM/ NODED(3000,50),AZIM(3000,50)
      INTEGER*2 NODED
      COMMCN /NODEGT/ NODEGT(25,4)
      INTEGER*2 NODEGT, IOPT
      LOGICAL*1 FLAG
      DIMENSION RMEAN(27),RSIGMA(210),RVEC(2,27),FLAG(16),WKVEC(27),
     &          R(2)
      DATA NR /1/
      DATA FLAG /16*.TRUE./
CF
      DOUBLE PRECISICN DSEED
CF 1.D0 < DSEED < 2147483647.D0
      DATA DSEED /13029.D0/
      DIMENSION IPT2(8),INTPT(159),XINT(159)
      INTEGER*2 INTPT
      DATA IPT2 /1,16,33,51,70,91,113,136/
      DATA INTPT /1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,
     &     0,1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,
     &     1,2,3,4,5,6,7,8,9,11,12,13,14,15,16,17,18,19,
     &     1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,
     &     0,1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20,
     &     0,1,2,3,4,5,6,7,8,9,10,10,11,12,13,14,15,16,17,18,19,20,
     &     0,1,2,3,4,5,6,6,7,8,9,10,11,12,13,13,14,15,16,17,18,19,20,
     &     0,1,2,3,4,5,5,6,7,8,9,10,10,11,12,13,14,15,15,16,17,18,19,20/
      DATA XINT /0.004,0.007,0.011,0.015,0.018,0.022,0.026,0.029,0.033,
     &     0.037,0.040,0.044,0.048,0.051,0.055,
     &     0.056,0.052,0.049,0.046,0.042,0.039,0.036,0.033,0.029,0.026,
     &     0.023,0.020,0.016,0.013,0.010,0.007,0.003,
     &     0.005,0.010,0.015,0.020,0.025,0.030,0.035,0.040,0.045,0.003,
     &     0.008,0.013,0.018,0.023,0.028,0.033,0.038,0.043,
     &     0.002,0.005,0.007,0.010,0.012,0.014,0.017,0.019,0.021,0.024,
     &     0.026,0.029,0.031,0.033,0.036,0.038,0.040,0.043,0.045,
     &     0.045,0.043,0.041,0.039,0.037,0.035,0.032,0.030,0.028,0.026,
     &     0.024,0.022,0.019,0.017,0.015,0.013,0.011,0.009,0.006,0.004,
     &     0.002,
     &     0.043,0.039,0.035,0.031,0.027,0.023,0.019,0.014,0.010,0.006,
     &     0.002,0.046,0.041,0.037,0.033,0.029,
     &     0.025,0.021,0.017,0.012,0.008,0.004,
     &     0.042,0.036,0.030,0.024,0.018,0.012,0.006,0.048,0.042,0.036,
     &     0.030,0.024,0.018,0.012,0.006,0.048,
     &     0.042,0.036,0.030,0.024,0.018,0.012,0.006,
     &     0.040,0.032,0.025,0.017,0.010,0.002,0.042,0.034,0.027,0.019,
     &     0.011,0.004,0.044,0.036,0.029,0.021,
     &     0.013,0.006,0.046,0.038,0.030,0.023,0.015,0.008/
      DIMENSICN GENNOD(10)
      DATA GENNOD /10*999./
      DIMENSICN SK(2,78)
      DATA SK /2.56,500.,3.63,250.,5.74,100.,8.12,50.,9.,43.,
     & 10.,35.1,11.,28.3,12.,23.3,13.,20.,14.,17.,15.,15.,16.,13.1,
     & 17.,11.66,18.,10.41,19.,9.38,20.,8.49,21.,7.73,22.,7.07,23.,6.5,
     & 24.,6.,25.,5.555,26.,5.165,27.,4.818,28.,4.511,29.,4.233,
     & 30.,3.985,31.,3.761,32.,3.557,33.,3.372,34.,3.203,35.,3.048,
     & 36.,2.904,37.,2.771,38.,2.647,39.,2.531,40.,2.423,41.,2.321,
     & 42.,2.224,43.,2.133,44.,2.046,45.,1.963,46.,1.884,47.,1.808,
     & 48.,1.735,49.,1.665,50.,1.597,51.,1.532,52.,1.468,53.,1.407,
     & 54.,1.347,55.,1.288,56.,1.231,57.,1.176,58.,1.121,59.,1.068,
     & 60.,1.015,61.,.9634,62.,.9125,63.,.8623,64.,.8128,65.,.7638,
     & 66.,.7152,67.,.6671,68.,.6194,69.,.5719,70.,.5246,71.,.4775,
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     & 72.,.4305,73.,.3835,74.,.3366,75.,.2895,76.,.2422,77.,.1948,
     & 78.,.1471,79.,.099,80.,.0505,81.,.0015,81.03,0.0/
      INTEGER LOW,HI,MID
      LOGICAL*1 FLAG2
      DATA FLAG2 /.FALSE./
C
C PPS IS THE PROBABILITY(P) THAT THE PHYLLOTAXIS(P) WILL SWITCH(S) DIRECTION
C
      DATA PPS /0.275/
      CRD =180. /3.141592654
C*************************************
C  DETERMINE THE NUMBER OF NODES
C*************************************
C
C  CALCULATE A RANDOM GENETIC EFFECT
C
      IF (FLAG2) GO TO 5
      DO 1 I=1,NTREES
CT
        GENNOD(I) =0.042289005 +SQRT(0.002688043) *RNOR(0)
CT        GENNOD(I) =0.042289005
    1 CONTINUE
      FLAG2 =.TRUE.
C
C  FIND AN "OPEN" STORAGE ROW IN THE NODED AND AZIM ARRAYS
C  CHANGE THE INDEX ON THE DO LOOP AS THE SIZE OF THESE ARRAYS INCREASE
C
    5 IF (NAPT(NO) .GT. 0) GO TO 9
CS
      DO 6 NANO=1,3000
        IF (NODED(NANO,1) .EQ. 999) GO TO 8
    6 CONTINUE
      WRITE(6,7)
    7 FORMAT(' THE NODE DISTANCE AND AZIMUTH ARRAYS ARE TOO SMALL!!!!!!')
      STOP
    8 NAPT(NO) =NANO
      GO TO 15
C
C STORE THE "GRANDMOTHER" POSITION FOR THE LENGTH CALCULATION
C
    9 NANO =NAPT(NO)
      IF (EAGE(NO) .EQ. 2) GO TO 13
      IOPT =ORD(NO) +1
      IEND =NNODES(NO,3)
      DO 10 I=1,IEND
        J =I +25
   10 NODEGT(I,IOPT) =NODED(NANO,J)
C
C  MOVE NODE POSITIONS AND AZIMUTHS TO THE TWO YEAR OLD POSITIONS
C
   13 NNODES(NO,2) =NNODES(NO,1)
      IEND =NNODES(NO,2)
      DO 14 I=1,IEND
        J =I +25
        NODED(NANO,J) =NODED(NANO,I)
        AZIM(NANO,J) =AZIM(NANO,I)
   14 CONTINUE
CE
   15 ERROR =0.1508128 *RNOR(0)
CE    15 ERROR =0.
CC
CC       WRITE(6,16) NO,LEN(NO,1),DURIN,NOTREE,GENNOD(NOTREE),ERROR
CC    16 FORMAT(' NO =',I2/' LEN(NO,1) =',F5.1/' DURIN =',F8.2/
```

```
CC      & ' NOTREE =',I2/' GENNOD(NOTREE) =',F10.6/' ERROR =',F10.7)
      IF (IEN(NO,1) .GT. 0) GO TO 18
      WRITE(6,17) NC
   17 FORMAT(' LEN(',I5,',1) IS LESS THAN OR EQUAL TO 0; CAN NOT',
     & ' PREDICT NNODES')
      CALL OUTBR(NC)
   18 IF (NOYR .NE. 2) GO TO 20
C
C  YEAR 2 FERTILIZER EFFECT
C  ADD +.5 TO CORRECT FOR ROUNDING TO ALL CALLS TO HFIX
C
      NNODES(NO,1) =HFIX(EXP(0.309 -0.440 *ALOG(LEN(NO,1))
     &       +0.103 *DURLN +GENNOD(NOTREE) +ERROR) *LEN(NO,1) +.5)
      GO TO 22
C
C  NO FERTILIZER EFFECT
C
   20 NNODES(NO,1) =HFIX(EXP(0.309 -0.440 *ALOG(LEN(NO,1))
     &-0.321 +0.103 *DURLN +GENNOD(NOTREE) +ERROR)*LEN(NO,1) +.5)
   22 IF (NNODES(NO,1) .LE. HFIX(LEN(NO,1) +0.5)) GO TO 25
CC       WRITE(6,23) NO,NNODES(NO,1),LEN(NO,1)
CC    23 FORMAT(' MORE NODES THAN THE BRANCH CAN ACCOMODATE: NO=',I5,
CC      &        ' NNODES(NO,1)=',I3,' LEN(NO,1)=',F5.1)
      NNODES(NO,1) =HFIX(LEN(NO,1) +0.5)
CC       WRITE(6,24) NNODES(NO,1)
CC    24 FORMAT(' NEW NUMBER OF NODES(NO,1)=',I5)
C*************************************
C DETERMINE NODE POSITIONS
C*************************************
C  DETERMINE THE NODE CLASS, POINTER ELEMENT FOR THE MEAN AND COVARIANCE
C  ARRAYS, AND STORE THE MEANS AND COVARIANCE MATRIX
C  IF NNODES =1, STORE THE LENGTH AND DROP TO THE AZIMUTH SECTION
C
   25 IF (NNODES(NO,1) .GT. 1) GO TO 26
         NODED(NANO,1) =HFIX(LEN(NO,1) +.5)
         NPTS =1
         GO TO 258
   26 IF (NNODES(NO,1) .GT. 15) GO TO 27
         NCL =NNODES(NO,1)
         NPT =NCL -1
         GO TO 30
   27 IF (NNODES(NO,1) .GT. 18) GO TO 28
         NCL =17
         NPT =15
         GO TO 30
   28 NCL =21
      NPT =16
      IF (NNODES(NO,1) .LE. 25) GO TO 30
CC
CC  ADD AN INTERPOLATOR IF NNODES(NO,1) .GT. 25
CC
      WRITE(6,29) NNODES(NO,1),NO
   29 FORMAT(' THE PREDICTED NUMBER OF NODES IS ',I2,' ON BRANCH ',I5/
     &        ' NNODES WAS RESET TO 25')
      NNODES(NO,1) =25
   30 NPTP1 =NPT +1
      NCLM1 =NCL -1
CE
CE       IF (.TRUE.) GO TO 61
      IBEG =IPOINT(2,NPT)
      NPTS =IPOINT(2,NPTP1) -IBEG
      DO 35 I=1,NPTS
         RSIGMA(I) =OSIGMA(IBEG)
```

```
      IBEG =IBEG +1
   35 CONTINUE
CC
CC       WRITE(6,36) (RSIGMA(I),I=1,NPTS)
CC    36 FORMAT(6E12.5)
CC       WRITE(6,37)  (FLAG(I),I=1,16)
CC    37 FORMAT(' ',16L4)
C
C  GGNSM CALCULATES THE ROOT OF SIGMA IF WKVEC(1) =0. TO KEEP IT FROM
C  TAKING A SECOND ROOT, I HAVE SET UP A NODE CLASS FLAG (NAMED FLAG)
C  TO INDICATE IF THIS COVARIANCE MATRIX HAS BEEN USED. ONCE IT HAS,
C  MARK(NPT) IS SET TO .FALSE., ROOT SIGMA IS STORED IN SIGMA, AND
C  WKVEC(1) IS SET TO .NE. 0.
C
      IF (FLAG(NPT)) GO TO 40
      WKVEC (1)=999.
      GO TO 45
   40 WKVEC(1) =0.0
C
C THIS SECTION CALCULATES NODE POSITION FOR NNODES =2 (UNIVARIATE
C RANDOM NUMBER GENERATOR)
C
   45 IF (NCL .GT. 2) GO TO 46
      IF (FLAG(1)) RSIGMA(1) =SQRT(RSIGMA(1))
      RVEC(1,1)  =RSIGMA(1)  *RNOR(0)
      GO TO 47
C
C THIS SECTION CALCULATES NODE POSITIONS FOR NNODES >2 (MULTIVARIATE
C RANDOM DEVIATE GENERATOR FROM THE COVARIANCE MATRIX)
C
   46 CALL GGNSM (DSEED,NR,NCLM1,RSIGMA,2,RVEC,WKVEC,IER)
   47 IF (.NOT. FLAG(NPT)) GO TO 50
      FLAG(NPT)  =.FALSE.
      IBEG =IPOINT(2,NPT)
      DO 50 I=1,NPTS
        OSIGMA(IBEG)  =RSIGMA(I)
        IBEG =IBEG +1
   50 CONTINUE
CC
CC         WRITE(6,55)
CC   55    FORMAT(' ',2X,'NODE 01',4X,'NODE 02',4X,'NODE 03',4X,'NODE 04',
CC      &          4X,'NODE 05',4X,'NODE 06',4X,'NODE 07',4X,'NODE 08',
CC      &          4X,'NODE 09',4X,'NODE 10',4X,'NODE 11',4X,'NODE 12'/
CC      &          ' ',2X'NODE 13',4X,'NODE 14',4X,'NODE 15',4X,'NODE 16',
CC      &          4X,'NODE 17',4X,'NODE 18',4X,'NODE 19',4X,'NODE 20',
CC      &          4X,'NODE 21',4X,'NODE 22',4X,'NODE 23',4X,'NODE 24'/
CC      &          ' ',2X,'NODE 25',4X,'NODE 26',4X,'NODE 27',4X,'NODE 28')
CC       WRITE(6,36) (RSIGMA(I),I=1,NPTS)
CC       WRITE(6,37)  (FLAG(I),I=1,16)
      IF (IER .EQ. 129) WRITE(6,60)
   60 FORMAT(' ERROR IN THE MULTIVARIATE CALL IN NODEAZ!!!!!')
   61 DO 80 I=1,NR
        MBEG =IPOINT(1,NPT)
        DO 70 J=1,NCLM1
CE
          RMEAN(J)  =CMEAN(MBEG)  + RVEC(I,J)
CE          RMEAN(J)  =CMEAN(MBEG)
CC
CC        WRITE(6,65)  I,J,MBEG,RMEAN(J),CMEAN(MBEG),RVEC(I,J)
CC   65   FORMAT(' ',I2,3X,I2,3X,I3,3X,F5.3,3X,F5.3,3X,F5.3)
          MBEG =MBEG +1
   70   CONTINUE
CC
```

```
CC          RMEAN(NNODES(NC,1)) =1.0000000
         RMEAN(NCL) =1.0000000
CC
CC          WRITE(6,75) (RMEAN(J),J=1,NNODES(NO,1))
CC          WRITE(6,75) (RMEAN(J),J=1,NCL)
   80 CONTINUE
CC   75 FORMAT(' ',12F11.7)
      NPTS =NNODES(NC,1)
      NNM1 =NPTS -1
      IF (NPTS .GT. 15 .AND. NPTS .NE. 17
     &    .AND. NPTS .NE. 21) GO TO 200
C
C THIS SECTION IS FOR BRANCHES WHERE NPTS =NNODES
C
      DO 100 I=1,NPTS
        NODED(NANO,I) =HFIX(RMEAN(I) *LEN(NO,1) +.5)
  100 CONTINUE
      GO TO 225
C
C THIS SECTION BACK-INTERPOLATES
C
  200 IF (NPTS .EQ. 16) NPT =1
      IF (NPTS .EQ. 18) NPT =2
      IF (NPTS .EQ. 19) NPT =3
      IF (NPTS .EQ. 20) NPT =4
      IF (NPTS .EQ. 22) NPT =5
      IF (NPTS .EQ. 23) NPT =6
      IF (NPTS .EQ. 24) NPT =7
      IF (NPTS .EQ. 25) NPT =8
      IBEG =IPT2(NPT)
      DO 220 I=1,NNM1
        NPT1 =INTPT(IBEG)
        NPT2 =NPT1 +1
        IF (NPT1 .GT. 0) GO TO 210
        NODED(NANO,I) =HFIX((RMEAN(NPT1) *NPTS *XINT(IBEG))
     &                  *LEN(NO,1) +0.5)
        GO TO 220
  210   NODED(NANO,I) =HFIX(((RMEAN(NPT2) -RMEAN(NPT1)) *NPTS
     &        *XINT(IBEG) +RMEAN(NPT1)) *LEN(NO,1) +0.5)
  220 IBEG =IBEG +1
      NODED(NANO,NPTS) =HFIX(LEN(NO,1) +.5)
C
C  FOR SOME BRANCHES, NODE(1) MAY BE =0, AND FOR OTHERS THE LAST TWO
C  NODES MAY BE AT THE SAME DISTANCE. THE NEXT FEW LINES ARE DESIGNED
C  TO CORRECT THESE POTENTIAL PROBLEMS. IF NODE(1) =0, I WILL ADD 1
C  TO EACH NODE DISTANCE UNTIL NO NODES ARE AT THE SAME DISTANCE.
C  IF THE LAST TWO NODES ARE AT THE SAME DISTANCE, I WILL SUBTRACT 1
C  FROM THE NEXT-TO-LAST NODE AND THEN COMPARE ITS DISTANCE TO THE
C  DISTANCE OF THE NEXT NODE IN. IF THESE ARE AT THE SAME POSITION,
C  THE PROCESS WILL BE REPEATED. THERE MAY BE AN EXTREMELY RARE
C  SITUATION WHERE NODE(1) WILL NOW BE =0. IF THIS IS THE CASE, THE
C  PROCESS WILL BE REPEATED.
C
  225 IF (NODED(NANO,1) .GT. 0) GO TO 240
  230 DO 235 I=1,NNM1
  231   CONTINUE
CC
CC          WRITE(6,255) NANO,I,NODED(NANO,I)
         NODED(NANO,I) =NODED(NANO,I) +1
         IF (I .GT. 1 .AND. NODED(NANO,I-1) .GE. NODED(NANO,I)) GO TO 231
         IF (NODED(NANO,I) .LT. NODED(NANO,I+1)) GO TO 240
  235 CONTINUE
  240 DO 245 I=1,NNM1
```

```
        J =NPTS -I
        IF (NODED(NANO,J) .NE. NODED(NANO,J +1)) GO TO 250
CC
CC        WRITE(6,255) NANO,J,NODED(NANO,J)
        NODED(NANO,J) =NODED(NANO,J) -1
  245 CONTINUE
  250 IF (NODED(NANO,1) .EQ. 0) GO TO 230
CC
CC  255 FORMAT(' NODE POSITION RESET: NAPT =',I4,'  NODENO =',I2,
CC     &        '  OLD DISTANCE =',I3)
C*************************************
C  CALCULATE AZIMUTHS
C*************************************
C
  258 IF (ORD(NO) .GT. 0) GO TO 265
C*******************
C  DETERMINE THE AZIMUTH FOR LEAVES/BRANCHES ATTACHED TO THE LEADER
C*******************
      AZIM(NANO,1) =UNI(0) *360.
      IF (NPTS .EQ. 1) GO TO 400
      AZTMP =AZIM(NANO,1)
C
C DETERMINE IF THE PHYLLOTAXIS SWITCHES DIRECTION
C
      PHYLIO =145.65616798
      RSW =UNI(0)
      IF (RSW .LE. PES) PHYLIO =-145.65616798
      DO 260 I=2,NPTS
        AZTMP =AZTMP +PHYLIO
        IF (AZTMP .GE. 360.) AZTMP =AZTMP -360.
        IF (AZTMP .LT. 0.) AZTMP =AZTMP +360.
CE
        AZIM(NANO,I) =AZTMP +43.0357 *RNOR(0)
CE        AZIM(NANO,I) =AZTMP
        IF (AZIM(NANO,I) .LT. 0) AZIM(NANO,I) =AZIM(NANO,I) +360.
        IF (AZIM(NANO,I) .GE. 360.) AZIM(NANO,I) =AZIM(NANO,I) -360.
  260 CONTINUE
      GO TO 400
C*******************
C  DETERMINE BRANCH AZIMUTH ON PRIMARY AND HIGHER ORDER BRANCHES
C*******************
  265 AZTMP =270.
      PROB =UNI(0)
      IF (PROB .GE. 0.5) AZTMP =90.
      DO 295 I=1,NPTS
        IF (NODED(NANO,I) .GT. 90) GO TO 300
        AZTMP =AZTMP +180.
        IF (AZTMP .GE. 360.) AZTMP =AZTMP -360.
C
C DETERMINE THE ANGULAR DEVIATION
C THIS EQUATION WAS DEVELOPED FOR NON-AXIAL DATA. DOUBLE THE ANGULAR DEVIATION
C TO CHANGE THE BIMODAL DISTRIBUTION INTO AN UNIMODAL DISTRIBUTION
C FOR THE VON MISES DEVIATE GENERATOR
C
CE
        ERROR =1.736470 *RNOR(0)
CE        ERROR =0.
        ANGDEV =(22.145950 +0.119937 *NODED(NANO,I) +ERROR) *2
        IF (ANGDEV .LT. 81.03) GO TO 268
        WRITE(6,267) ANGDEV
  267   FORMAT(' ANGULAR DEVIATION RESET; OLD VALUE =',F8.3)
        AKBAT =0.0
        GO TO 290
```

```
  268   CONTINUE
CE
CE        IF (.TRUE.) GO TO 293
C
C DETERMINE THE CONCENTRATION PARAMETER (K) FROM THE ANGULAR DEVIATON (S)
C THE BINARY SEARCH WAS MODIFIED FROM HUGHES, PFLEEGER, AND ROSE; ADVANCED
C PROGRAMMING TECHNIQUES: A SECOND COURSE IN PROGRAMMING USING FORTRAN
C
        LOW =1
        HI =78 +1
  270   MID =(LOW +HI) /2
        IF (ANGDEV .NE. SK(1,MID)) GO TO 275
          AKHAT =SK(2,MID)
          GO TO 290
  275   IF (ANGDEV .LT. SK(1,MID)) HI =MID
        IF (ANGDEV .GT. SK(1,MID)) LOW =MID
        IF (HI .NE. (LOW +1)) GO TO 270
C
C INTERPOLATE
C
        AKHAT =((SK(2,HI) -SK(2,LOW)) /(SK(1,HI) -SK(1,LOW)))
     &          *(ANGDEV -SK(1,LOW)) +SK(2,LOW)
  290   CONTINUE
CC        WRITE(6,291) AKHAT
CC  291   FORMAT(' AKHAT=',F10.5)
        CALL GGVMS(DSEED,AKHAT,1,R)
C
C CORRECT FOR DOUBLING THE ANGULAR DEVIATION AND CONVERT FROM RADIANS
C TO DEGREES
C
        R(1) =(R(1) /2) *CRD
CE
        AZIM(NANO,I) =AZTMP +R(1)
CE  293   AZIM(NANO,I) =AZTMP
        IF (AZIM(NANO,I) .LT. 0.) AZIM(NANO,I) =AZIM(NANO,I) +360.
        IF (AZIM(NANO,I) .GT. 360.) AZIM(NANO,I) =AZIM(NANO,I) -360.
  295 CONTINUE
      GO TO 400
C
C THIS SECTION DETERMINES AZIMUTH FOR BRANCHES WITH NODE DISTANCE >90 CM
C
  300 DO 305 J=I,NPTS
        IF (J .EQ. 1) AZMEAN =UNI(0) *360.
        AZTMP =AZTMP +132.857
        IF (AZTMP .GE. 360.) AZTMP =AZTMP -360.
CE
        ERROR =22.7041 *RNOR(0)
CE        ERROR =0.
        AZIM(NANO,J) =AZTMP +ERROR
        IF (AZIM(NANO,J) .LT. 360.) AZIM(NANO,J) =AZIM(NANO,J) +360.
        IF (AZIM(NANO,J) .GE. 360.) AZIM(NANO,J) =AZIM(NANO,J) -360.
  305 CONTINUE
  400 CONTINUE
CC
CC      WRITE(6,2002)
CC 2002 FORMAT(' END OF NODEAZ')
      RETURN
      END
C*********************************************************************
C
C     THIS SUBROUTINE KILLS BRANCHES
C
C*********************************************************************
```

```
      SUBROUTINE KILL
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),O2N(3000),O3A(3000),O3N(3000),O4A(3000),O4N(3000),
     & ORD(3000),BAGE(3000),PANG(3000),PAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,O1N,O2A,O2N,O3A,O3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
      LOGICAL*1 COND
      COMMON /NODAZM/ NODED(3000,50),AZIM(3000,50)
      INTEGER*2 NODED
      COMMON /NO/ NYEARS,NTREES,NOYR
      INTEGER*2 NYEARS,NTREES
      COMMON /NOBR/ NOBRT,NOBROT,NOTREE
      INTEGER*2 NOBRT,NOBROT,NOTREE
C
C  Y1MORT IS THE PROBABILITY OF A TREE DYING BACK THE FIRST YEAR
C  Y2MORT IS THE PROBABILITY OF A TREE DYING THE SECOND YEAR IF IT DIED
C  BACK THE FIRST YEAR
C
      DATA Y1MORT /0.174/, Y2MORT /0.125/
      DIMENSION GENSUR(10),OSURV(4),AGEORD(4),NNSURV(5,5),OCOND(5)
      INTEGER*2 NNSURV
      LOGICAL*1 OCOND
      DATA GENSUR /10*999./, OSURV /0.894285,1.090303,0.9389483,0.0/,
     &     AGEORD /-0.08941134,-0.2002018,-0.1584490,0.0/
CB
CB SKIP THE SURVIVAL EFFECT FOR THE BOLES
CB
CB      GO TO 2
      IF (NOYR .NE. 1) GO TO 2
      DO 1 I=1,NTREES
CT
        GENSUR(I) =-0.1337232420 +SQRT(0.010154131) *RNOR(0)
CT        GENSUR(I) =-0.1337232420
    1 CONTINUE
    2 DO 999 NOBR =1,NOBRT
        IF (ORD(NOBR) .GT. 0) GO TO 10
C*************************************
C THIS SECTION KILLS THE TRUNKS
C*************************************
C  THIS SECTION LOOKS FOR FIRST YEAR PROBABILITY OF DEATH
C
        IF (NOYR .NE. 1) GO TO 5
        PSURV1 =UNI(0)
        IF (PSURV1 .GT. Y1MORT) GO TO 999
        BAGE(NOBR) =0
        LEN(NOBR,1) =0
        GO TO 999
C
C  THIS SECTION LOOKS FOR SECOND YEAR PROBABILITY OF DEATH
C
    5   IF (NOYR .NE. 2 .OR. BAGE(NOBR) .GT. 1) GO TO 10
        PSURV2 =UNI(0)
        IF (PSURV2 .GT. Y2MORT) GO TO 999
        BAGE(NOBR) =0
        LEN(NOBR,1) =0
        NNODES(NOBR,1) =0
        COND(NOBR) =.FALSE.
        GO TO 999
C*************************************
```

```
C THIS SECTION KILLS THE BRANCHES
C*************************************
C
C SKIP DEAD BRANCHES
C
CE SKIP THE SECTION THAT KILLS BRANCHES FOR THE PRESENT
   10   IF (.NOT.COND(NOBR)) GO TO 40
CE   10   IF (.TRUE.) GO TO 40
        IF (BAGE(NOBR) .LT. 2) GO TO 40
C
C FIND THE POINTER FOR THE GENSUR ARRAY
C
        NOTREE =TREE(NOBR)
        IF (ORD(NOBR) .GT. 2) GO TO 25
        IORD =ORD(NOBR) +1
        GO TO 30
   25   IORD =4
   30   CONTINUE
        IBA =BAGE(NOBR)
        DO 35 I=2,IBA
          J =I -1
          IF (NDAUT(NOBR,J) .LT. 1) GO TO 35
C
C ADD 0.5 TO ROUND CORRECTLY
C
CE
        ERROR =0.2584234 *RNOR(0)
CE        ERROR =0.
          NNSURV(IORD,J) =NNCDES(NOBR,I) -(HFIX((0.3812708
     &        +AGEORD(IORD) *I +OSURV(IORD) +GENSUR(NOTREE)
     &        +ERROR) *NDAUT(NOBR,J) +0.5))
   35   CONTINUE
C
C THIS SECTION KILLS DAUGHTERS
C
   40   IF (ORD(NOBR) -1) 55,60,45
   45   IF (ORD(NOBR) -3) 70,80,50
   50   IF (ORD(NOBR) -5) 90, 100,110
C ORDER 0
   55   IF (COND(NOBR)) GO TO 150
          GO TO 120
C ORDER 1
   60   IF (.NOT.COND(NOBR)) GO TO 125
CE
CE        IF (OCOND(1)) GO TO 155
        IF (OCOND(1) .AND. TN(NOBR) .GE. NNSURV(1,TA(NOBR) -1))
     &  GO TO 155
          COND(NOBR) =.FALSE.
          GO TO 125
C ORDER 2
   70   IF (.NOT.COND(NOBR)) GO TO 130
CE
CE        IF (OCOND(2)) GO TO 160
        IF (OCOND(2) .AND. O1N(NOBR) .GE. NNSURV(2,O1A(NOBR) -1))
     &  GO TO 160
          COND(NOBR) =.FALSE.
          GO TO 130
C ORDER 3
   80   IF (.NOT.COND(NOBR)) GO TO 135
CE
CE        IF (OCOND(3)) GO TO 165
        IF (OCOND(3) .AND. O2N(NOBR) .GE. NNSURV(3,O2A(NOBR) -1))
     &  GO TO 165
```

```
          COND(NOBR) =.FALSE.
          GO TO 135
C ORDER 4
   90   IF (.NOT.COND(NOBR)) GO TO 140
CF
CF        IF (OCOND(4)) GO TO 170
        IF (OCOND(4) .AND. O3N(NOBR) .GE. NNSURV(4,O3A(NOBR) -1))
     &  GO TO 170
          COND(NOBR) =.FALSE.
          GO TO 140
C ORDER 5
  100   IF (.NOT.COND(NOBR)) GO TO 999
CF
CF        IF (OCOND(5)) GO TO 999
        IF (OCOND(5) .AND. O4N(NOBR) .GE. NNSURV(5,O4A(NOBR) -1))
     &  GO TO 999
          COND(NOBR) =.FALSE.
          GO TO 999
  110   WRITE(6,115)
  115   FORMAT(' GREATER THAN 5 BRANCH ORDERS IN THE SUBROUTINE KILL')
  120   OCOND(1) =.FALSE.
  125   OCOND(2) =.FALSE.
  130   OCOND(3) =.FALSE.
  135   OCOND(4) =.FALSE.
  140   OCOND(5) =.FALSE.
        GO TO 999
  150   OCOND(1) =.TRUE.
  155   OCOND(2) =.TRUE.
  160   OCOND(3) =.TRUE.
  165   OCOND(4) =.TRUE.
  170   OCOND(5) =.TRUE.
  999 CONTINUE
      RETURN
CC      DEBUG INIT(GENSUB,ERROR,NNSURV,OCOND)
      END
C*********************************************************************
C
C     THIS SUBROUTINE PRUNES DEAD BRANCHES
C
C*********************************************************************
      SUBROUTINE PRUNE
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),C2N(3000),O3A(3000),O3N(3000),O4A(3000),C4N(3000),
     & ORD(3000),BAGE(3000),PANG(3000),PAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,C1N,O2A,C2N,O3A,O3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
      LOGICAL*1 COND
      COMMON /NOBR/ NOBRT,NOBROT,NOTREE
      INTEGER*2 NOBRT,NOBRCT,NOTREE
      COMMON /NODAZM/ NODED(3000,50),AZIM(3000,50)
      INTEGER*2 NODED
      NOBRCT =NOBRT
      NOBRT =0
      DO 20 I=1,NOBRCT
        IF (COND(I)) GO TO 1
        NODED(NAPT(I),1) =999
        GO TO 20
    1   NOBRT =NOBRT +1
        TREE(NOBRT) =TREE(I)
```

```
        TA(NOBRT) =TA(I)
        TN(NOBRT) =TN(I)
        O1A(NOBRT) =C1A(I)
        O1N(NOBRT) =C1N(I)
        O2A(NOBRT) =C2A(I)
        O2N(NOBRT) =C2N(I)
        O3A(NOBRT) =C3A(I)
        O3N(NOBRT) =C3N(I)
        O4A(NOBRT) =C4A(I)
        O4N(NOBRT) =C4N(I)
        ORD(NOBRT) =ORD(I)
        PAGE(NOBRT) =PAGE(I)
        PANG(NOBRT) =PANG(I)
        PAZ(NOBRT) =PAZ(I)
        GROM(NOBRT) =GROM(I)
        NODE(NOBRT) =NODE(I)
        NODEG(NOBRT) =NODEG(I)
        AZ(NOBRT) =AZ(I)
        DO 5 J=1,6
          ANG(NOBRT,J) =ANG(I,J)
          LEN(NOBRT,J) =LEN(I,J)
          NNODES(NOBRT,J) =NNODES(I,J)
    5   CONTINUE
        COND(NOBRT) =COND(I)
        NAPT(NOBRT) =NAPT(I)
        DO 10 J=1,5
          NDAUT(NOBRT,J) =NDAUT(I,J)
   10   CONTINUE
        DO 15 J=1,7
          X(NOBRT,J) =X(I,J)
          Y(NOBRT,J) =Y(I,J)
          Z(NOBRT,J) =Z(I,J)
   15   CONTINUE
   20 CONTINUE
      RETURN
      END
C*************************************************************************
C
C     THIS SUBROUTINE CREATES IDENTIFICATION FOR NEW BRANCHES
C
C*************************************************************************
      SUBROUTINE NEWID(NC)
      INTEGER*2 NC
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),O2N(3000),O3A(3000),O3N(3000),O4A(3000),O4N(3000),
     & ORD(3000),PAGE(3000),PANG(3000),PAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,O1N,O2A,O2N,O3A,O3N,O4A,O4N,
     &          ORD,PAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
      LOGICAL*1 COND
      COMMON /NOBR/ NOBRT,NOBROT,NOTREE
      INTEGER*2 NOBRT,NOBROT,NOTREE
      COMMON /NO/ NYEARS,NTREES,NOYR
      INTEGER*2 NYEARS,NTREES
      IF (NOYR .NE. 1) GO TO 20
C
C  GENERATE ID FOR NEW TREES
C
      DO 15 I=1,NC
        NOBRT =NOBRT +1
```

```
      TREE(NOBRT) =NOBRT
C
C THE NEXT SEVERAL STATEMENTS CALCULATE RANDOM TREE NUMBERS TO CHECK
C THE SORT SUBROUTINE. IF THIS OPTION IS USED, USE THE CALL TO SORT
C FOUND AFTER THE '10 CONTINUE' STATEMENT AND USE THE CALL TO PRINT
C FOUND IN MAIN
C  ADD +.5 TO CORRECT FOR ROUNDING TO ALL CALLS TO HFIX
C
C       Z =UNI(0)
C       TREE(NOBRT) =HFIX(Z*100 +.5)
C
C PRINT TREE NUMBER TO DETERMINE WHY TWO TREES HAVE THE SAME ID
C
C     WRITE(6,5) TREE(NOBRT)
C   5 FORMAT(' RANDOM TREE NUMBER =',I3)
      TA(NOBRT) =0
      TN(NOBRT) =0
      O1A(NOBRT) =0
      O1N(NOBRT) =0
      O2A(NOBRT) =0
      O2N(NOBRT) =0
      O3A(NOBRT) =0
      O3N(NOBRT) =0
      O4A(NOBRT) =0
      O4N(NOBRT) =0
      ORD(NOBRT) =0
      PAGE(NOBRT) =0
      PANG(NOBRT) =99.
      PAZ(NOBRT) =999.
      GROM(NOBRT) =0.
      DO 10 J=1,6
        ANG(NOBRT,J) =0.
        IEN(NOBRT,J) =0.
   10   NNODES(NOBRT,J) =0
      NODE(NOBRT) =0
      NODEG(NOBRT) =1
      AZ(NOBRT) =999.
      COND(NOBRT) =.TRUE.
      NAPT(NOBRT) =0
      DO 11 J=1,5
   11   NDAUT(NOBRT,J) =0
C
C DETERMINE THE ORIGINAL COORDINATES OF THE SEEDLINGS. IF THE TREES
C ARE GROWING IN A PLANTATION, THIS IS THE PLACE IN THE PROGRAM TO ADD
C CODE TO DETERMINE THEIR LOCATION
C
      X(NOBRT,1) =0.
      Y(NOBRT,1) =0.
      Z(NOBRT,1) =0.
   15 CONTINUE
C     CALL SORT
      GO TO 1000
C
C  GENERATE ID FOR NEW BRANCHES
C
   20 NNDAUT =NDAUT(NO,1)
      DO 60 I=1,NNDAUT
        NOBRT =NOBRT +1
        TREE(NOBRT) =TREE(NO)
        TA(NOBRT) =TA(NO)
        TN(NOBRT) =TN(NO)
        O1A(NOBRT) =O1A(NO)
        O1N(NOBRT) =O1N(NO)
```

```
      O2A(NOBRT) =C2A(NO)
      O2N(NOBRT) =C2N(NO)
      O3A(NOBRT) =C3A(NO)
      C3N(NOBRT) =C3N(NO)
      O4A(NOBRT) =C4A(NO)
      O4N(NOBRT) =C4N(NO)
      ORD(NOBRT) =ORD(NO) +1
      IF (ORD(NOBRT) -2) 24,25,22
   22 IF (ORD(NOBRT) -4) 30,35,23
   23 IF (ORD(NOBRT) -6) 40,45,45
C ORDER 1
   24 TA(NOBRT) =2
      GO TO 55
C ORDER 2
   25 O1A(NOBRT) =2
      GO TO 55
C ORDER 3
   30 O2A(NOBRT) =2
      GO TO 55
C ORDER 4
   35 O3A(NOBRT) =2
      GO TO 55
C ORDER 5
   40 O4A(NOBRT) =2
      GO TO 55
   45 WRITE(6,50)
   50 FORMAT(' THE TREE HAS MORE THAN 5 BRANCH ORDERS!!!!!!!')
      STOP
   55 BAGE(NOBRT) =1
      PANG(NOBRT) =99.
      PAZ(NOBRT) =999.
      GROM(NOBRT) =0.
      NODE(NOBRT) =0
      NODEG(NOBRT) =1
      AZ(NOBRT) =999.
      DO 56 J=1,6
        ANG(NOBRT,J) =0.
        LEN(NOBRT,J) =0.
   56   NNODES(NOBRT,J) =0
      DO 57 J=1,5
   57   NDAUT(NOBRT,J) =0
      COND(NOBRT) =.TRUE.
      NAFT(NOBRT) =0
      DO 58 J=1,7
        X(NOBRT,J) =0.
        Y(NOBRT,J) =0.
        Z(NOBRT,J) =0.
   58 CONTINUE
   60 CONTINUE
 1000 CONTINUE
CC
CC    WRITE(6,2002)
CC 2002 FORMAT(' END OF NEWID')
      RETURN
      END
C*********************************************************************
C
C     THIS SUBROUTINE DETERMINES BRANCH COORDINATES
C
C*********************************************************************
      SUBROUTINE COORD(NOBR,NODAUT,FLAG)
      INTEGER*2 NOBR,NODAUT
      LOGICAL*1 FLAG
```

```
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),O2N(3000),O3A(3000),O3N(3000),O4A(3000),O4N(3000),
     & ORD(3000),BAGE(3000),PANG(3000),PAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,O1N,O2A,O2N,O3A,O3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
      LOGICAL*1 COND
      INTEGER*2 BA,BAM1,BAP1
C CIR =CONVERT FROM DEGREES TO RADIANS =(2*PI)/360.
C CRD =CONVERT FROM RADIANS TO DEGREES =360./(2*PI)
      DATA CDR /0.017453293/, CRD /57.29577951/
CC
CC       DATA NERR /0/
      BA =BAGE(NOBR)
      BAM1 =BA -1
      BAP1 =BA +1
      IF (FLAG) GO TO 15
C*****************************************
C THIS SECTION IS FOR EXISTING BRANCHES
C*****************************************
      IF (ORD(NOBR) .NE. 0) GO TO 5
C*******************
C TRUNK
C*******************
      X(NOBR,BAP1) =X(NOBR,BA)
      Y(NOBR,BAP1) =Y(NOBR,BA)
      Z(NOBR,BAP1) =Z(NOBR,BA) +LEN(NOBR,1)
      GO TO 10
C*******************
C BRANCHES
C*******************
    5 PHI =ANG(NOBR,1) *CDR
C
C ALL AZIMUTHS WERE MEASURED WHILE LOOKING DOWN THE BRANCH FROM ITS
C APEX. ALSO, BECAUSE MATHEMATICIANS MEASURE ANGLES IN A COUNTERCLOCKWISE
C DIRECTION, THETA WAS CHANGED TO -THETA.
C
      THETA =-AZ(NOBR) *CDR
      X(NOBR,BAP1) =LEN(NOBR,1)*SIN(PHI)*COS(THETA)
     &             +X(NOBR,BA)
      Y(NOBR,BAP1) =LEN(NOBR,1)*SIN(PHI)*SIN(THETA)
     &             +Y(NOBR,BA)
      Z(NOBR,BAP1) =LEN(NOBR,1)*COS(PHI)
     &             +Z(NOBR,BA)
      IF (ABS(X(NOBR,BA)) .LE. 0.1E-6) X(NOBR,BA) =0.
      IF (ABS(Y(NOBR,BA)) .LE. 0.1E-6) Y(NOBR,BA) =0.
   10 IF (ABS(Z(NOBR,BA)) .LE. 0.1E-6) Z(NOBR,BA) =0.
      RETURN
C*****************************************
C THIS SECTION IS FOR NEW BRANCHES
C*****************************************
   15 PHI =PANG(NODAUT) *CDR
      THETA =-PAZ(NODAUT) *CDR
      IF (ORD(NODAUT) .GT. 1) GO TO 20
C*******************
C ORDER 1
C*******************
C
C DETERMINE POINT #1
C
```

```
      X(NODAUT,1) =X(NOBR,BAM1)
      Y(NODAUT,1) =Y(NOBR,BAM1)
      NN =NODE(NODAUT)
      Z(NODAUT,1) =Z(NOBR,BAM1) +FLOAT(NN)
C
C DETERMINE POINT #2
C
      X(NODAUT,2) =LEN(NODAUT,1)*SIN(PHI)*COS(THETA)
     &              +X(NODAUT,1)
      Y(NODAUT,2) =LEN(NODAUT,1)*SIN(PHI)*SIN(THETA)
     &              +Y(NODAUT,1)
      Z(NODAUT,2) =LEN(NODAUT,1)*COS(PHI)
     &              +Z(NODAUT,1)
      IF (ABS(X(NODAUT,2)) .LE. 0.1E-6) X(NODAUT,2) =0.
      IF (ABS(Y(NODAUT,2)) .LE. 0.1E-6) Y(NODAUT,2) =0.
      IF (ABS(Z(NODAUT,2)) .LE. 0.1E-6) Z(NODAUT,2) =0.
C
C STORE THE ANGLES RELATIVE TO GRAVITY
C
      AZ(NODAUT) =FAZ(NODAUT)
      ANG(NODAUT,1) =FANG(NODAUT)
      RETURN
C*******************
C ORDER 2 AND HIGHER ORDER BRANCHES
C*******************
C
C DETERMINE POINT #1
C
   20 NN =NODE(NODAUT)
      FRACT =(FLOAT(NN)) /GRCM(NODAUT)
      X(NODAUT,1) =(X(NOBR,BA) -X(NOBR,BAM1)) *FRACT +X(NOBR,BAM1)
      Y(NODAUT,1) =(Y(NOBR,BA) -Y(NOBR,BAM1)) *FRACT +Y(NOBR,BAM1)
      Z(NODAUT,1) =(Z(NOBR,BA) -Z(NOBR,BAM1)) *FRACT +Z(NOBR,BAM1)
      IF (ABS(X(NODAUT,1)) .LE. 0.1E-6) X(NODAUT,1) =0.
      IF (ABS(Y(NODAUT,1)) .LE. 0.1E-6) Y(NODAUT,1) =0.
      IF (ABS(Z(NODAUT,1)) .LE. 0.1E-6) Z(NODAUT,1) =0.
CC
CC       WRITE(6,21)NOBR,NODAUT,NN,BA,BAM1,FRACT,X(NOBR,BAM1),Y(NOBR,BAM1),
CC      &            Z(NOBR,BAM1),X(NOBR,BA),Y(NOBR,BA),Z(NOBR,BA)
CC    21 FORMAT(' POINT #1'/' NOBR=',I4,' NODAUT=',I4,' NN=',I5,' BA=',
CC      &        I2,' BAM1=',I2,' FRACT=',F8.4/' X1=',F10.5,'Y1=',F10.5,
CC      &        'Z1=',F10.5/' X2=',F10.5,' Y2=',F10.5,'Z2=',F10.5)
CC       CALL OUTBR(NOBR)
CC       CALL OUTBR(NODAUT)
CC       CALL ERR
C
C DETERMINE POINT #2
C
      XP =LEN(NODAUT,1)*SIN(PHI)*COS(THETA)
      YP =LEN(NODAUT,1)*SIN(PHI)*SIN(THETA)
      ZP =LEN(NODAUT,1)*COS(PHI)
      IF (ABS(XP) .LE. 0.1E-6) XP =0.
      IF (ABS(YP) .LE. 0.1E-6) YP =0.
      IF (ABS(ZP) .LE. 0.1E-6) ZP =0.
CC
CC       WRITE(6,40) PHI,THETA,XP,YP,ZP
CC    40 FORMAT(' PHI=',F6.1,' THETA=',F8.1/' XP=',F10.5,' YP=',F10.5,
CC      &        ' ZP=',F10.5)
C
C NOTE: WHEN THE COORDINATE AXES ARE ROTATED, THE NEW X-AXIS POINTS
C       DOWN INSTEAD OF UP. SUBTRACTING 180 DEGREES FROM THIS NUMBER AND
C       CHANGING THE SIGN OF ANG(NODAUT,1) CORRECTS THIS.
      PHI1 =-ANG(NOBR,2) *CDR
```

```
      THETA1 =(-AZ(NCBR) *CDR) -3.141592654
C
C NCTE: AT THIS PCINT X, Y, AND Z ARE THE CHANGE IN THE COCRDINATES
C       ALCNG THEIR AXES
C
      X(NOCAUT,2) =XP*CCS(PHI1)*COS(THETA1) -YP*SIN(THETA1)
     &              +ZP*SIN(PHI1)*COS(THETA1)
      Y(NOCAUT,2) =XP*CCS(PHI1)*SIN(THETA1) +YP*COS(THETA1)
     &              +ZP*SIN(PHI1)*SIN(THETA1)
      Z(NOCAUT,2) =-XP*SIN(PHI1) +ZP*COS(PHI1)
CC
CC       WRITE(6,45) PHI1,THETA1,X(NODAUT,2),Y(NOCAUT,2),Z(NCDAUT,2)
CC    45 FORMAT(' PHI1=',F6.1,' THETA1=',F8.1/
CC      &        ' X(NCDAUT,2)=',F10.5,' Y(NCDAUT,2)=',F10.5,
CC      &        ' Z(NCDAUT,2)=',F10.5)
      IF (ABS(X(NOCAUT,2)) .LE. 0.1E-6) X(NODAUT,2) =0.
      IF (ABS(Y(NOCAUT,2)) .LE. 0.1E-6) Y(NODAUT,2) =0.
      IF (ABS(Z(NODAUT,2)) .LE. 0.1E-6) Z(NODAUT,2) =0.
      ANG(NOCAUT,1) =(ACOS(Z(NODAUT,2) /LEN(NODAUT,1))) *CRD
CC
CC       WRITE(6,50) NCDAUT,ANG(NCDAUT,1)
CC    50 FORMAT(' NODAUT=',I4,' ANG(NCDAUT,1)=',F10.5)
      IF (X(NCDAUT,2)) 100,120,80
   80 IF (Y(NCDAUT,2)) 160,90,160
   90 AZ(NCDAUT) =0. *CRD
CC
CC       WRITE(6,95)
CC    95 FORMAT(' STATEMENT 90')
      GO TC 180
  100 IF (Y(NCDAUT,2)) 170,110,170
  110 AZ(NCDAUT) =3.141592654 *CRD
CC
CC       WRITE(6,115)
CC   115 FORMAT(' STATEMENT 110')
      GO TC 180
  120 IF (Y(NCDAUT,2)) 130,150,140
  130 AZ(NCDAUT) =-1.5707963 *CRD
CC
CC       WRITE(6,135)
CC   135 FORMAT (' STATEMENT 130')
      GO TC 180
  140 AZ(NCDAUT) =+1.5707963 *CRD
CC
CC       WRITE(6,145)
CC   145 FORMAT (' STATEMENT 140')
      GO TC 180
  150 AZ(NCDAUT) =3.141592654 *CRD
      ANG(NODAUT,1) =0. *CRD
CC
CC       WRITE(6,155)
CC   155 FORMAT (' STATEMENT 150')
C
  160 AZ(NCDAUT) =-ATAN(Y(NCDAUT,2) /X(NCDAUT,2)) *CRD
      IF (AZ(NODAUT) .LT. 0.) AZ(NODAUT) =AZ(NODAUT) +360.
CC
CC       WRITE(6,165)
CC   165 FORMAT (' STATEMENT 160')
CC       CAIL CUTER(NCER)
CC       CAIL CUTER(NCDAUT)
CC       NERR =NERR +1
CC       IF (NERR .GE. 5) CAIL ERR
      GO TC 180
C
```

```
C -PI/2 <= AZ <= PI/2, SO ADD 180 DEGREES FOR POINTS WHERE DELTA X <0
C
  170 AZ(NODAUT) =-ATAN(Y(NODAUT,2) /X(NODAUT,2)) *CRD +180.
CC
CC       WRITE(6,165)
CC   165 FORMAT (' STATEMENT 170')
CC       CALL CUTER(NCER)
CC       CALL CUTER(NODAUT)
CC       NERR =NERR +1
CC       IF (NERR .GE. 5) CALL ERR
  180 X(NODAUT,2) =X(NODAUT,2) +X(NODAUT,1)
      Y(NODAUT,2) =Y(NODAUT,2) +Y(NODAUT,1)
      Z(NODAUT,2) =Z(NODAUT,2) +Z(NODAUT,1)
      IF (ABS(X(NODAUT,2)) .LE. 0.1E-6) X(NODAUT,2) =0.
      IF (ABS(Y(NODAUT,2)) .LE. 0.1E-6) Y(NODAUT,2) =0.
      IF (ABS(Z(NODAUT,2)) .LE. 0.1E-6) Z(NODAUT,2) =0.
      RETURN
      END
C*********************************************************************
C
C     THIS SUBROUTINE SORTS THE DATA
C
C*********************************************************************
      SUBROUTINE SORT
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),O2N(3000),O3A(3000),O3N(3000),O4A(3000),O4N(3000),
     & ORD(3000),BAGE(3000),PANG(3000),PAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,O1N,O2A,O2N,O3A,O3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
      LOGICAL*1 COND
      COMMON /NOER/ NOBRT,NOBROT,NOTREE
      INTEGER*2 NOBRT,NOBROT,NOTREE
      DIMENSION E(6), F(6), G(7), H(7), C(7), K(102)
      INTEGER*2 K
      LOGICAL*1 I
      EQUIVALENCE (K(13),A),(K(15),B),(K(17),C),(K(21),D),
     &            (K(23),E(1)),(K(35),F(1)),(K(59),L),
     &            (K(61),G(1)),(K(75),H(1)),(K(89),O(1))
      INTEGER KORE /1000/
      CALL FSORT(' SORT FIELDS=(1,2,A,3,2,A,5,2,A,7,2,A,9,2,A,11,2,A,13,
     &2,A,15,2,A,17,2,A,19,2,A,21,2,A),FORMAT=FI,SIZE=E100 ',
     &' RECORD TYPE=F,LENGTH=(204) ','FINEFOUT',KORE)
      DO 10 I=1,NOBRT
        K(1) =TREE(I)
        K(2) =TA(I)
        K(3) =TN(I)
        K(4) =O1A(I)
        K(5) =O1N(I)
        K(6) =O2A(I)
        K(7) =O2N(I)
        K(8) =O3A(I)
        K(9) =O3N(I)
        K(10) =O4A(I)
        K(11) =O4N(I)
        K(12) =BAGE(I)
        A =PANG(I)
        B =PAZ(I)
        K(19) =NODE(I)
        K(20) =NODEG(I)
```

```
      C =GROM(I)
      D =AZ(I)
      DO 5 J=1,6
        E(J) =ANG(I,J)
        F(J) =LEN(I,J)
 5    CONTINUE
      K(47) =NNODES(I,1)
      K(48) =NNODES(I,2)
      K(49) =NNODES(I,3)
      K(50) =NNODES(I,4)
      K(51) =NNODES(I,5)
      K(52) =NNODES(I,6)
      K(53) =NDAUT(I,1)
      K(54) =NDAUT(I,2)
      K(55) =NDAUT(I,3)
      K(56) =NDAUT(I,4)
      K(57) =NDAUT(I,5)
      K(58) =ORD(I)
      L =COND(I)
      K(60) =NAPT(I)
      DO 7 J=1,7
        G(J) =X(I,J)
        H(J) =Y(I,J)
        C(J) =Z(I,J)
 7    CONTINUE
      CALL FINP(K)
10 CONTINUE
   CALL FSCRT
   DO 20 I=1,NOERT
      CALL FOUT(K)
      TREE(I) =K(1)
      TA(I) =K(2)
      TN(I) =K(3)
      O1A(I) =K(4)
      O1N(I) =K(5)
      O2A(I) =K(6)
      O2N(I) =K(7)
      O3A(I) =K(8)
      O3N(I) =K(9)
      O4A(I) =K(10)
      O4N(I) =K(11)
      BAGE(I) =K(12)
      PANG(I) =A
      PAZ(I) =E
      NODE(I) =K(19)
      NODEG(I) =K(20)
      GROM(I) =C
      AZ(I) =D
      DO 15 J=1,6
        ANG(I,J) =E(J)
        LEN(I,J) =F(J)
15    CONTINUE
      NNODES(I,1) =K(47)
      NNODES(I,2) =K(48)
      NNODES(I,3) =K(49)
      NNODES(I,4) =K(50)
      NNODES(I,5) =K(51)
      NNODES(I,6) =K(52)
      NDAUT(I,1) =K(53)
      NDAUT(I,2) =K(54)
      NDAUT(I,3) =K(55)
      NDAUT(I,4) =K(56)
      NDAUT(I,5) =K(57)
```

```
        ORD(I) =K(58)
        COND(I) =L
        NAPT(I) =K(60)
        DO 17 J=1,7
          X(I,J) =G(J)
          Y(I,J) =H(J)
          Z(I,J) =C(J)
   17   CONTINUE
   20 CONTINUE
CC
CC      WRITE(6,2002)
CC 2002 FORMAT(' END OF SORT')
      RETURN
      END
C*********************************************************************
C
C      THIS SUBROUTINE OUTPUTS DATA
C
C*********************************************************************
      SUBROUTINE OUTPUT(FLAG)
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),C2N(3000),O3A(3000),O3N(3000),O4A(3000),C4N(3000),
     & ORD(3000),PAGE(3000),PANG(3000),PAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,C1N,O2A,C2N,O3A,C3N,O4A,O4N,
     &          ORD,PAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
      LOGICAL*1 COND
      COMMON /NOER/ NCERT,NCERCT,NOTREE
      INTEGER*2 NOERT,NCERCT,NOTREE
      COMMON /NO/ NYEARS,NTREES,NOYR
      INTEGER*2 NYEARS,NTREES
      COMMON /NODAZM/ NODED(3000,50),AZIM(3000,50)
      INTEGER*2 NODED
      LOGICAL*1 FLAG
      WRITE(6,5)
    5 FORMAT('0 T',38X,'P',9X,'G    MN  GN',60X,'C    N'/'  R',8X,
     & 9('C   '),3X,'A    P    R    O   O',13X,'ANGLES',20X,'LENGTHS',14X,
     & 'O    A'/'  E',2('  T'),
     & 2('  1'),2('  2'),2('  3'),2('  4'),'  R  B  N    A    O    D',
     & '   D   A ',55X,'N    P'/'  E',5('  A  N'),'  D  A  G    Z    M',
     & '    E   E   Z   1   2   3   4   5   6    1    2    3    4    5',
     & '    6  D    T')
      WRITE(6,6)
    6 FORMAT('+',126('_'))
      WRITE(6,7)
    7 FORMAT(' ',99X,'NNODES'/' ',92X,'1    2    3    4    5    6')
      WRITE(6,8)
    8 FORMAT('+',90X,29('_'))
CE
      WRITE(6,9)
    9 FORMAT(' ',100X,'NDAUT'/' ',97X,'2    3    4    5    6')
      WRITE(6,8)
CC
CC     WRITE(6,11)
CC   11 FORMAT(' ',97X,'COORDINATES (X,Y,Z)'/' ',87X,'1    2    3    4',
CC     &        '    5    6    7')
CC      WRITE(6,12)
CC   12 FORMAT('+',84X,35('_'))
      DO 18 I=1,NCERT
      WRITE(6,13)TREE(I),TA(I),TN(I),O1A(I),O1N(I),O2A(I),C2N(I),O3A(I),
```

```
     & O3N(I),O4A(I),C4N(I),ORD(I),BAGE(I),PANG(I),PAZ(I),GROM(I),
     & NODE(I),NODEG(I),AZ(I),(ANG(I,J),J=1,6),(LEN(I,J),J=1,6),
     & COND(I),NAPT(I),(NNODES(I,J),J=1,6)
   13 FORMAT(' ',13(I2,1X),F3.0,2(F5.0),2(I4),F5.0,6(F4.0),6(F5.0),
     &         1X,L1,I5/' ',88X,6(I5))
CE
      IF (BAGE(I) .GT. 1) WRITE(6,14) (NDAUT(I,J),J=1,5)
   14 FORMAT(' ',93X,5(I5))
CC
CE
CC         WRITE(6,15) (X(I,J),J=1,7),(Y(I,J),J=1,7),(Z(I,J),J=1,7)
CC   15    FORMAT(3(' ',84X,7(F5.0)/))
   18 CONTINUE
      IF (FLAG) GO TO 45
CC SKIP THE OUTPUT OF THE NODE POSITIONS FOR THE PRESENT
      IF (.NOT.FLAG) GO TO 45
      WRITE(6,20)
   20 FORMAT('0CURRENT GROWTH'/' NAPT'/' NODE'/' AZIMUTH'/'      1     2',
     & '     3     4     5     6     7     8     9    10    11    12    13    14',
     & '    15    16    17    18    19    20    21    22    23    24    25'/
     & ' PREVIOUS GROWTH'/' NODE'/' AZIMUTH'/'     26    27    28    29',
     & '    30    31    32    33    34    35    36    37    38    39    40    41',
     & '    42    43    44    45    46    47    48    49    50')
      WRITE(6,21)
   21 FORMAT('+',125('_'))
      DO 45 I=1,NOERT
        IF (.NOT.COND(I)) GO TO 45
        NPTS =NNODES(I,1)
        II =NAPT(I)
        WRITE(6,23) II
   23   FORMAT(' ',I5)
CC
CC         WRITE(6,24)
CC   24    FORMAT('+_____')
        WRITE(6,25) (NODED(II,J),J=1,NPTS)
   25   FORMAT(' ',25I5)
        WRITE(6,30) (AZIM(II,J),J=1,NPTS)
   30   FORMAT(' ',25F5.0)
        NPTS =NNODES(I,2) +25
        IF (NODED(II,26) .GE. 999) GO TO 45
        WRITE(6,35) (NODED(II,J),J=26,NPTS)
   35   FORMAT(' ',25I5)
        WRITE(6,40) (AZIM(II,J),J=26,NPTS)
   40   FORMAT(' ',25F5.0)
   45 CONTINUE
      RETURN
      END
C*********************************************************************
C
C       THIS SUBROUTINE OUTPUTS DATA FOR ONE BRANCH AND IS USED FOR DEBUGGING
C
C*********************************************************************
      SUBROUTINE OUTER(I)
      INTEGER*2 I
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),O2N(3000),O3A(3000),O3N(3000),O4A(3000),O4N(3000),
     & ORD(3000),BAGE(3000),PANG(3000),PAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,O1N,O2A,O2N,O3A,O3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
```

```
      LOGICAL*1 COND
      WRITE(6,13)TREE(I),TA(I),TN(I),O1A(I),C1N(I),O2A(I),O2N(I),O3A(I),
     & O3N(I),O4A(I),C4N(I),ORD(I),BAGE(I),PANG(I),PAZ(I),GROM(I),
     & NODE(I),NODEG(I),AZ(I),(ANG(I,J),J=1,6),(LEN(I,J),J=1,6),
     & COND(I),NAPT(I),(NNODES(I,J),J=1,6)
   13 FORMAT(' ',13(I2,1X),F3.0,2(F5.0),2(I4),F5.0,6(F4.0),6(F5.0),
     &         1X,L1,I5/' ',88X,6(I5))
      IF (BAGE(I) .GT. 1) WRITE(6,14) (NDAUT(I,J),J=1,5)
   14 FORMAT(' ',93X,5(I5))
CC
CC       WRITE(6,15) (X(I,J),J=1,7),(Y(I,J),J=1,7),(Z(I,J),J=1,7)
CC    15 FORMAT(3(' ',84X,7(F5.0)/))
      RETURN
      END
C*********************************************************************
C
C       THIS SUBROUTINE OUTPUTS DATA FOR ELCTS
C
C*********************************************************************
      SUBROUTINE OUTPUT
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),C2N(3000),O3A(3000),O3N(3000),O4A(3000),C4N(3000),
     & ORD(3000),BAGE(3000),PANG(3000),PAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,C1N,O2A,C2N,O3A,C3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
      LOGICAL*1 COND
      COMMON /NOER/ NOERT,NOERCT,NOTREE
      INTEGER*2 NOERT,NOERCT,NOTREE
      DO 20 I=1,NOERT
        WRITE(8,10) TREE(I),BAGE(I),(X(I,J),J=1,7),(Y(I,J),J=1,7),
     &              (Z(I,J),J=1,7)
   10   FORMAT (2I2,3(/7F8.3))
   20 CONTINUE
      RETURN
      END
C*********************************************************************
C
C     THIS SUBROUTINE SAMPLES BRANCHES TO VALIDATE THE MODEL
C
C*********************************************************************
      SUBROUTINE VALID
      COMMON /TREEID/ TREE(3000),TA(3000),TN(3000),O1A(3000),O1N(3000),
     & O2A(3000),C2N(3000),O3A(3000),O3N(3000),O4A(3000),C4N(3000),
     & ORD(3000),BAGE(3000),PANG(3000),PAZ(3000),GROM(3000),
     & NODE(3000),NODEG(3000),AZ(3000),ANG(3000,6),LEN(3000,6),
     & NNODES(3000,6),COND(3000),NAPT(3000),NDAUT(3000,5),
     & X(3000,7),Y(3000,7),Z(3000,7)
      INTEGER*2 TREE,TA,TN,O1A,C1N,O2A,C2N,O3A,C3N,O4A,O4N,
     &          ORD,BAGE,NODE,NODEG,NNODES,NAPT,NDAUT
      REAL LEN
      LOGICAL*1 COND
      COMMON /NOER/ NOERT,NOERCT,NOTREE
      INTEGER*2 NOERT,NOERCT,NOTREE
      INTEGER*2 NOER,IBPT1,IBPT2
C CDR =CONVERT FROM DEGREES TO RADIANS =(2*PI)/360.
C CRD =CONVERT FROM RADIANS TO DEGREES =360./(2*PI)
C       DATA CDR /0.017453293/, CRD /57.29577951/
C ROTANG IS THE ANGLE (75 DEGREES) THE TREE IS ROTATED IN A CLOCKWISE
C DIRECTION TO GET TEE VALIDATION DATA
```

```
      DATA ROTCOS/0.258819045/,ROTSIN/-0.965925826/,ROTANG/-1.308996939/
      DATA SIDE /62.9960525/, HSIDE /31.4980263/
      DIMENSION XB(7), YB(7)
      LOGICAL*1 FLAG
CE
CE      DIMENSION IZ(7)
      ZMAX =0.
      RMAX =0.
      NOBR =0
      WRITE(8,1)
    1 FORMAT(' 999999999999999999999999999999999999999999999999999999')
C*************************************
C DETERMINE MAXIMUM HEIGHT AND RADIUS
C*************************************
   10 NOBR =NOBR +1
      IF (CRD(NOBR) .GT. 0) GO TO 30
CE
CE THIS NEXT SECTION OUTPUTS DATA FOR THE HOLE FOR VALIDATION
CE
CE      DO 12 J=1,7
CE        IZ(J) =IFIX(Z(NOBR,J) +0.5)
CE   12 CONTINUE
CE      WRITE(8,15) TREE(NOBR),(IZ(J),J=1,7)
CE   15 FORMAT(I2,7(1X,I3))
CE END OF SECTION FOR VALIDATION
   20 IF (NOBR .GE. NOBRT) RETURN
C*******************
C DETERMINE THE TEST POINTS ALONG THE Z-AXIS
C*******************
      IBAP1 =PAGE(NOBR) +1
      ZMAX =Z(NOBR,IBAP1)
      Z50 =ZMAX /2.
      Z50T =Z50 +SIDE
      Z75 =ZMAX *3. /4.
      Z75T =Z75 +SIDE
      GO TO 10
   30 IBPT1 =NOBR
C*******************
C DETERMINE THE TEST POINTS IN THE X-Y PLANE
C*******************
   40 IBAP1 =PAGE(NOBR) +1
      DO 50 J=1,IBAP1
        DIST =SQRT((X(NOBR,J)**2) +(Y(NOBR,J)**2))
        IF (DIST .GT. RMAX) RMAX =DIST
   50 CONTINUE
      IBPT2 =NOBR
      IF (NOBR .LT. NOBRT) GO TO 60
      FLAG =.FALSE.
      GO TO 70
   60 NOBR =NOBR +1
      IF (CRD(NOBR) .GT. 0) GO TO 40
      FLAG =.TRUE.
   70 R50 =RMAX /2.
C
C C =CUBE
C M,C,P,T =MINUS, CENTER, PLUS, TOP
C P1,P2 =POINTS 1 AND 2
C
      CMP1 =-R50 -HSIDE
      CMP2 =-R50 +HSIDE
      CCP1 =-HSIDE
      CCP2 =HSIDE
      CPP1 =R50 -HSIDE
```

```
      CPP2 =R50 *HSIDE
      CTP1 =-SIDE
      CTP2 =0.
C*************************************
C ROTATE THE BRANCHES SO THAT THE SAMPLE BOXES LIE ALONG THE X AND Y AXES
C*************************************
      DO 550 II=IBPT1,IBPT2
        IEA =EAGE(II)
        IBAP1 =BAGE(II) +1
C
C ORDER 1
C
        IF (ORD(II) .GT. 1) GO TO 90
        IOTAGE =BAGE(II)
        XR(1) =X(II,1)
        YR(1) =Y(II,1)
        DO 80 J=2,IBAP1
          XR(J) =X(II,J) *ROTCOS +Y(II,J) *ROTSIN
          YR(J) =-X(II,J) *ROTSIN +Y(II,J) *ROTCOS
   80   CONTINUE
        GO TO 220
C
C ORDER 2+ BRANCHES
C
   90   DO 210 J=1,IBAP1
          IF (X(II,J)) 120,140,100
  100     IF (Y(II,J)) 180,110,180
  110     THETA =0.
CC
CC          WRITE(6,115)
CC  115     FORMAT(' STATEMENT 110')
          GO TO 200
  120     IF   (Y(II,J)) 190,130,190
  130     THETA =3.141592654
CC
CC          WRITE(6,135)
CC  135     FORMAT(' STATEMENT 130')
          GO TO 200
  140     IF (Y(II,J)) 150,170,160
  150     THETA =-1.5707963
CC
CC          WRITE(6,155)
CC  155     FORMAT (' STATEMENT 150')
          GO TO 200
  160     THETA =+1.5707963
CC
CC          WRITE(6,165)
CC  165     FORMAT (' STATEMENT 160')
          GO TO 200
  170     THETA =3.141592654
CC
CC          WRITE(6,175)
CC  175     FORMAT (' STATEMENT 170')
C
  180     THETA =-ATAN(Y(II,J) /X(II,J))
          IF (THETA .LT. 0.) THETA =THETA +6.283185308
CC
CC          WRITE(6,185)
CC  185     FORMAT (' STATEMENT 180')
          GO TO 200
C
C -PI/2 <= AZ <= PI/2, SO ADD 180 DEGREES FOR POINTS WHERE DELTA X <0
C
```

```
  190     THETA =-ATAN(Y(II,J) /X(II,J))  +3.141592654
CC
CC          WRITE(6,185)
CC  185     FORMAT (' STATEMENT 190')
  200     THETA =THETA +ROTANG
          RHO =SQRT (X(II,J)**2 +Y(II,J)**2)
          XR(J) =RHO *COS(THETA)
          YR(J) =RHO *SIN (THETA)
  210   CONTINUE
C*************************************
C SAMPLE THE BRANCHES
C*************************************
C NOTE: THIS SECTION HAS BEEN WRITTEN TO ACCOUNT FOR THE "WORST CASE"
C       WHERE A BRANCH IS IN ALL FIVE CUBES.
  220   DO 550 J=1,IEA
          K =J +1
          IF (Z(II,J) .LE. Z75 .AND. Z(II,K) .LE. Z75) GO TO 230
          IF (Z(II,J) .GE. Z75T .AND. Z(II,K) .GE. Z75T) GO TO 550
          IF (XR(J) .LE. CCP1 .AND. XR(K) .LE. CCP1) GO TO 230
          IF (XR(J) .GE. CCP2 .AND. XR(K) .GE. CCP2) GO TO 230
          IF (YR(J) .LE. CTP1 .AND. YR(K) .LE. CTP1) GO TO 230
          IF (YR(J) .GE. CTP2 .AND. YR(K) .GE. CTP2) GO TO 230
C
C SAMPLE CUBE 1
C M =MINUS (NEGATIVE); P =PLUS (POSITIVE); L =LOWER; U =UPPER
C
          XM =CCP1
          XP =CCP2
          YM =CTP1
          YP =CTP2
          ZL =Z75
          ZU =Z75T
          ICUBE =1
          GO TO 270
  230     IF (Z(II,J) .LE. Z50 .AND. Z(II,K) .LE. Z50) GO TO 550
          IF (Z(II,J) .GE. Z50T .AND. Z(II,K) .GE. Z50T) GO TO 550
          IF (XR(J) .LE. CMP1 .AND. XR(K) .LE. CMP1) GO TO 550
          IF (XR(J) .GE. CMP2 .AND. XR(K) .GE. CMP2) GO TO 240
          IF (YR(J) .LE. CCP1 .AND. YR(K) .LE. CCP1) GO TO 240
          IF (YR(J) .GE. CCP2 .AND. YR(K) .GE. CCP2) GO TO 240
C
C SAMPLE CUBE 4
C
          XM =CMP1
          XP =CMP2
          YM =CCP1
          YP =CCP2
          ZL =Z50
          ZU =Z50T
          ICUBE =4
          GO TO 270
  240     IF (XR(J) .LE. CCP1 .AND. XR(K) .LE. CCP1) GO TO 550
          IF (XR(J) .GE. CCP2 .AND. XR(K) .GE. CCP2) GO TO 260
          IF (YR(J) .LE. CMP1 .AND. YR(K) .LE. CMP1) GO TO 550
          IF (YR(J) .GE. CMP2 .AND. YR(K) .GE. CMP2) GO TO 250
C
C SAMPLE CUBE 3
C
          XM =CCP1
          XP =CCP2
          YM =CMP1
          YP =CMP2
          ZL =Z50
```

```
      ZU =Z50T
      ICUBE =3
      GO TO 270
250   IF (YR(J) .LE. CPP1 .AND. YR(K) .LE. CPP1) GO TO 260
      IF (YR(J) .GE. CPP2 .AND. YR(K) .GE. CPP2) GO TO 550
C
C SAMPLE CUBE 5
C
      XM =CCP1
      XP =CCP2
      YM =CPP1
      YP =CPP2
      ZL =Z50
      ZU =Z50T
      ICUBE =5
      GO TO 270
260   IF (XR(J) .LE. CPP1 .AND. XR(K) .LE. CPP1) GO TO 550
      IF (XR(J) .GE. CPP2 .AND. XR(K) .GE. CPP2) GO TO 550
      IF (YR(J) .LE. CCP1 .AND. YR(K) .LE. CCP1) GO TO 550
      IF (YR(J) .GE. CCP2 .AND. YR(K) .GE. CCP2) GO TO 550
C
C SAMPLE CUBE 2
C
      XM =CPP1
      XP =CPP2
      YM =CCP1
      YP =CCP2
      ZL =Z50
      ZU =Z50T
      ICUBE =2
C
C "CHOP" THE BRANCH SECTIONS SO THAT ONLY THE PART IN THE CUBE IS SAMPLED
C
270   X1 =XR(J)
      X2 =XR(K)
      Y1 =YR(J)
      Y2 =YR(K)
      Z1 =Z(II,J)
      Z2 =Z(II,K)
      IF (X1 .LT. XM) GO TO 280
      IF (X2 .LT. XM) GO TO 290
      GO TO 300
280   X1 =XM
      GO TO 300
290   X2 =XM
300   IF (X1 .GT. XP) GO TO 310
      IF (X2 .GT. XP) GO TO 320
      GO TO 330
310   X1 =XP
      GO TO 330
320   X2 =XP
330   IF (Y1 .LT. YM) GO TO 340
      IF (Y2 .LT. YM) GO TO 350
      GO TO 360
340   Y1 =YM
      GO TO 360
350   Y2 =YM
360   IF (Y1 .GT. YP) GO TO 370
      IF (Y2 .GT. YP) GO TO 380
      GO TO 390
370   Y1 =YP
      GO TO 390
380   Y2 =YP
```

```
  390     IF (Z1 .LT. ZL) GO TO 400
          IF (Z2 .LT. ZL) GO TO 410
          GO TO 420
  400     Z1 =ZL
          GO TO 420
  410     Z2 =ZL
  420     IF (Z1 .GT. ZU) GO TO 430
          IF (Z2 .GT. ZU) GO TO 440
          GO TO 450
  430     Z1 =ZU
          GO TO 450
  440     Z2 =ZU
  450     IO1A =C1A(II)
          IO2A =C2A(II)
          IO3A =C3A(II)
          IO4A =C4A(II)
          IF (ORD(II) -2) 490,500,460
  460     IF (ORD(II) -4) 510,520,470
  470     WRITE (6,480)
  480     FORMAT(' TRYING TO SAMPLE A FIFTH ORDER BRANCH IN "VALID"')
          GO TO 550
  490     IO1A =IBA +1 -J
          GO TO 530
  500     IO2A =IBA +1 -J
          GO TO 530
  510     IO3A =IBA +1 -J
          GO TO 530
  520     IO4A =IBA +1 -J
  530     IENG =IFIX(SQRT((X2-X1)**2 +(Y2-Y1)**2 +(Z2-Z1)**2) +0.5)
C SINCE THE MEASUREMENTS IN THE VALIDATION DATA SET ARE RECORDED TO THE
C NEAREST CM, FIX THE VALUES OF THE AZIMUTH AND INCLINATION SO THAT
C THE FORMATS OF THE TWO DATA SETS MATCH.
          IAZ =IFIX(AZ(II) +0.5)
          IANG =IFIX(ANG(II,J) +0.5)
CC
CC          WRITE(6,531) X1,X2,Y1,Y2,Z1,Z2,IENG
CC  531     FORMAT(' X1=',F6.2,' X2=',F6.2,' Y1=',F6.2,' Y2=',F6.2,
CC     &          ' Z1=',F6.2,' Z2=',F6.2,' LENG=',I6)
          WRITE(8,540) TREE(II),ICUBE,IC1AGE,IC1A,IO2A,IC3A,IO4A,
     &                 LENG,IAZ,IANG
  540     FORMAT(I2,I1,2X,5I1,I3,I4,I3)
          GO TO (230,550,250,240,260), ICUBE
  550 CONTINUE
      IF (FLAG) GO TO 20
      RETURN
CC
CC      DEBUG INIT(Z50,Z50T,Z75,Z75T,CMP1,CMP2,CCP1,CCP2,CPP1,CPP2,
CC     &           CTP1,CTP2,ZMAX,RMAX,TEETA,RHO,XB,YB,
CC     &           XM,XP,YM,YP,ZI,ZU,II,ICUBE)
      END
C*********************************************************************
C
C      THIS SUBROUTINE STOPS THE PROGRAM
C
C*********************************************************************
      SUBROUTINE ERR
      STOP
      END
```

# APPENDIX B

# MODEL INPUT

This appendix lists the data used to run the model. The first two lines give the length of the run and the number of trees. The third line gives the soil field capacity, and the -3 bar and -15 bar soil moisture tension values. Line four gives the dates of the first and last days of the growing season, and plot latitude. The next four lines give monthly values for mean temperatures and their standard deviations, and for total precipitations and their standard deviations. The rest of this data set gives information needed to predict node position for each node class. The first number in each block of data gives the number of nodes associated with that node class, minus one. (The minus one is used because all node positions are relative node positions, and the last of these positions is always 1.0). The next line(s) gives (give) mean relative node distances. The last set of lines in each data block gives the lower diagonal of the variance-covariance matrix for each node class.

```
    6
    3
20.6177 20.5453 10.9784
105.0 288.0 37.00
 38.92 40.15 47.58 56.98 66.11 74.06 77.84 76.75 71.15 60.32 50.58 41.53
 5.117 4.184 3.772 2.381 2.113 1.917 1.435 1.553 2.158 2.540 2.515 3.843
 3.453 3.148 3.700 3.095 3.687 3.708 4.965 4.836 3.922 3.145 2.947 3.091
 1.544 1.172 1.253 1.120 1.592 1.364 2.042 2.262 2.216 1.806 1.564 1.322
 1
0.4325758
 9.71518E-03
 2
0.18223230.4925330
 3.51838E-03
 3.19554E-03 1.41540E-02
 3
0.09734260.25528390.6113564
 1.13814E-03
 1.28513E-03 5.29218E-03
 7.80383E-04 4.55551E-03 7.06494E-03
 4
0.06291150.17551800.41178100.7098648
 5.55186E-04
 7.32136E-04 3.72398E-03
 7.63401E-04 4.17393E-03 6.56423E-03
 6.18995E-04 3.19617E-03 5.03847E-03 5.33823E-03
 5
0.04813790.13948510.32871540.55731380.8001740
 3.76669E-04
 6.96226E-04 2.91569E-03
 9.12916E-04 4.20093E-03 7.42013E-03
 9.52919E-04 3.69190E-03 6.78373E-03 7.70364E-03
 5.88451E-04 2.31440E-03 4.27738E-03 4.94568E-03 4.10466E-03
 6
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 4.28940E-04
 9.32670E-04 3.25399E-03
 1.23075E-03 4.38897E-03 6.95744E-03
 1.26592E-03 4.30496E-03 6.88812E-03 7.60819E-03
 1.06790E-03 3.50897E-03 5.63424E-03 6.38688E-03 6.03843E-03
 5.07930E-04 1.74345E-03 2.85881E-03 3.34020E-03 3.30721E-03 2.44531E-03
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 8.56941E-04 2.69829E-03
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 1.18894E-03 3.99970E-03 6.46238E-03 8.18744E-03
 1.10222E-03 3.52498E-03 5.82000E-03 7.37697E-03 7.51388E-03
 7.52143E-04 2.35169E-03 4.04167E-03 5.31076E-03 5.66675E-03 4.96365E-03
 3.48518E-04 1.04631E-03 1.79343E-03 2.35533E-03 2.52359E-03 2.29954E-03
 1.40976E-03
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 3.96440E-04 1.41808E-03
 5.82040E-04 2.21945E-03 4.02284E-03
 6.00103E-04 2.31701E-03 4.33928E-03 5.08450E-03
 5.91911E-04 2.31040E-03 4.31639E-03 5.21248E-03 6.05328E-03
 4.46307E-04 1.84943E-03 3.53160E-03 4.41330E-03 5.22418E-03 5.18290E-03
 2.75375E-04 1.18292E-03 2.34854E-03 3.01622E-03 3.61448E-03 3.75619E-03
 3.05214E-03
 1.31096E-04 4.98371E-04 1.06013E-03 1.40953E-03 1.67139E-03 1.85697E-03
 1.57382E-03 1.05126E-03
```

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 2.59333E-04 1.19814E-03 2.49787E-03 3.04564E-03
 2.47432E-04 1.16180E-03 2.47987E-03 3.13987E-03 3.54370E-03
 1.96700E-04 1.00085E-03 2.11772E-03 2.80629E-03 3.33878E-03 3.60470E-03
 1.26218E-04 7.26086E-04 1.50283E-03 2.05768E-03 2.56654E-03 2.89469E-03
 2.69955E-03
 4.19137E-05 3.76006E-04 7.59404E-04 1.06533E-03 1.37597E-03 1.64679E-03
 1.55627E-03 1.08113E-03
 2.90341E-05 1.74495E-04 3.91607E-04 5.84055E-04 7.74576E-04 9.29245E-04
 8.46587E-04 5.64685E-04 4.16114E-04
10
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 4.88562E-04 1.86547E-03 2.92766E-03 3.80745E-03
 3.93123E-04 1.77293E-03 2.79484E-03 3.74616E-03 3.93600E-03
 3.08427E-04 1.58471E-03 2.52165E-03 3.49335E-03 3.79323E-03 3.92014E-03
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 2.75233E-03
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 2.33142E-03 2.21708E-03
 1.43316E-04 5.37976E-04 7.74954E-04 1.18621E-03 1.31867E-03 1.38243E-03
 1.41702E-03 1.42354E-03 1.15426E-03
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 7.47195E-04 6.87765E-04 5.21381E-04 3.55259E-04
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 2.86440E-03
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 2.56883E-03 2.58005E-03
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 1.46466E-04 5.74647E-04 9.13055E-04 1.29300E-03 1.62104E-03
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 1.30478E-03
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 9.57611E-04 8.77924E-04
 4.42589E-05 1.72693E-04 3.05914E-04 4.18275E-04 5.64766E-04 6.22621E-04
 6.76075E-04 7.75248E-04 8.58546E-04
 1.60032E-05 1.38236E-04 2.97498E-04 3.72344E-04 4.57980E-04 4.64040E-04
 5.09207E-04 5.43587E-04 6.37035E-04 8.10356E-04
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 4.82157E-04 4.98869E-04 6.04296E-04 8.61276E-04 1.03758E-03
 2.56713E-05 1.86994E-04 3.76363E-04 4.61379E-04 5.06314E-04 5.15491E-04
 4.82064E-04 4.35336E-04 4.97892E-04 7.86002E-04 9.57764E-04 9.56788E-04
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 4.90730E-04 3.51625E-04 3.49624E-04 6.74367E-04 8.69407E-04 9.10331E-04
 9.58394E-04
-1.45426E-06 1.00737E-04 2.04364E-04 2.14416E-04 1.83561E-04 1.74983E-04
 1.30477E-04 1.06807E-04 1.52124E-04 4.05373E-04 5.45468E-04 5.79404E-04
 6.03778E-04 4.37408E-04
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