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Crown geometry, light interception and photosynthesis
of selected Populus x euramericana clones: A modeling approach

by

Timothy Aaron Max

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
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INTRODUCTION

Intensive silvicultural systems are currently being evaluated because they may provide a viable alternative for forest managers faced with trying to increase forest production on a stable or decreasing land base. Intensive silvicultural systems could be installed close to the plant and used in conjunction with more traditional sources of fiber to insure a uniform flow of mill input. These systems are generally envisioned as consisting of densely spaced, rapidly growing hardwood species. The age at harvest will probably be between five and ten years with harvesting accomplished by the coppice method. The management practices of fertilization and, ideally, irrigation will be employed to provide optimum levels of water and nutrients. Such systems have been described by McAlpine et al. (1966), and others.

Before intensive silvicultural systems can be recommended as a reasonable management alternative they must be proved feasible on the basis of biological and economic evaluations. Some of the questions that require answers are:

- (1) What plant material should be used in these systems?
- (2) What density of planting is desirable?
- (3) Can such systems survive for many years of coppice harvesting?
- (4) How can these systems be protected from insect and disease attacks?
- (5) What are the characteristics of wood fiber produced in this

manner?

- (6) What growth and yield can be expected?
- (7) Are these systems economically feasible?

Some of these questions can be answered using existing data and knowledge.

The answers to other questions require the use of extensive data not currently available.

To perform an economic analysis of these systems, reliable data must be available on the growth and yield produced by such systems. Traditionally in forestry such growth and yield information was collected from similar stands already in existence. This, of course, cannot be done for the case at hand. Two other alternatives exist. One is to conduct extensive field trials to generate the necessary information on growth and yield as well as other variables of interest. While field testing is undeniably necessary it could probably best be used at a later stage of decision making. At an early stage of decision making the many potentially acceptable species and hybrids in conjunction with a wide range of stand treatments renders field experiments alone too expensive and time consuming if an alternative is available to provide the necessary information. This alternative is to develop a mathematical model which will simulate growth and yield with sufficient accuracy to permit preliminary decision making on the basis of data generated by model simulations based on laboratory and controlled-environment experiments. Field trials could then be conducted on the plant material and stand treatments selected in preliminary simulation experiments.

A suitable mathematical growth and yield simulation model must be sufficiently accurate so that effects on yield of changes in environmental and physiological variables can be analyzed and evaluated. Hence, the model should be based as much as possible on biological principles rather than just empirical relationships. This is also necessary because much of the data on which the model is based is derived from laboratory research, especially for physiological variables. The model must couple in a meaningful fashion the information from the laboratory experimentation with environmental variables and limited field trial information to predict responses of the desired plant material to various treatments applied to field-grown stands.

A first attempt at such a model has been developed by Promnitz and Rose (1974). In this model the forest stand is considered as a system comprised of individual trees and their interactions with other trees and the environment. A growth model of an individual tree, the basic unit of the system, was developed by Promnitz (1972). The use of the individual tree as the basic unit of the system is important because a tree is the basic unit most often used in laboratory research. Also, this will expedite the simulation of stands consisting of mixtures of genotypes, now viewed as necessary from a stand protection point of view. The most reasonable approach of estimating stand response is as follows.

- (1) Identify the types and frequency of genotypes in the stand.
- (2) Estimate the average response for each genotype for the given stand conditions.
- (3) Weight the response of each genotype by the frequency of

occurrence to estimate overall stand response.

This approach is easily implemented when the individual tree is the basic unit of the model. If the stand is the basic modeling unit then the responses of mixed stands must be empirically determined. Because of nonlinear responses it is inappropriate to average variables of interest over all genotypes and then use these average values to determine stand response.

The model as it now exists is at an early stage of development. The basis is a photosynthate allocation model for individual tree growth as developed by Promnitz (1972). Other components of the model were taken from various literature sources where these components had, for the most part, been developed in a general theoretical framework and had been applied to one or more species by way of example. These components have not necessarily been applied to a stand of young deciduous trees. Therefore each section of the model must be carefully examined on both a theoretical and empirical basis, and more accurate modifications of the present model must be made or new models must be developed on the basis of these evaluations.

One very important section of the stand growth simulation model deals with the behavior of light in the crown and its effect on photosynthesis. Light is clearly very important to a plant community and ultimately provides the energy and carbon for growth. Where water and nutrients are supplied by irrigation and fertilization, efficient use of light energy becomes even more important because light interception and utilization may be the factor most limiting growth. Thus a more thorough understanding of light interception as related to photosynthesis may

provide the necessary criterion for the selection of more photosynthetically efficient plants. Biologically realistic mathematical models of light interception and photosynthesis will help to provide this understanding.

This study was undertaken to develop a biologically realistic model for light interception as related to photosynthesis in young hybrid Populus clones. The model for light interception currently used, discussed in detail in the next section, is general and empirical in nature. The identity of individual trees and individual leaves is not maintained. The objective of this study was to develop a model of light interception and photosynthesis that maintains as basic units the individual tree and the individual leaves within a tree. This was necessary from several points of view. First of all this approach would provide a model that is most compatible with the central photosynthate allocation model for individual tree growth. Thus the individual tree is preserved as the basic unit of the simulation model and the identity of individual leaves is maintained within each tree. If the individual leaf is maintained as a distinct unit in the model, then photosynthetic response curves as derived under laboratory conditions are easily utilized because the individual leaf is the experimental unit used in the determination of these curves. Furthermore this approach will provide for the expansion of the photosynthate allocation growth model. It is known that certain portions of the crown provide the photosynthate for different aspects of tree growth. For example, the upper part of the crown provides the photosynthate for stem elongation while the middle

and lower section of the crown support stem thickening (Larson and Gordon 1969). By maintaining the individuality of leaves within the crown it is hoped that the overall model can be expanded to predict how a tree will grow as well as how much it will grow.

The specific objectives of this study were (1) to develop a model for light interception as related to photosynthesis that maintains the biological identity of individual trees and individual leaves within a tree and is appropriate for application to young Populus trees, (2) to empirically fit the necessary equations of the model to data collected from young Populus trees, and (3) to test the sensitivity of the model through simulation of photosynthesis.

LITERATURE REVIEW

Introduction

In the voluminous literature dealing with various aspects of the total light regime within plant communities terms have not been given standard definitions and have not been used consistently throughout the literature. The meaning of some terms has changed as new ideas have developed. In other cases authors have used different terms to represent essentially the same concepts. A few essential terms are defined explicitly and used consistently throughout this paper. For clarity and consistency, ideas and results from the literature are discussed using the terms defined here rather than using the terms used in the original papers.

All of the light in and around a community of plants is described by the following terms:

- (1) Direct light--unobstructed radiation received from the sun assumed to consist of parallel rays.
- (2) Diffuse light, also referred to as skylight--light resulting from a bright sky that is present even when direct radiation is obscured.
- (3) Transmitted light--any light which has passed through a plant part.
- (4) Reflected light--any light which is reflected from a plant part.
- (5) Photosynthetically active radiation (PAR)--the portion of the electromagnetic spectrum with wavelengths between 380 nm and 710 nm generally considered as providing the energy for photosynthetic processes.

Most of the early papers considered diffuse light only. Only recently have direct light and diffuse light been treated in the same plant community. Relatively little work has been done on transmitted or reflected light. Also, there have been two rather distinctly different types of studies done with regard to light within a forest stand. The first type treats the canopy as a whole and tries to relate the difference between the light above the canopy and the light at the forest floor to various measures of the stand. The other approach is to divide the canopy into horizontal layers and to try to describe the vertical distribution of light within a forest canopy.

Light Extinction by the Whole Canopy

Several studies have been conducted to relate the percentage of diffuse light penetrating the entire canopy to measures of the stands such as age, crown closure percentage and number of stems per unit area. Wellner (1946, 1948) and Miller (1959) both studied the relationship of diffuse light to stand age and crown closure. Both found a curvilinear relationship between the percentage of diffuse light penetrating the canopy and crown closure percentage. Roussel (1953, 1962) proposed that the percentage of diffuse light penetrating the canopy was inversely related to the number of stems per hectare. In these studies diffuse light includes all indirect light regardless of whether the light is skylight, transmitted light or reflected light. These relationships are unsatisfactory because the variables used to describe the stand, crown closure percentage and number of stems per hectare, are not measures that sensitively reflect the ability of the canopy to intercept radiation.

Brocks (1939) and Nägeli (1940) investigated the spacial variation of light beneath forest canopies. Brocks observed the spacial variation of diffuse light that penetrated a Quercus robur forest during leaf expansion. He observed that on clear days significantly more light penetrated the canopy from the direction pointing toward the sun. In heavily shaded sites most of the light penetrated the canopy near the zenith. Nägeli measured diffuse light variation in mixed deciduous stands by taking measurements on overcast days. He concluded, in agreement with Brocks, that most diffuse light penetrates the stand near the zenith.

Researchers who have worked with direct radiation within a forest canopy report conflicting results. Park (1931), Nägeli (1940) and Allard (1947) found direct light in the forest nearly as intense as the incident light outside the forest. Dineur (1951) and Schultz (1960) found lower values for direct radiation inside temperate Quercus robur stands and tropical lowland rain forests respectively. Ashton (1958), working in a Brazilian rain forest, and Reid (1962), working in temperate deciduous forests of Wisconsin, both found a wider range of direct radiation values within a forest, as compared to the incident radiation outside the forest.

The intensity of solar radiation is a fairly simple function of altitude, for any particular set of atmospheric conditions (Anderson 1964a). The intensity of direct solar radiation decreases markedly with decreasing solar altitude. Hence, the greatest intensity of direct solar radiation occurs at noon. Reid (1962) concluded that at any time of the year, the major contribution of sunflecks will be in the hours around noon.

Sunflecks are areas of direct light that penetrate the surface of the canopy. This direct light may be intercepted by a lower portion of the canopy or may reach the ground. Anderson (1964b) showed that nearly all direct irradiance penetrated the canopy of a mixed deciduous woodland in the four hours around noon.

Diffuse Light within a Plant Canopy

All the work discussed thus far was concerned with determining the amount of either direct or diffuse light that penetrated the entire canopy of a forest stand. Transmitted and reflected light were not explicitly considered, nor was the changing intensity and composition of the light as it traveled vertically through the canopy.

A major advance in the study of the relation of light to the plant community was made by the development of the 'stratified clip' method by Monsi and Saeki (1953) in Japan and Davidson and Philip (1958) in Australia. This method relates the vertical distribution of diffuse light and the distribution of plant parts in the canopy; successive harvests of horizontal layers of the canopy are made to determine cumulative leaf area and dry matter; and the cumulative leaf area above any layer is then related to the average light intensity at that level.

Previous workers, such as Trapp (1938), Rademacher (1950), Nägeli (1940), Schimitschek (1948) and Kauttu (1952), used light measurements at various heights in existing stands to show that light intensity changed with height within a forest canopy. Sauberer (1937) and Reid (1962) showed that a marked reduction in light occurs in each layer of a multistoried temperate forest, among the tree and shrub canopies and the

herb layer. These workers demonstrated by actual measurement that the intensity of light changed as it passed through a forest canopy, but they did not relate the vertical distribution of light to the cumulative leaf area.

Monsi and Saeki (1953), on both experimental and theoretical grounds, suggested that a negative exponential relationship existed between the vertical extinction of diffuse light and the cumulative leaf area index. Others such as Davidson and Philip (1958) and Brougham (1958) proposed similar treatment. The improvement of this model over the models previously proposed resulted from the use of the independent variable, leaf area index, which is a measure of a canopy's capacity to intercept radiation. Also the model proposed by Monsi and Saeki is a negative exponential whereas the model given by Roussel was hyperbolic.

In the original paper of Monsi and Saeki (1953) the light extinction model was used in conjunction with experimentally determined light response curves to predict dry-matter production of various communities with some success. The theoretical derivation of Monsi and Saeki (1953) assumed an isotropic sky, a sky in which radiance was equal at all altitudes. Hence, only indirect or diffuse radiation was considered and no allowance was made for direct radiation. Attenuation of radiation was entirely attributed to interception by leaves; the effect of stems and other plant parts was ignored. Transmitted and reflected light were not considered directly.

The equation proposed by Monsi and Saeki (1953) is the same formulation as 'Beer's law.' This 'law' states that the extinction of a monochromatic beam of parallel rays of light in a homogeneous solution of particles of molecular dimensions can be described by a negative exponential relationship. It is clear that a canopy of leaves penetrated by diffuse solar radiation does not meet the assumptions for Beer's law. Extensive experimentation has shown, however, that the negative exponential relationship describes the vertical dissipation of light in the canopy of a plant community with some degree of success.

Verhagen et al. (1963) proposed a more general model. In this model the intensity of light at any level was assumed to be proportional to the derivative of the function used to describe the vertical attenuation of light as a function of leaf area index and inversely proportional to the light absorption coefficient of the leaves. The form of the function used to describe the vertical attenuation of light could be changed to accommodate various canopies. The model by Monsi and Saeki is then a special case of this more general model in which the function used to describe light attenuation is assumed to be a negative exponential.

Duncan et al. (1967) modified the model proposed by Monsi and Saeki (1953) to allow the extinction of diffuse light to depend explicitly on leaf angle and the angle of origin of the radiation. The original model given by Monsi and Saeki (1953) was changed only in the exponent. The new exponent proposed by Duncan et al. was the leaf area index multiplied by the Wilson-Reeve ratio divided by the sine of the elevation angle appropriate for the sky position under consideration. The Wilson-Reeve

ratio described by Wilson (1960) and Reeve (1960) is the ratio of the actual leaf area to the shadow that the leaf area would cast for light originating from a given sky position. This model was improved because of the inclusion of the additional descriptive information on leaf angles and the altitude angle of the incident light.

These models for the extinction of diffuse light assume the canopy can be divided into horizontal layers. Leaf area is assumed to be randomly distributed within horizontal layers and independently distributed among horizontal layers. Hence the identity of the individual plant is lost. Furthermore, all leaf area at a specified level is assumed to be uniformly irradiated by the intensity of light at that level. This probably will not be true. Also it is often not clear in these papers what wavelengths of light are being measured when extinction curves are determined empirically. In connection with photosynthesis, only PAR is important. So only this portion of the spectrum should be measured when developing light extinction curves since the PAR may be depleted in a stand while other radiation is still in abundance.

Direct Light within a Plant Canopy

The models discussed in the previous section attempted to describe the vertical distribution of diffuse light within a plant canopy. Direct solar radiation is the most important source of light energy available to the plant community (Ross 1970). But, in general, direct light and diffuse light require different mathematical treatments and theories (Anderson 1964b; Duncan et al. 1967). Hence, in recent years, some emphasis has been placed on developing models adequate for the

description of the interception of direct radiation. Most of the models currently available are based on the concept of point quadrat analysis developed by J. W. Wilson (1959, 1960, 1961, 1963, 1965).

Point quadrat analysis assumes that very long, thin needles are passed through the canopy in fixed directions, r , described by the zenith and azimuth angles of the needle. The canopy is divided into horizontal layers according to F , the downward cumulative leaf area index. Then $X(F, r)$ is the number of contacts a needle makes with the foliage of the layer denoted by the value of F in the direction denoted by r . So $X(F, r)$ is a random variable with value 0, 1, ..., n , if there have been 0, 1, ..., n , contacts respectively in the interval from the surface of the stand to the depth F in the stand. $P_n(F, r)$ is defined as the probability of the random event $X(F, r) = n$. Then $P_0(F, r)$ is the probability of encountering a gap in the canopy to the level F in the direction r . That is to say, $P_0(F, r)$ is the probability that a light ray will penetrate the canopy to the level F , in the direction denoted by r .

The probability, $P_n(F, r)$, depends, of course, on the geometry of the canopy under consideration. A model for $P_n(f, r)$ used by many authors is the Poisson model (e.g., Duncan et al. 1967). The assumptions necessary for this treatment are:

- (1) The canopy consists of a large number of stochastically independent horizontal layers.
- (2) The probability of observing more than one contact within a small layer is infinitely small compared with the probability

of one contact.

- (3) The probability of observing one contact within a small layer is approximately proportional to the depth of the layer.

Then $P_n(F, r)$ follows the Poisson probability distribution and the probability that a light ray is intercepted is a negative exponential function of depth in the crown, leaf angle and r , the direction of the incident light ray as shown by Duncan et al. (1967). This formulation applies when the leaf area of the canopy consists of small segments randomly distributed within a given layer.

Positive and negative binomial distributions have been used to describe the probability $P_n(F, r)$ by Monteith (1965), Wit (1965), Mototani (1968) and others. The assumptions for the positive binomial model are:

- (1) The canopy is divided into a finite number of equal and stochastically independent layers.
- (2) Only zero or one contact within a layer is possible.
- (3) The probability of one contact within a layer is equal to the foliage area index of the layer projected in the direction r .

Then the probability of a light ray penetrating to level F in the canopy can be calculated by use of the binomial probability distribution. The negative binomial has the same assumption (1) listed for the positive binomial model and similar appropriate assumptions (2) and (3). The positive binomial model is used to describe foliage that is regularly or uniformly dispersed within a layer (Acock et al. 1970; Nilson 1971). On the other hand, the negative binomial model is used to describe foliage

in which the leaf area within a layer is concentrated in clumps rather than being uniformly dispersed. Both of the binomial models tend to the Poisson model as the thickness of the independent layers becomes arbitrarily small.

Nilson (1971) proposed the use of Markov models based on the theory of Markov chains to describe the probability of light penetration to a specified level in the canopy. This approach allows the partial relaxation of assumption (1) required in all of the other models discussed. The canopy must still be divided into equal horizontal layers but these layers are not required to be independent. The probability of a ray being intercepted at any given level depends on the foliage arrangement of that layer as well as the light that has been intercepted by layers higher in the canopy.

In the models for direct light as with the models for indirect light the canopy is artificially divided in horizontal layers. The leaves are assumed to be randomly distributed within each layer by some governing model. The layers are assumed independent in all but Nilson's Markov model. In all cases the identity of the individual plants that make up the stand is lost. Another criticism of such models mentioned by Ross (1970) is that the models are one-dimensional rather than three-dimensional. Application of such one-dimensional models should be made only to relatively dense stands that possess high leaf area indices. Furthermore, most of the discussion of the direct-light models has been on a theoretical level. Little work has been directed at actually testing the models or estimating appropriate parameters from experimental data.

In most of the modeling attempts where both direct and indirect light are considered, different models are used to describe the interception of direct and indirect light. A problem then exists when calculating photosynthetic rates for the plant. In the cases presented in the literature photosynthesis was calculated separately for leaf area receiving direct and indirect radiation. This approach introduces additional errors into the results because some of the leaf area receives both direct and indirect radiation and photosynthetic response functions are generally nonlinear. The ideal approach would be to identify the leaf area receiving both direct and indirect radiation and that leaf area receiving only indirect radiation. The photosynthetic rate for each of the leaf areas would be calculated using the intensity of radiation received. In the one case this would be the intensity of indirect radiation whereas in the other case this would be the intensity of both direct and indirect radiation.

MODEL DEVELOPMENT

Introduction

The model developed in this paper is distinctly different from models previously described in the literature. The basic unit for this model is the individual tree. In addition, the identity of individual leaves within a tree is maintained. This is important because the tree is the basic biological unit of a stand, and the stand can be viewed as an aggregate of individuals with their associated interactions. In such a modeling attempt it is usually necessary to incorporate information derived from laboratory experiments that use individual trees or individual leaves within a tree as the experimental unit. Maintaining the identity of these units will greatly facilitate the incorporation of such information into the model.

Retaining the biological identity of individual trees and individual leaves within trees invalidates the use of the models currently proposed in the literature. All of them, whether for direct or indirect light, require the canopy to be divided into horizontal layers within which leaf area is assumed to be randomly or uniformly distributed. This assumption is not met for stands consisting of young trees and in general fails to recognize the importance of the crown geometry of individual plants.

The specific objectives are:

- (1) To predict the leaf area of an individual tree receiving direct radiation from the sun for various positions of the sun. This total area will consist of contributions from some or all of the individual leaves each receiving radiation at a different

angle of incidence.

- (2) To predict the leaf area of an individual tree receiving indirect radiation from various segments of the sky.

This model is developed with primary emphasis on keeping the relationships as biologically realistic as possible. The development of relationships should be motivated as much as possible by biological reasoning rather than mathematical simplicity, although some reasonable compromise between the two must always be adopted.

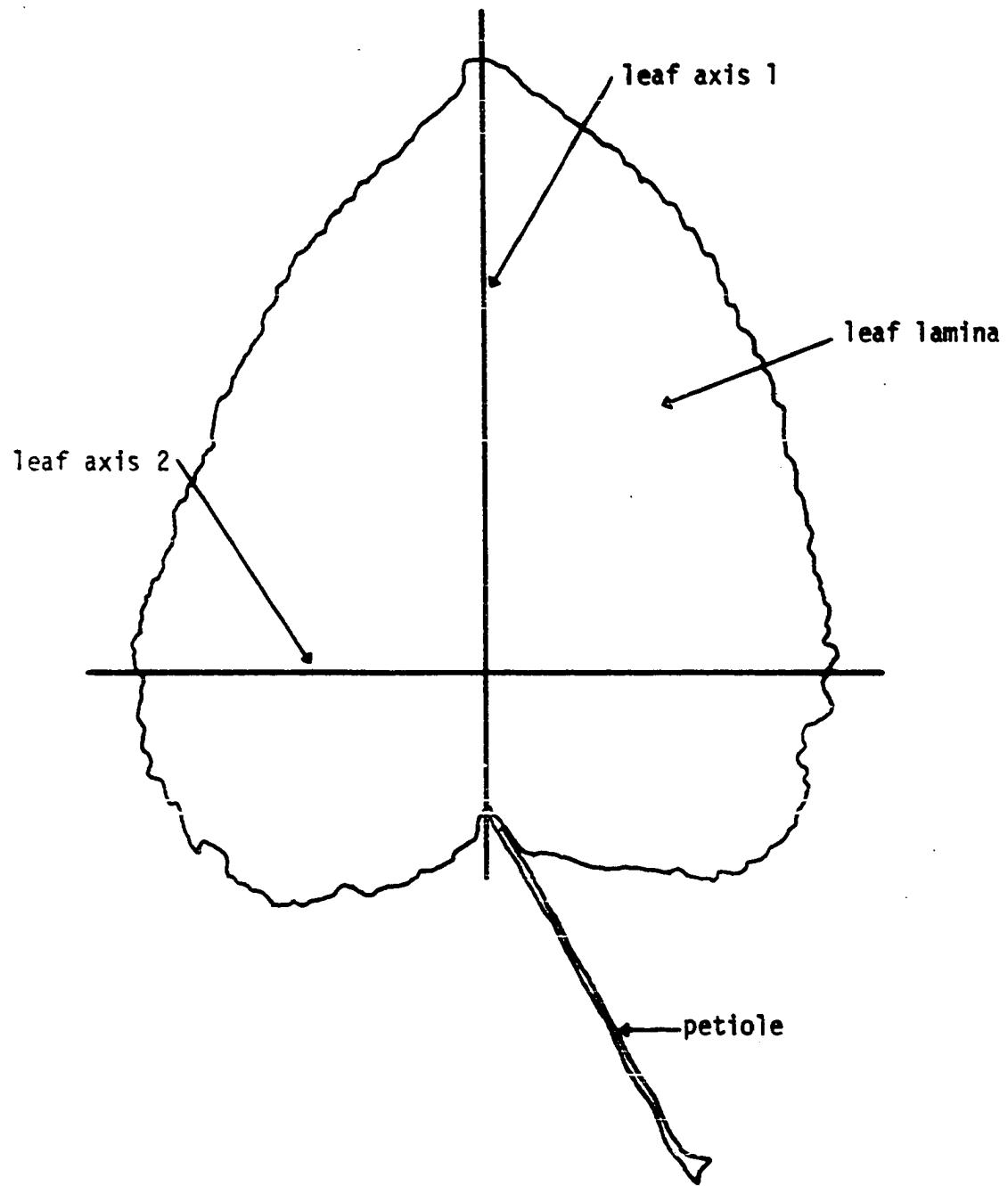
The two specific objectives of the modeling endeavor have been traditionally treated as quite different problems. Upon closer examination, however, a striking similarity is found. The important difference between the treatment here and previous modeling attempts is the complete separation of light intensity measurement and the measurement of the leaf area illuminated by various light intensities. Previously, researchers have attempted to relate the intensity of diffuse light in a stand with depth in the canopy where depth is calculated as a function of cumulative foliage area. This requires the measurement of light intensity in the stand of interest which usually is not a simple task. I propose to deal only with leaf area, in both the direct and indirect light models. If a model is developed that predicts the leaf area of a tree exposed to direct radiation for a specified sun position, then this model also predicts the leaf area that can 'see' that specified portion of the sky when the sun is not there. Thus, this leaf area is the area which receives indirect radiation from that designated segment of the sky. Hence, for any portion of the sky, the same model should predict

the leaf area exposed to direct radiation, if the sun is in that portion of the sky, or the leaf area exposed to indirect radiation from the specified section of the sky, if the sun is elsewhere. Therefore, both of the specific model objectives can be attained by the same basic model. Hence, primary emphasis is devoted to the development of the model in reference to direct light. This work, however, is directly applicable to the consideration of diffuse light. This approach will relate the leaf area illuminated by indirect light to the sky position from which the light originated. Hence, the formulation for sky brightness, the source of indirect radiation, can be more general than has been assumed in the past. Most previous researchers have assumed a uniformly bright sky as a source of indirect radiation. This assumption conflicts with empirical evidence. Anderson (1964a) states on empirical grounds that the sky is brighter at the zenith. Duncan et al. (1967) say that the sky is brighter near the sun and also state that clouds probably produce patterns of variable brightness in the sky. The incorporation of a more complex model of sky brightness into the present model could be accomplished with little difficulty whereas in previous models such modification would have been impossible.

Definition of Leaf Axes

For the convenience of reading as well as writing two axes are defined on Populus leaves. The definitions are illustrated in Figure 1. Leaf axis 1 is defined to be the line connecting the petiole of the leaf to the leaf tip. Leaf axis 2 is defined to be a line perpendicular to leaf axis 1 and placed at the point of maximum leaf width. Leaf length is then measured along axis 1 and leaf width is measured along axis 2.

Figure 1. A typical poplar leaf illustrating the placement of leaf axis 1 and leaf axis 2



Model I

Model I was an initial attempt at partially fulfilling the stated objectives. This model is important because it provided insight into some of the basic problems of crown geometry modeling, and also provided some of the basic ideas necessary for the development of a more comprehensive model.

Model I is designed to deal only with light interception when incident light is parallel to the main stem, i.e., when the sun is directly over the tree. The details of this model are developed in Appendix A.

The model assumes a phyllotaxy described by the fraction two-fifths. This is the generally accepted description of young Populus phyllotaxy as reported by several authors (e.g. Larson and Gordon 1969). Leaf shape is assumed to be triangular. Petiole length and leaf size are assumed to be the same for any two leaves such that one of the leaves shades the other leaf as illustrated in Figure 25. Leaves are assumed to be tilted only along leaf axis 1.

If the petiole lengths and leaf dimensions are known then, under the stated assumptions, the leaf area exposed to direct radiation can be calculated. The equations necessary for the calculation of the area exposed to light are developed in Appendix A.

One of the problems with Model I is that rather stringent assumptions are required in order to make the model analytically solvable. Errors are introduced when the model is assumed to represent a particular plant which deviates from these assumptions. The first assumption requires the plant to have a strict phyllotaxy described by the fraction

two-fifths. This means that for any leaf n , leaf $n+6$ will be directly beneath and completely shaded by leaf n unless the petiole of leaf $n+6$ is longer than the petiole of leaf n . This pattern of phyllotaxy is correct in a general sense but not in the strict sense required by this model. Observations indicate that there is usually a significant angular separation between the petioles of leaves n and $n+6$ so that leaf $n+6$ will receive some direct light. This seems logical since if the phyllotaxic pattern was rigidly controlled by the fraction two-fifths the crown could not be a very efficient radiation trap.

Another important assumption is that leaf shape is triangular. This assumption was required so that when the leaf was rotated on axis 1 and projected onto a horizontal plane the projected leaf area would have a well-known geometrical shape. Actually Populus leaves are generally quite rounded and hence the model should underestimate the leaf area that is shaded by another leaf. A more realistic assumption that would still permit the derivation of the appropriate formulas is that the shape of the leaf be considered a quadrilateral as illustrated in Figure 26. The appropriate formulas for this assumption have been developed in Appendix A.

The assumption requiring leaf size and petiole length to be equal for any two leaves for which one leaf shades the other is not too unrealistic. Such shading occurs only for leaves that are relatively close to each other in the crown and hence have a relatively small difference in leaf plastichron age (LPA). Such leaves can be expected to have similar leaf sizes and petiole lengths under normal conditions.

The model also requires some simplifying assumptions concerning leaf

angles. Leaf axis 1 is assumed to be horizontal. All leaves are assumed to be rotated on axis 1 through a characteristic angle. These leaf angles will be discussed in more detail later. In practice, however, leaf axis 1 is often not horizontal. Furthermore, the angle at which leaf axis 2 is tilted is not constant for all leaves in the crown but varies with position in the crown.

The obvious criticism of this model is that even if the assumptions were valid, the model only accounts for one sun position, that is, when the sun is directly over the plant. However, the model is useful. It illustrates some of the basic problems of constructing such models. And it illustrates the need for imposing assumptions that may compromise biological reality for the sake of analytical simplicity. The model also provides some of the basic insights into the overall problem which stimulated further developments.

Model II

An ideal model for crown geometry as related to light interception might work as follows. Each leaf would be represented by a small segment of a plane whose location in space is known. The plane segments would have the size and shape of the leaves they represent. The locations of the plane segments would depend upon internodal distances, petiole lengths and the orientation of the leaves. Then for any given sky position, the model would project all of the small planes representing leaves onto the two-dimensional plane normal to a vector pointing to the sky position under consideration. The model would keep track of all overlapping of the small planes, the distance that the small plane segments were from

the plane of projection, and the angles between normal vectors to the small plane segments and a normal to the plane of projection. With this information, the leaf area of any individual leaf receiving radiation directly from the sun when the sun is at the specified sky position could be determined; and the angle of incidence of this radiation would be known. Thus, this ideal model would work in a completely general way much as Model I worked in the limited case of the light source being directly overhead. The development of such an ideal model is currently not possible. However, the idea of working with projected leaf area is intriguing and forms the basis for the development of the model discussed in this section.

Model II is designed to accommodate all sun positions. As noted before, a main shortcoming of Model I was that only one sun position was described by the model. However, Model I was analytically functional without the empirical estimation of any parameters except for the assessment of errors caused by deviations from the assumptions. The scope of Model II is designed to be much broader than Model I since all sun positions are considered by Model II. In exchange for this generality, parameters are introduced into the model which must be empirically estimated.

One of the main goals of Model II is the attempt to model the interception of light by a tree on the basis of light interception of the individual leaves. This approach is intuitively appealing because of the basic biological identity of individual leaves. Furthermore, photosynthetic response curves derived in the laboratory for leaves of different ages could then be directly incorporated into the model.

The fundamental idea of this model is to assess shading of leaf area, and hence also the area not shaded, by the projection of the leaf area onto a two dimensional plane. Consider the sun in any given position and the direct radiation coming from that position in the form of parallel rays. Consider an imaginary plane, designated the reference plane, normal to the sun's rays and located between the sun and the individual tree under consideration. The tree under consideration is assumed to have a single stem. On this single stem are n leaves numbered one through n with corresponding leaf plastichron ages zero through $n-1$ respectively. Let A_i represent the area of the i^{th} leaf and A'_i represent the area of the orthogonal projection of A_i onto the reference plane. Then the total leaf area on the tree is $\sum_{i=1}^n A_i$. Now $\sum_{i=1}^n A'_i$ is the sum of the projected leaf areas and hence is the maximum area in the reference plane that could intercept the direct radiation falling normally on the reference plane. To assess shading, the intersection of the projected leaf areas is considered. If $A'_i \cap A'_j \neq \emptyset$ for any i and j , $i \neq j$, then either leaf i shades leaf j or leaf j shades leaf i when light is normal to the reference plane. If $A'_i \cap A'_j = \emptyset$, then no shading of leaf i by j or of leaf j by leaf i occurs for this sun position. Now UA_i is the union of the projected leaf areas and hence is the area in the reference plane that intercepts solar radiation for the specified sun position.

There are many possible ways in which a young tree crown might be considered. I have chosen three for consideration here. The first method treats the whole crown as an indivisible unit. The second method divides the crown in three horizontal sections based on the physiological development of the leaves within each section. The top part of the crown, con-

sisting of leaves of LPA zero through LPA eight, is the immature or expanding leaf zone. The lower portion of the crown, consisting of the oldest five leaves, is the senescent leaf zone. The remainder of the leaves, located in the middle of the crown, comprise the mature leaf zone. This division is somewhat arbitrary, but should divide the crown into sections having physiologically similar leaves. The third method considers the crown as consisting of a collection of individual leaves. Each of these approaches has its own advantages and disadvantages.

The crown considered as a whole unit

Suppose the crown is considered as a whole unit. Then ΣA_i^n is the total leaf area of the crown. This total crown leaf area depends simply on the number of leaves on the tree and the size of those leaves. The sum of the projected leaf areas for all of the leaves in the crown is $\Sigma A_i^{n'}$ and is the maximum area available for the interception of radiation that is normal to the reference plane considered. This quantity, $\Sigma A_i^{n'}$, depends upon the position of the reference plane and the angular orientation of the leaves with respect to this reference plane. Clearly for a crown with any appreciable leaf area there will be shading of some of the leaf area. So $U A_i^{n'}$ is the union of the $A_i^{n'}$'s in the reference plane and hence is the area of radiation captured by the plant. This quantity, $U A_i^{n'}$, depends upon the position of the reference plane and, in a very complex way, upon leaf shape, leaf size with respect to position in the crown, internodal distances, petiole lengths, phyllotaxy and the angular position of the leaves in space. Clearly

$$\sum_{i=1}^n A_i' \leq \sum_{i=1}^n A_i \leq \sum_{i=1}^n A_i'$$

for any particular reference plane.

The total leaf area of the tree, $\sum_{i=1}^n A_i'$, can be calculated by measuring the area of each leaf on the tree. Or, more easily, the total leaf area can be estimated by estimating the area of each leaf using independent variables such as leaf length and width and then summing these individual leaf estimates to estimate total leaf area. To facilitate the estimation of $\sum_{i=1}^n A_i'$, however, the area of each leaf should be estimated.

The quantity, $\sum_{i=1}^n A_i'$, can be estimated by projecting the estimated area of each of the leaves onto the reference plane and then summing these projected areas. This projection is accomplished as discussed in Appendix B. To project the leaf area onto any given reference plane the angle between a normal to the leaf's surface and a normal to the reference plane must be known. Let γ_i denote this angle. Then for any leaf, i , and a given reference plane

$$A_i' = A_i \cos \gamma_i$$

and

$$\sum_{i=1}^n A_i' = \sum_{i=1}^n A_i \cos \gamma_i$$

This formulation demonstrates the dependency of $\sum_{i=1}^n A_i'$ on the leaf area present, the A_i 's, and the orientation of the leaves. The orientation of a leaf with respect to the reference plane determines γ_i . Now in the simple case where all foliage is horizontal, γ_i is the same for all leaves and depends only on the altitude of a vector normal to the reference plane. Let γ^* be the angle between the positive z-axis, which is coincident with the main stem of the plant, and a normal to the reference

plane. Then, in this case of horizontal foliage, $\gamma_i = \gamma^*$ for all i.

Hence, as expected

$$\sum A_i' = (\sum A_i) \cos \gamma^*.$$

These calculations are possible since a normal to the surface of any leaf can be constructed using the method described in Appendix B. The requirements for calculating a normal vector to a leaf's surface are that the direction in which the leaf points and the angles associated with leaf inclination are known. The direction in which a leaf points is determined by the phyllotaxy and the orientation of the plant with respect to the reference plane. The angles associated with leaf inclination can be measured or they can be predicted if relationships between leaf angles and the position of the leaf within the crown have been developed.

The actual leaf area in the reference plane receiving radiation, $\sum A_i'$, must be empirically determined. A technique for such empirical determinations will be discussed later.

The quantity of primary interest,

$$P_T = \frac{\sum A_i'}{\sum A_i} \quad (1)$$

is the proportion of the projected leaf area in the reference plane, in this example for the total crown, that receives radiation. P_T is defined to be zero if $\sum A_i'$ is zero. In this development we have assumed that the crown is considered as a whole unit without explicitly maintaining the identity of the individual leaves which are regularly distributed around the main stem according to the phyllotaxic pattern. Under these conditions a reasonable simplifying assumption might be that $\sum A_i'$ and $\sum A_i$ are

invariant under any rotation of the tree on its main stem. These quantities, $\bar{U}A_i^n$ and ΣA_i^n , and hence P_T , would only depend upon the altitude of the reference plane for a given tree. $\bar{U}A_i^n$ depends upon tree growth and leaf arrangement characteristics as well as leaf area. ΣA_i^n depends upon leaf area and leaf orientations. It is reasonable to expect, then, that the ratio, P_T , will reflect individual tree efficiency in the arrangement of leaves for radiation capture and will be relatively stable over moderate changes in leaf area. It is further reasonable to expect that this ratio is, at least in part, genetically determined, and will vary among clones. Hence an estimated value of P_T could be used to predict the quantity $\bar{U}A_i^n$ for crowns with slightly different values of total projected leaf area.

The ultimate goal of this modeling endeavor is to predict photosynthesis of an individual tree based on the leaf area exposed to radiation and the amount of radiation absorbed by this exposed leaf area. To accomplish this it is necessary to make some additional simplifying assumptions. First, in this case where the crown is considered as a whole unit, a photosynthetic response curve must be assumed that is appropriate for the average unit of leaf area in the whole crown. Individual leaves or sections of leaves are not differentiated in this approach. Second, an average value for the angle of incidence of direct radiation must be used. This angle of incidence is important since it is used to determine the actual leaf area exposed to radiation and also to calculate the amount of the incident radiation that is absorbed by the exposed leaf area. Recall the relationship between projected and actual leaf area

$$A_i' = A_i \cos \gamma_i$$

Then if P_i is the proportion of the projected leaf area receiving radiation then the actual leaf area receiving radiation is

$$P_i A_i' / \cos \gamma_i$$

and the angle of incidence of this radiation is γ_i . P_T is the proportion of the total projected leaf area receiving radiation for a specified sky position. An assumed or calculated value, $\bar{\gamma}_T$, is the average angle of incidence for the whole crown. Then the area calculated to receive direct radiation when the sun is in the specified position, is

$$P_T \sum_{i=1}^n A_i' / \cos \bar{\gamma}_T$$

and the angle of incidence of this radiation is assumed to be $\bar{\gamma}_T$. The actual leaf area receiving radiation is

$$\sum_{i=1}^n P_i A_i' / \cos \gamma_i$$

with angle of incidence γ_i for that portion of the area of leaf i receiving radiation. But under this approach of treating the crown as a whole unit the value of P_i for each i is not known.

Let ψ_1 and ψ_2 be spherical coordinates used to identify any desired sky position. The coordinate system assumed is OXYZ where OX is due east, OY is due south and OZ is vertically upward. The tree under consideration is at the origin with main stem coincident with the positive Z-axis.

The plant receives indirect radiation from all sky positions. Assuming the sun to be a point source of light, the plant receives direct radiation only from one sky position at any given time. Traditionally, photosynthesis has been calculated separately for direct and indirect light because generally different models have been used to describe the

reception of direct and indirect light. But the direct light falls on a subset of leaf material receiving indirect light. The result has been an overestimation of photosynthesis because of the nonlinearity of photosynthetic response functions. An attempt is made in this model to correct this error.

Consider first indirect radiation. Let the intensity of indirect, photosynthetically active radiation from the sky position designated by ψ_1 and ψ_2 be denoted by $I_{ID}(\psi_1, \psi_2)$. Previous researchers have assumed this function to be constant or a function of ψ_2 only. The assumption was made that P_T was independent of ψ_1 and depended only on ψ_2 . This may be shown explicitly by writing $P_T(\psi_2)$. Clearly the amount of projected leaf area and the average angle of incidence also depend upon the sky position considered. Let $A_p'(\psi_1, \psi_2)$ be the total leaf area projected onto the reference plane designated by ψ_1, ψ_2 . Let $\bar{\gamma}_T(\psi_1, \psi_2)$ be the average angle between the normals to the leaves and the vector pointing to the sky position designated by ψ_1, ψ_2 . If it is assumed that the indirect radiation incident on the plant is uniformly distributed over the leaf area then the average intensity of this radiation per unit leaf area is

$$\bar{I}_{ID} = \frac{1}{\sum A_i} \int_0^{2\pi} \int_0^{\pi/2} P_T(\psi_2) A_p'(\psi_1, \psi_2) I_{ID}(\psi_1, \psi_2) \sin(\psi_2) d\psi_2 d\psi_1.$$

The tree is also receiving direct radiation. Let ψ_{1S}, ψ_{2S} denote the position of the sun. Then the leaf area

$$P_T(\psi_{1S}) A_p'(\psi_{1S}, \psi_{2S}) / \cos(\bar{\gamma}_T(\psi_{1S}, \psi_{2S}))$$

is receiving full sunlight with average angle of incidence $\cos(\bar{\gamma}_T(\psi_{1S}, \psi_{2S}))$

and indirect radiation of average intensity \bar{I}_{ID} . Photosynthesis of the plant is then calculated in two parts. The first part for the leaf area exposed to direct light which receives radiation of full sunlight at the specified average angle of incidence plus indirect light at the average intensity. The rest of the leaf area of the plant receives only indirect light at the average intensity.

There are several problems associated with the whole crown approach. One problem is that only one photosynthetic response curve is used to represent all the leaf area in the crown. It would be more realistic if different photosynthetic response functions could be used for leaves in the crown that are physiologically different. Another problem is the calculation of actual leaf area receiving radiation. This really depends upon which leaf area is irradiated and the associated angle between that leaf area and the vector pointing to the sky position from which the radiation is coming. In this case we have assumed that an average angle can be used to calculate the actual leaf area irradiated and that this average angle can be used as the angle of incidence of all the radiation falling on this leaf area. This is unsatisfactory in view of the non-linearity of the functions involved and could result in sizeable errors in the calculation of photosynthesis.

The crown considered as three segments

In an attempt to overcome some of the difficulties encountered in treating the crown as a whole unit, I tried a slightly different approach. This approach divides the crown into three regions; the immature leaf zone, the mature leaf zone and the senescent leaf zone. The immature,

mature and senescent leaf zones consist of those leaves with leaf numbers one through eight, nine through n-5 and n-4 through n respectively.

The fundamental ideas of this segmented-crown model are identical to those discussed in the previous section dealing with the crown as a whole unit with only a few exceptions. In dealing with the crown as three segments the proportion of projected leaf area receiving radiation for each section of the crown is estimated separately. Let the subscripts I, M, S designate the immature, mature and senescent zones of the crown respectively. Then

$$P_I = \frac{\sum_{i=1}^8 U A_i}{\sum_{i=1}^8 A_i} \quad (2)$$

is the proportion of projected leaf area in the immature zone that receives radiation for a specified reference plane. Similarly

$$P_M = \frac{\sum_{i=9}^{n-5} U A_i}{\sum_{i=9}^{n-5} A_i} \quad (3)$$

and

$$P_S = \frac{\sum_{i=n-4}^n U A_i}{\sum_{i=n-4}^n A_i} \quad (4)$$

are the proportions of projected leaf areas that receive radiation from the specified sky position for the mature and senescent zones respectively.

The calculation of light interception and the resultant photosynthesis proceeds as when the crown was considered as a whole unit. Photosynthesis, however, is calculated separately for each segment of the crown. Total photosynthesis of the crown is then the sum of the photosynthesis of the three crown segments. As before, some simplifying assumptions are needed to make these calculations. The main assumption is that P_I , P_M and P_S are invariant with respect to rotations of the tree on its main axis.

There are two main advantages of the segmented crown approach. One advantage is that different photosynthetic response curves can be assumed for each segment of the crown which allows different parts of the crown to respond differently to intercepted light. The other advantage relates to the calculation of actual leaf area exposed to radiation and the angle of incidence of this radiation. In this approach, as before, an average value for this angle of incidence must be assumed. However, by calculating photosynthesis by crown segment, a different angle of incidence can be used for each segment of the crown. This should reduce errors caused by using an overall average value of this angle of incidence to calculate actual irradiated leaf area, the light energy absorbed by this leaf area and the resultant photosynthetic rates.

The crown considered as individual leaves

The third approach to crown modeling is the most biologically realistic. In this attempt, the crown is viewed as consisting of all component leaves in an effort to eliminate some of the problems associated with the two preceding approaches in which leaf material was grouped. For any

given sun position, the quantity $\frac{n}{UA_i}$ is broken down into the component contributions by each leaf. I define $(SA)_i'$ as the sunlit portion of the projected area of leaf i , A_i' , for the particular sun position considered. Clearly $0 \leq (SA)_i' \leq A_i'$ where if $(SA)_i' = 0$, then the leaf is completely shaded. If $(SA)_i' = A_i'$ then all of the leaf is in sunlight. Note that

$$\frac{n}{UA_i} = \sum (SA)_i'$$

so $(SA)_i'$ is the contribution from leaf i to the total projected leaf area receiving radiation for the specified sun position. The proportion of the projected leaf area for an individual leaf i receiving radiation for a specified sun position is

$$P_i = \frac{(SA)_i'}{A_i'} \quad (5)$$

The calculation of radiation absorption and photosynthesis is performed on an individual leaf basis. In the two previous models the value of the proportion of projected leaf area receiving radiation was assumed invariate with respect to rotation of the tree on its main stem. This simplifying assumption was justified because many leaves covering the range of possible positions contributed to the calculation of the proportions. When dealing with the P_i for an individual leaf, such an assumption is clearly invalid. Thus P_i will vary with the position of the leaf in the crown as specified by LPA, and the angular displacement in the horizontal plane between the sun position considered and the direction in which the leaf is pointing.

To calculate A_i' it is necessary to calculate the angle γ_i which is the angle between a normal to the leaf and a normal to the reference

plane. The angle of incidence of light falling on leaf i if that light is normal to the reference plane is clearly γ_i . So the intensity of light absorbed by the leaf is the intensity of the light normal to the reference plane reduced by multiplying by the cosine of the angle of incidence. The angle γ_i is also used to calculate the leaf area receiving this radiation. If $(SA)_i'$ is the amount of projected leaf area receiving radiation then the actual amount of leaf area receiving radiation is

$$(SA)_i = (SA)_i' / \cos \gamma_i.$$

Consider indirect light falling on leaf i . Clearly leaf i receives indirect radiation from many sky positions. As before we must assume that this indirect radiation is uniformly spread over the whole area of leaf i . Again assume $I_{ID}(\psi_1, \psi_2)$ describes radiation flux as a function of sky position. Then the total indirect radiant energy received by leaf i from all sky positions is

$$I_{i, ID} = \int_0^{2\pi} \int_{-\pi/2}^{\pi/2} \frac{P_i(\psi_1, \psi_2) A_i'(\psi_1, \psi_2)}{\cos(\gamma_i(\psi_1, \psi_2))} I_{ID}(\psi_1, \psi_2) \sin \psi_2 d\psi_2 d\psi_1$$

Assuming this radiation is uniformly distributed over the total leaf area then the average intensity of indirect radiation falling on leaf i is

$$\bar{I}_{i, ID} = I_{i, ID} / A_i$$

In addition to this indirect light falling on leaf i , part of the leaf may be receiving direct light. The amount of the area of leaf i receiving direct radiation depends upon the position of the sun determined by $\psi_{S1}(t), \psi_{S2}(t)$ as a function of time of day for the appropriate latitude and longitude. At any time, t , the area of leaf i in direct light is

$$A_{i, DIR}(t) = \frac{P_i(\psi_{1S}(t), \psi_{2S}(t)) A_i'(\psi_{1S}(t), \psi_{2S}(t))}{\cos(\gamma_i(\psi_{1S}(t), \psi_{2S}(t)))}.$$

Then the photosynthesis of the leaf is calculated in two parts. One part for that part of the leaf receiving only indirect light. The other part for that part of the leaf receiving both indirect and direct light. For the part of the leaf receiving both direct and indirect light the intensity of light received on this leaf area is

$$I_i(t) = \bar{I}_{i,DIR} + I_{DIR} \cos(\gamma_i(\psi_{S1}(t), \psi_{S2}(t)))$$

where I_{DIR} is the intensity of PAR in direct sunlight. The leaf area receiving this radiation is

$$A_{i,DIR}(t).$$

The photosynthetic rate of the leaf part receiving direct radiation can then be calculated using the photosynthetic response curve appropriate for the leaf in question. The rest of the leaf area

$$A_i - A_{i,DIR}(t)$$

receives indirect radiation at intensity $\bar{I}_{i,DIR}$. Hence the photosynthetic rate for this part of the leaf can be calculated.

There are several advantages in using the approach in which the crown is viewed as a collection of individual leaves. It facilitates the use of photosynthetic response curves derived in the laboratory on the basis of the experimental photosynthetic responses of individual leaves. This is important since response to light is different for leaves of different LPA. In addition, the cosine law for light interception is observed explicitly and also the actual leaf area receiving radiation is more accurately estimated. This is a result of using the angle of incidence of light for each individual leaf rather than an average value for several leaves. Furthermore, the individual leaf model should encourage the refinement of other models in the overall growth and yield modeling effort.

One disadvantage of this approach is that the P_i 's can not be assumed to be constant if the tree is rotated on its main stem. In general P_i depends on both ψ_1 and ψ_2 whereas in the previous two formulations these proportions changed only with ψ_2 .

FITTING THE MODEL TO DATA

An important section of this study concerned the collection of data from young hybrid poplar clones. The data collected from these plants are used to describe some of the characteristics of their crown geometry, and also to empirically estimate some of the components of the models.

Four Populus x euramericana clones were used in this experiment; they are identified as 5321, 5323, 5326 and 5377. Information describing the origin and parentage of these clones is given in Appendix C.

Uniform tip cuttings of all four clones were taken on October 26, 1973, and rooted under mist in Jiffy-7 peat pellets. Twelve rooted cuttings of each of the four clones were planted in eight-inch pots on November 30, 1973, in an artificial substrate (2:1 ratio of Jiffy-Mix and Perlite). The plants were then grown under standard conditions in the greenhouse until they were harvested for measurement when they reached a total height of 60 cm, 75 cm, or 90 cm. Three heights were used to insure a range in total leaf number and total leaf area per tree. This procedure provided for measurement four trees of each of the four clones at each of the three specified heights.

Leaf Angles

Two leaf angles were measured on each leaf of each tree. These two angles, in addition to the direction the leaf pointed, as indicated by the phyllotaxy, are sufficient to determine the plane in space in which the leaf lies and to construct a normal vector to the leaf. These angles were used to investigate some aspects of the crown geometry of the four clones. The angles were measured using a simple clinometer constructed

by the author.

The measurement of two angles to determine leaf inclination has not been reported. All previous work I reviewed discussed foliage inclination only in terms of one angle. Measuring only one angle is clearly inadequate for the purposes of this study because one angle cannot unambiguously describe the inclination of the typical poplar leaf. One angle is measured by placing the clinometer under the leaf along leaf axis 1. This angle is designated ϕ_3 corresponding to the notation of Appendix B. The clinometer was constructed so that the angle between the vertical, or the plant's main stem, and leaf axis 1 could be read directly from the instrument (Figure 2). If leaf axis 1 is horizontal then ϕ_3 is equal to ninety degrees.

The other angle, designated δ_3 , is measured with the clinometer held generally parallel to leaf axis 2. Specifically if leaf axis 1 is horizontal then this angle is measured along leaf axis 2 and is the angle leaf axis 2 makes with the vertical. So if the leaf is parallel to the horizontal, ϕ_3 and δ_3 are both ninety degrees. If leaf axes 1 and 2 are not parallel to the x-y plane then the measuring device is rotated along the leaf surface about its midpoint, which is just below the intersection of axes, until the projection of leaf axis 1 and the new axis of measurement would be perpendicular in the x-y plane. The measured angle is then the angle between the vertical and the right hand end of this axis when the axis is viewed from the leaf tip (Figure 3).

A different description might more clearly illustrate the problems of measuring these angles. Assume that a leaf is horizontal and is situated in a three dimensional coordinate system such that leaf axis 1

Figure 2. Illustration of the measurement of leaf angle ϕ_3
with the clinometer placed along leaf axis 1

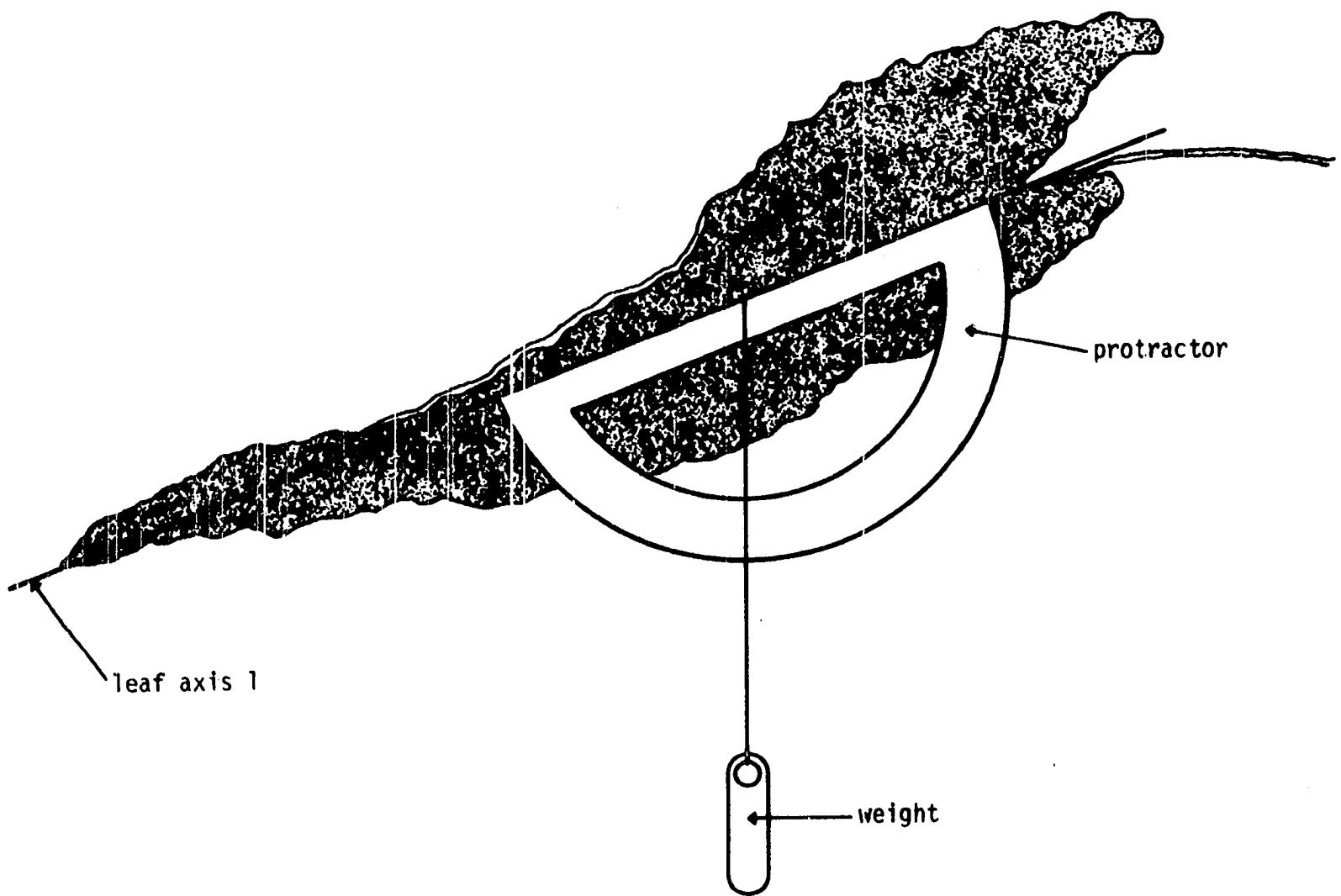
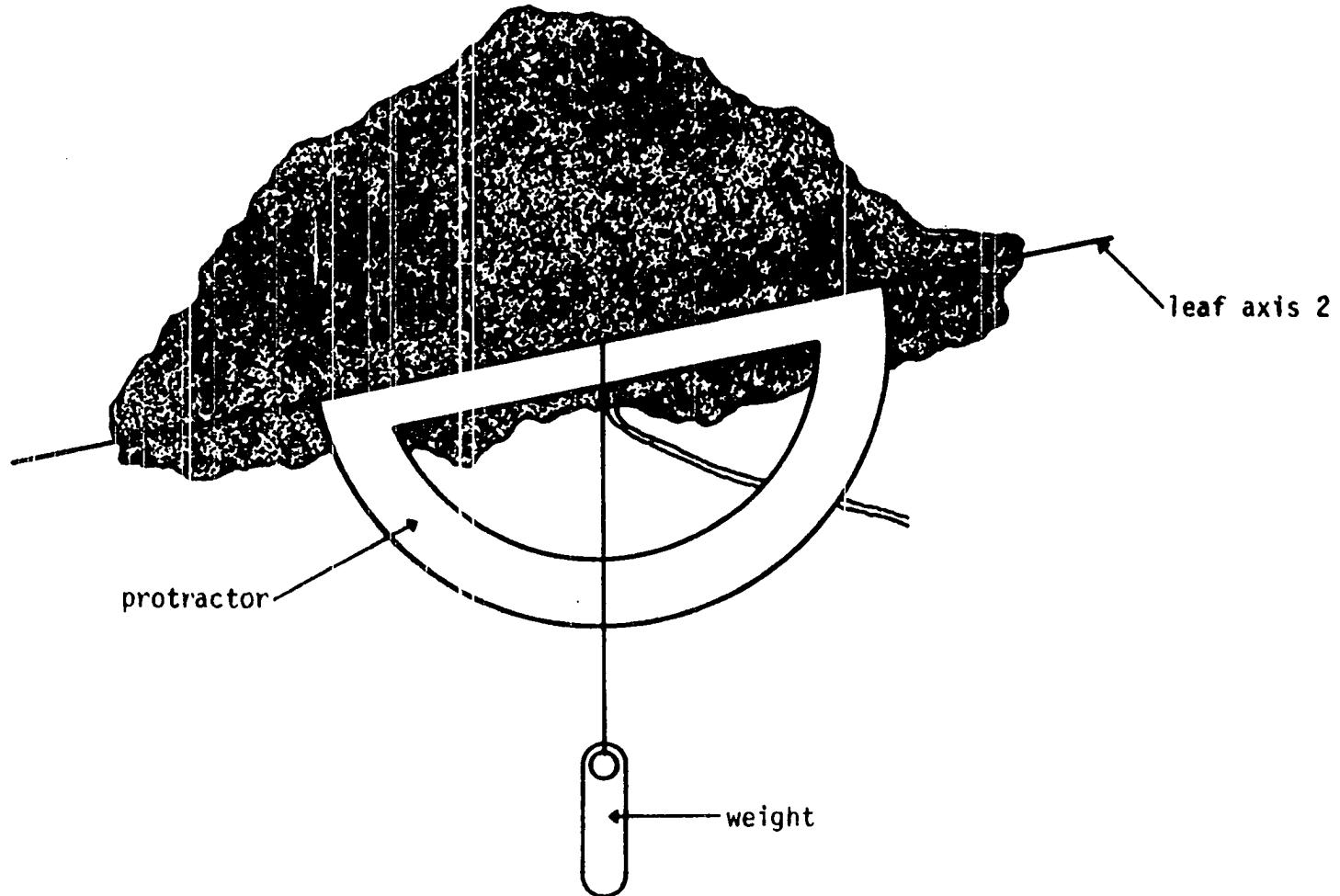


Figure 3. Illustration of the measurement of leaf angle δ_3 with
the clinometer placed along leaf axis 2



and leaf axis 2 coincide with the x-axis and y-axis respectively and the leaf tip lies on the positive x-axis. Any angular orientation of this leaf can then be obtained by first rotating the leaf on leaf axis 2 through some specified angle, thus raising or lowering the tip of the leaf. Next the leaf is rotated on leaf axis 1 through some angle so that leaf axis 2 is no longer parallel to the x-y plane. Now the projection of leaf axis 1 is coincident with the x-axis. The angle ϕ_3 is the angle between the positive z-axis and leaf axis 1. The problem is that the projection of leaf axis 2 is no longer necessarily coincident with the y-axis. The angle δ_3 is then the angle between the positive z-axis and the line determined by the intersection of the plane of the leaf and quadrant I of the y-z plane.

In trying to describe the crown geometry of the four clones the relationships between the two leaf angles and LPA were investigated. These relationships are important for predicting values for angles when the model is applied to trees for which the values of these angles have not been measured. Both angles were quite variable and for this reason the observations were averaged by LPA within each clone. These means consisted of twelve observations except for some of the oldest leaf categories. The means were then used to fit empirical relationships between the leaf angles and LPA.

It was difficult to find a model to fit the relationship of ϕ_3 as a function of LPA. Following the ideas of Bliss (1970), with some substantial modifications, the nonlinear model

$$Y = \beta_1 + \beta_2 X_3^{\beta_3} \beta_4^{X_3} \sin(\pi + 2\pi \beta_5 X_1 \log X_2 / |X_1|) \quad (6)$$

was fitted using a nonlinear regression procedure where

$$Y = \text{value of the angle } \delta_3 \text{ in degrees}$$

$$X_1 = \text{LPA-constant for translation of the x-axis}$$

$$X_2 = 1 + |X_1|$$

$$X_3 = \text{LPA} + 1.$$

The fitted curves and observed means for the four clones are shown in Figures 4, 5, 6 and 7. The estimated parameters, the standard errors of the estimated parameters and the values of R^2 are given in Table 1.

This curve form is basically a sine curve with modified amplitude and period. The amplitude is assumed to vary with LPA according to the model $\beta_2 X_3^{\beta_3} \beta_4^{X_3}$, a curve form suggested in Freese (1964). The period is assumed to increase logarithmically. The x-axis has been translated so that π corresponds to LPA 10.5, 8.5, 9.5 and 9.5 for clones 5321, 5323, 5326 and 5377 respectively.

A similar but slightly simpler model was used to represent the relationship between leaf angle δ_3 and LPA. A nonlinear regression procedure was used in fitting this model also. The model is

$$Y = \beta_1 + (\beta_2 + \beta_3 X) \cos (2\pi \beta_4 \log (X)) \quad (7)$$

where

$$Y = \begin{cases} \text{the angle } \delta_3 \text{ in degrees if } 0^\circ \leq \delta_3 \leq 90^\circ \\ \text{the angle } 180^\circ - \delta_3 \text{ if } 90^\circ < \delta_3 \leq 180^\circ \end{cases}$$

$$X = \text{LPA} + 1.$$

The fitted curves and observed means for the four clones are shown in Figures 8, 9, 10 and 11. The estimated parameters, the standard errors of the estimated parameters and the values of R^2 are given in Table 2.

Table 1. Coefficients, standard errors of the coefficients, number of observations and values of R^2 for fitting the model given by Equation 6

Clone	Coefficient	SE ^a	n ^b	R^2
5321	77.5395	0.7998	32	0.9511
	25.2463	1.1018		
	-1.0045	0.1537		
	1.1350	0.0171		
	0.2554	0.0666		
5323	113.4916	0.7231	26	0.9534
	272.1691	13.1177		
	1.9517	0.4223		
	0.3197	0.0685		
	0.2693	0.0055		
5326	99.8108	1.0253	28	0.8751
	62.9587	4.9589		
	-1.0984	0.2049		
	1.0961	0.0261		
	0.2507	0.0073		
5377	101.6570	1.2929	29	0.8053
	71.4540	7.1725		
	-1.2963	0.2780		
	1.1182	0.0340		
	0.2451	0.0092		

^aSE = Standard error of the coefficient.

^bn = Number of observations.

Figure 4. Observed values and fitted equation for leaf angle ϕ_3 versus LPA as given in Equation 6 for clone 5321

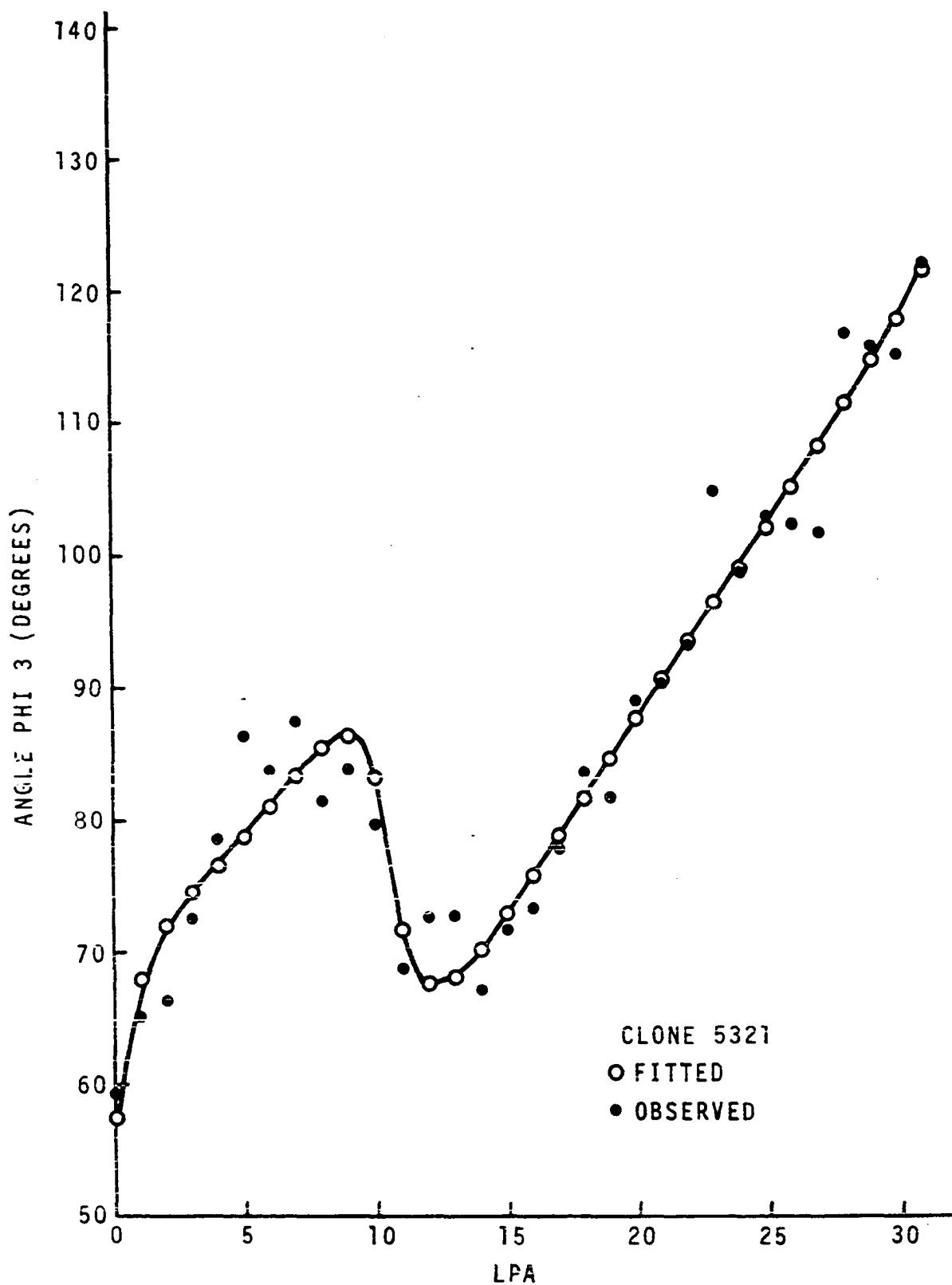


Figure 5. Observed values and fitted equation for leaf angle ϕ_3 versus LPA as given in Equation 6 for clone 5323

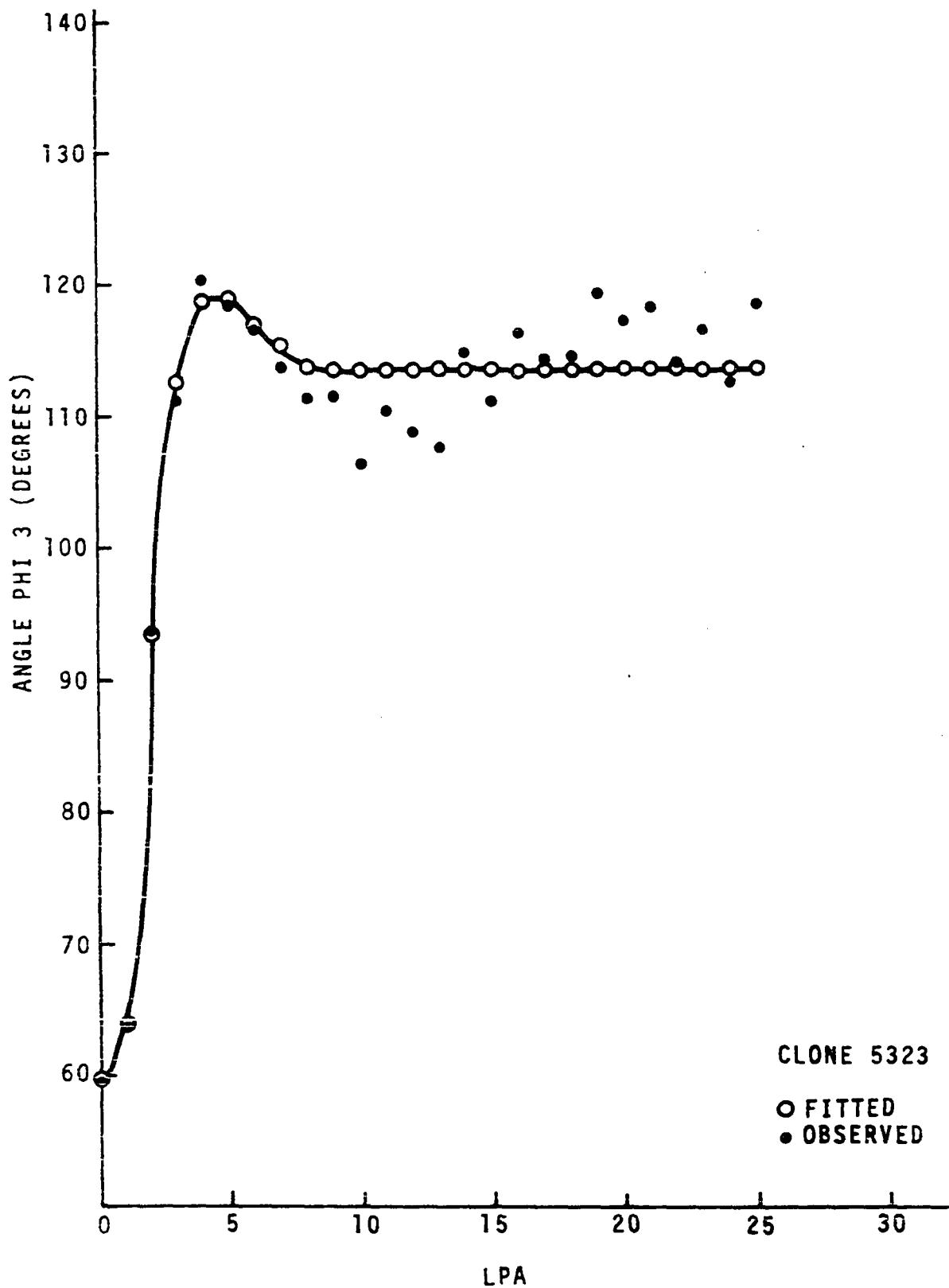


Figure 6. Observed values and fitted equation for leaf angle ϕ_3 versus LPA as given in Equation 6 for clone 5326

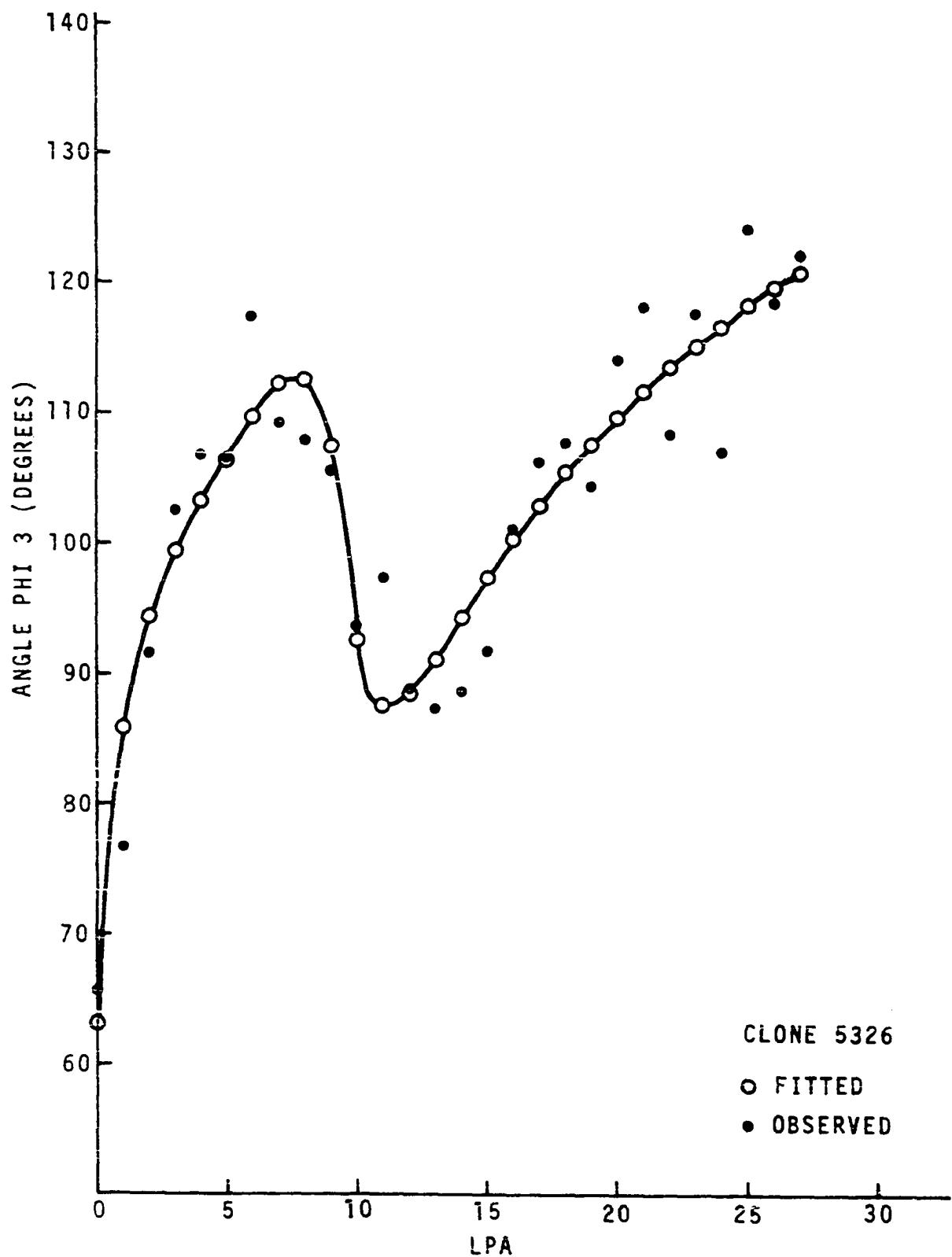


Figure 7. Observed values and fitted equation for leaf angle ϕ_3 versus LPA as given in Equation 6 for clone 5377

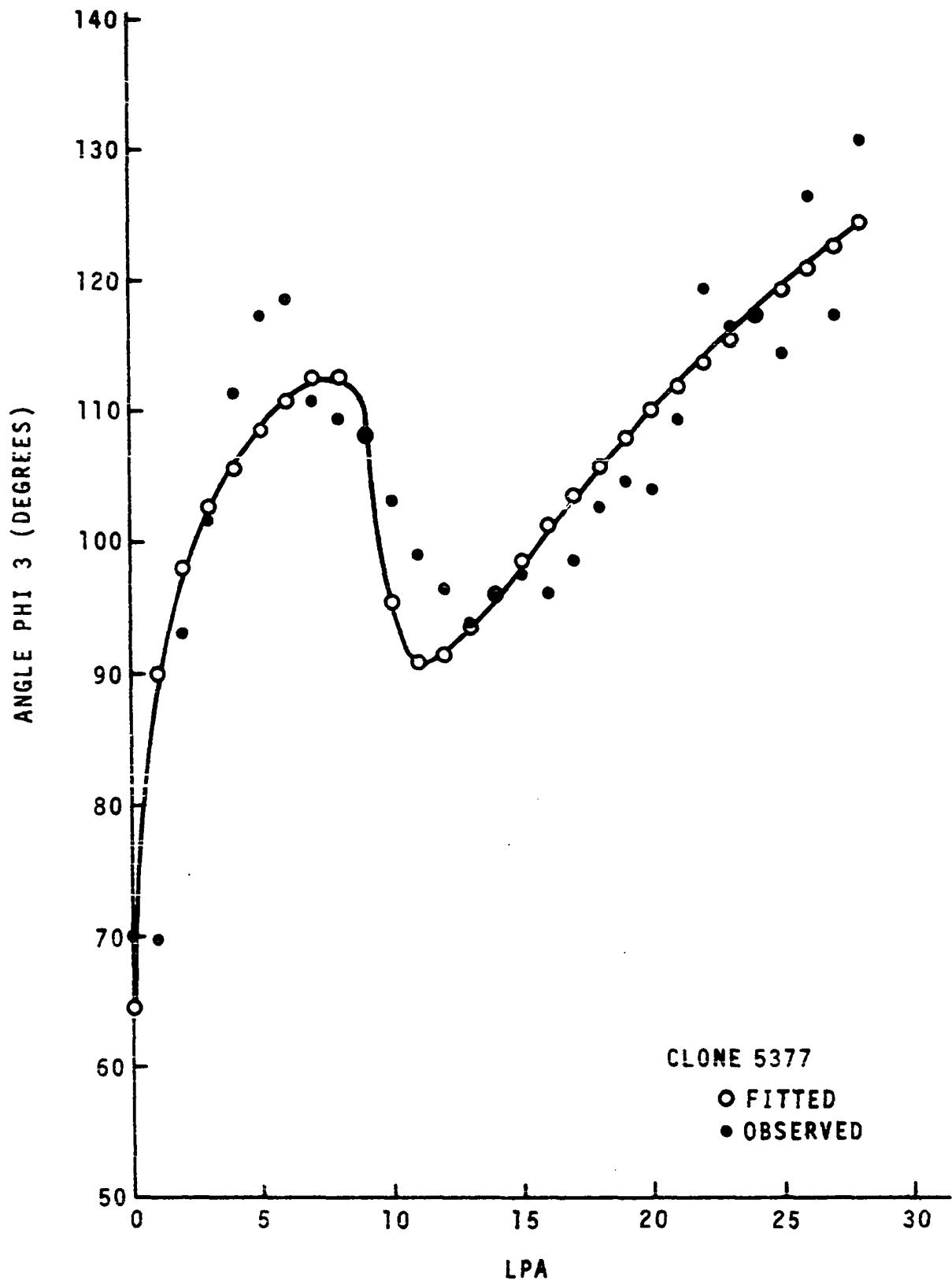


Table 2. Coefficients, standard errors of the coefficients, number of observations and values of R^2 for fitting the model given by Equation 7

Clone	Coefficient	SE ^a	n ^b	R^2
5321	60.3709	1.0870	33	0.8700
	20.4983	2.5584		
	-0.2108	0.1353		
	0.2743	0.0069		
5323	62.5651	2.0489	26	0.7061
	21.6430	2.9766		
	-1.6223	0.3063		
	0.2151	0.0089		
5326	43.3969	2.0056	28	0.8992
	37.4327	2.9433		
	-3.1797	0.2245		
	0.1971	0.0050		
5377	43.3886	1.5383	28	0.9430
	38.6950	2.4357		
	-3.1768	0.1598		
	0.1844	0.0054		

^aSE = Standard error of the coefficient.

^bn = Number of observations.

Figure 8. Observed values and fitted equation for leaf angle δ_3 versus LPA as given in Equation 7 for clone 5321

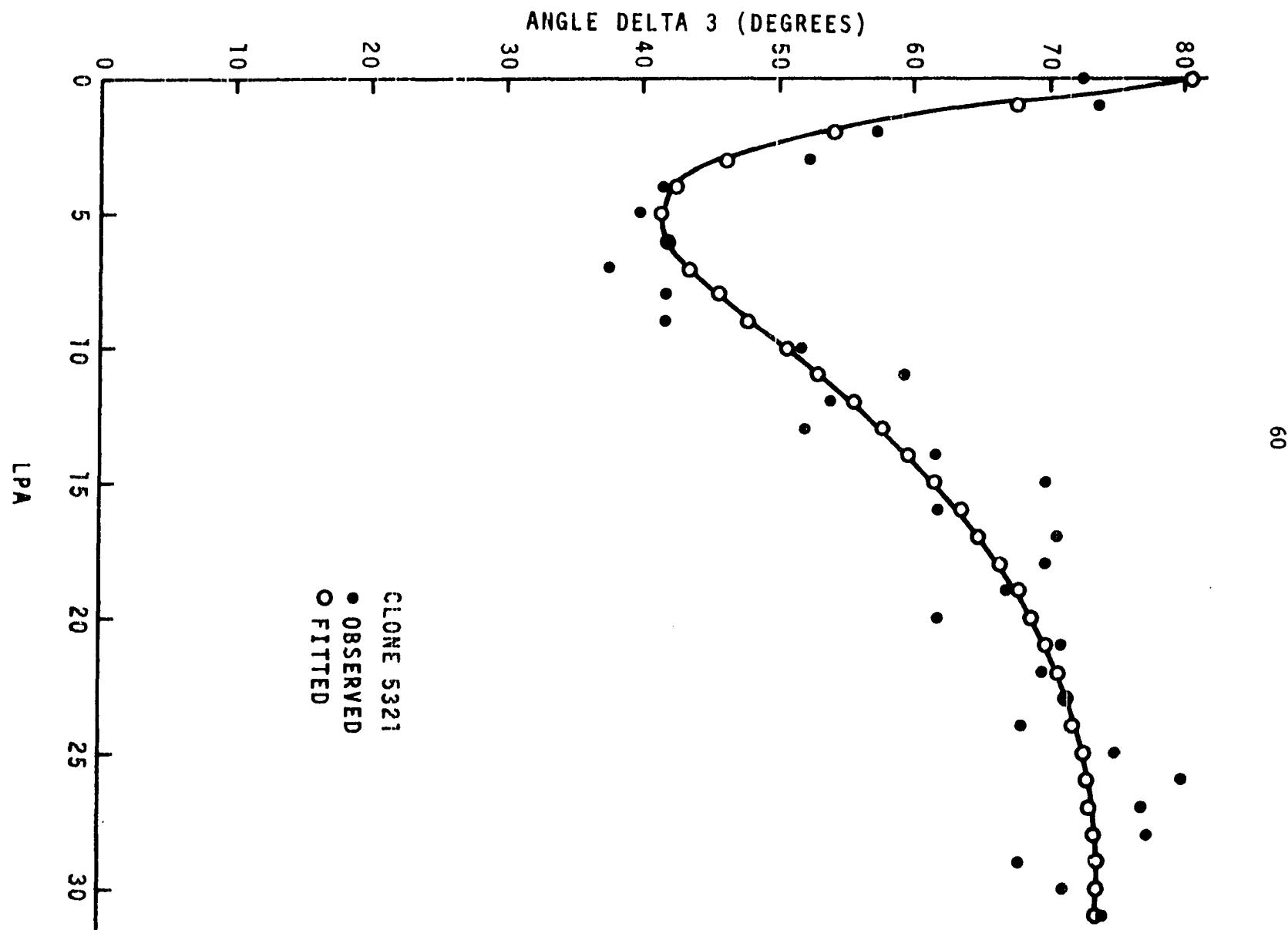


Figure 9. Observed values and fitted equation for leaf angle δ_3 versus LPA as given in Equation 7 for clone 5323

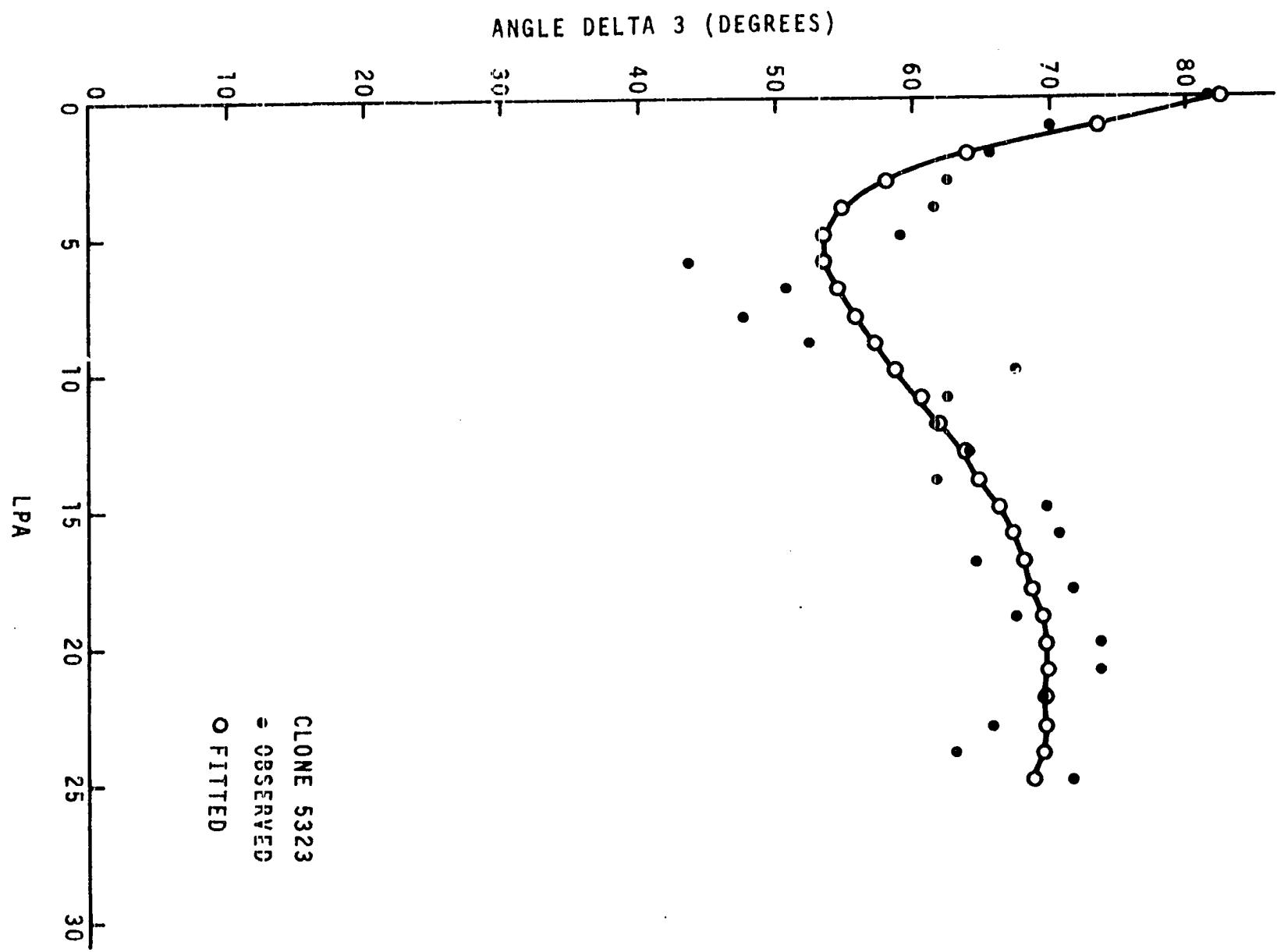


Figure 10. Observed values and fitted equation for leaf angle δ_3 versus LPA as given in Equation 7 for clone 5326

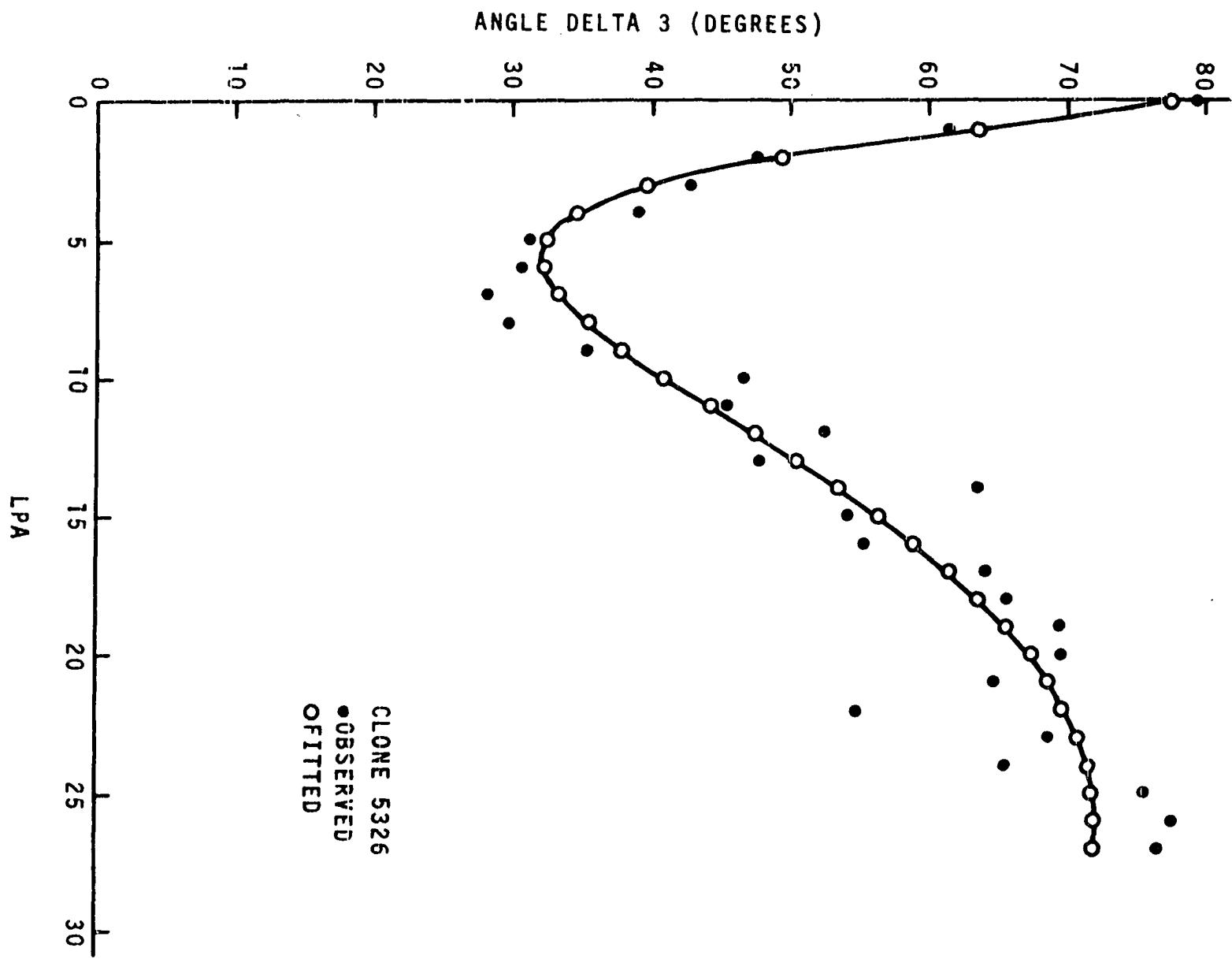
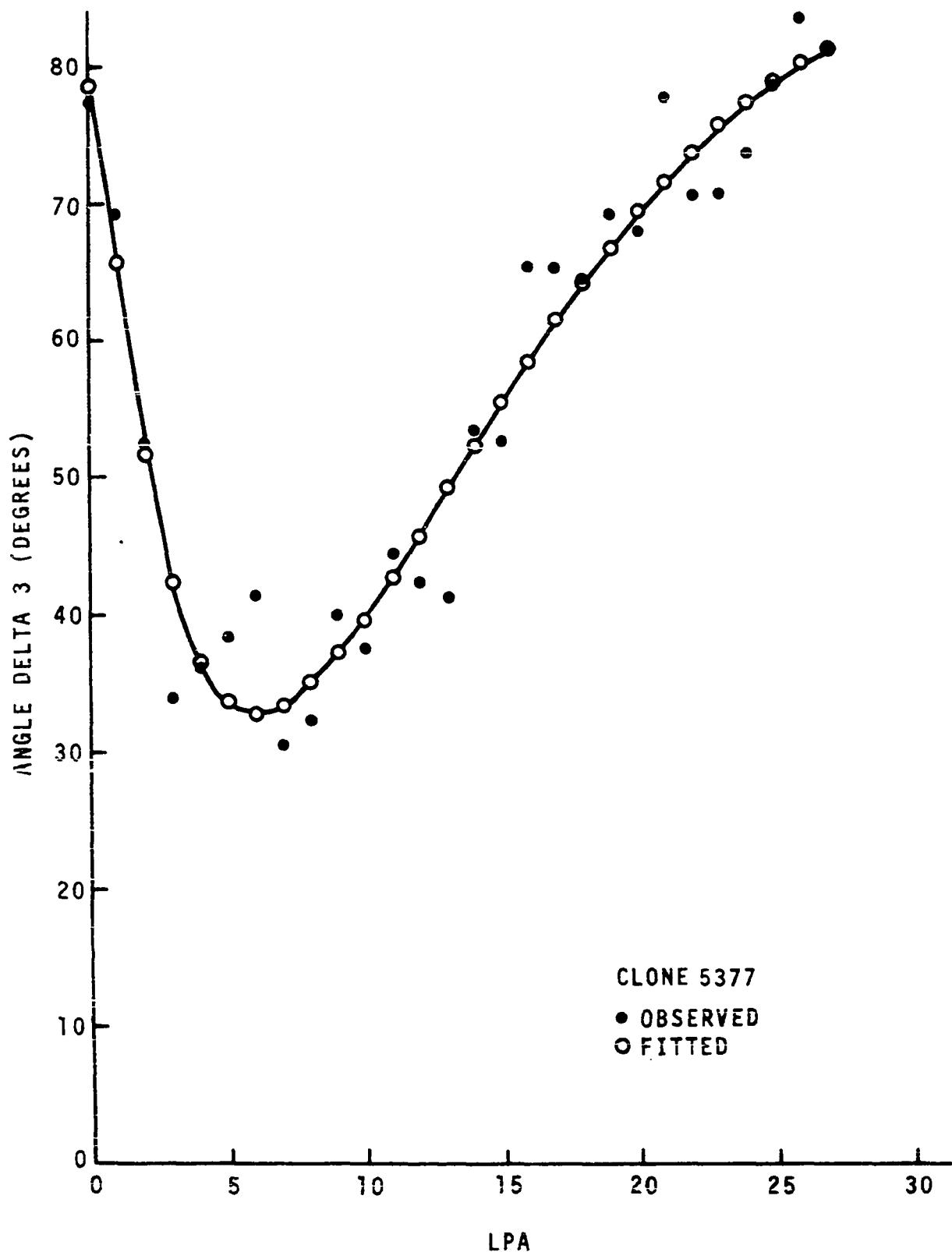


Figure 11. Observed values and fitted equation for leaf angle δ_3 versus LPA as given in Equation 7 for clone 5377



In this model the amplitude is assumed to be a linear function of LPA, and the period is again assumed to be a logarithmic function of LPA. Notice the way in which Y, the independent variable in Equation 7, was formed. Upon reviewing the original plot of δ_3 against LPA, it was noted that the data above $\delta_3 = 90^\circ$ was essentially the mirror image of the data below $\delta_3 = 90^\circ$, indicating that regardless of the direction a leaf rotated on leaf axis 1 the pattern was identical. There seemed to be no preferential direction of tilt; that is, there were approximately equal numbers of leaves tilted in each direction.

In summary, then, the top leaves in the crown are erect with very little tilt to one side or the other. Both angle ϕ_3 , which measures erectness of the leaf along leaf axis 1, and angle δ_3 , which measures the angle of tilt of the leaf, change rapidly between LPA zero and LPA five. The angle ϕ_3 increases until the leaves are nearly horizontal along leaf axis 1 somewhere between LPA five and LPA eight. In this same period the angle of tilt changes from the leaf being almost horizontal along leaf axis 2 to where the leaf is tilted to its greatest extent between LPA five and LPA eight. The angle of tilt, δ_3 , then declines slowly with increasing LPA until the angle of tilt is small for large LPAs. The leaves become more erect after LPA eight until about LPA twelve. Then the erectness gradually decreases with increasing leaf angle.

Estimation of Leaf Area Exposed to Radiation

The proportion of projected leaf area receiving radiation from any designated sky position must be known or estimated so that photosynthesis of the plant can be simulated. These quantities are P_T if the crown is considered as a whole unit, P_I , P_M and P_S if the crown is viewed as consisting of three segments, and P_i for each leaf if the crown is viewed as consisting of individual leaves. These quantities depend on the crown geometry and growth pattern of the plants. The theoretical derivation of values of parameters based on crown geometry and growth characteristics was the approach taken in the development of Model I. An extension of the strictly theoretical approach is currently impossible to implement in a general framework. For this reason empirical techniques were developed to estimate the necessary parameters.

Methods

A photographic method was developed to assess the amount of leaf area receiving radiation for a given sky position. A photograph is taken of a tree with the camera at a specified orientation with respect to the tree. The film acts as a reference plane for the sky position simulated by the appropriate placement of the camera. The film then records the projected leaf area as seen from the designated sky position. The leaf area which is shaded, and hence does not receive radiation from this sky position, is not visible in the photograph. By measuring the leaf area which appears in the photograph for each leaf on the tree, data is obtained which can be used to estimate P_T , P_I , P_M , P_S and the P_i 's. These methods are completely described in Appendix D.

Results

Measurements from the photographs provided values of $(SA)_i'$ for each leaf and for each sun position considered. Measurements were taken to determine leaf orientation and leaf area. Hence A_i' , the area of leaf i projected onto a given reference plane, could be estimated. When the crown is considered as a unit then

$$P_T = \frac{\sum_{i=1}^n A_i'}{\sum_{i=1}^n A_i} = \frac{\sum_{i=1}^n (SA)_i'}{\sum_{i=1}^n A_i} \quad (8)$$

for a particular sun altitude. The relationship between the mean value of \hat{P}_T and altitude angle for the four clones is demonstrated in Figure 12 and indicates that all the clones follow the same basic trend with small differences between clones.

The same procedure was used in the case when the crown was considered as consisting of three segments. Proportion of projected leaf area exposed to radiation from a particular sky position was estimated as

$$\hat{P}_I = \frac{\sum_{i=1}^8 (SA)_i'}{\sum_{i=1}^8 A_i} \quad (9)$$

$$\hat{P}_M = \frac{\sum_{i=9}^{n-5} (SA)_i'}{\sum_{i=9}^{n-5} A_i} \quad (10)$$

$$\hat{P}_S = \frac{\sum_{i=n-4}^n (SA)_i'}{\sum_{i=n-4}^n A_i} \quad (11)$$

since for these trees the immature leaf zone was defined to consist of the youngest eight leaves, the senescent leaf zone was defined to consist of the oldest five leaves with all intervening leaves belonging to the mature leaf zone. The relationship between the mean values of these

quantities and altitude of the sky position for the four clones is demonstrated in Figures 13, 14 and 15. The most important figure is Figure 14 for the mature section of the crown since mature leaves have the highest photosynthetic response to light intensity. In Figure 14, clones 5321 and 5377 are essentially identical and tend to have values for P_M higher than the other two clones. The general conclusion, however, is that the clones do not differ greatly in magnitude or trend of proportion of leaf area receiving radiation as a function of solar altitude.

The case when the crown is viewed as consisting of individual leaves is considerably more complex. In this case tree orientation is extremely important. In general the proportion of a leaf's area exposed to radiation for a particular sky position depends upon LPA, which indicates the relative position or depth of the leaf within the crown, altitude of the sky position considered and the horizontal angular displacement of the leaf with respect to a particular sky position. In particular, for a given clone, these proportions are influenced by growth characteristics of that clone, for example, internodal distances, petiole lengths and leaf areas. Even if only the former factors are considered, an extensive data base would be required to determine the relationship between these variables. Some of these difficulties are illustrated in Figure 16 which is a plot of P_i versus LPA for sun altitude 60° . These results demonstrate that the top leaves are fully irradiated and, as LPA increases, P_i decreases. The pattern of this decrease will depend upon whether a leaf is on the side of the plant near or away from the sun. To reduce these difficulties, the angular displacement of leaves was divided into four equal categories from 0° to 180° .

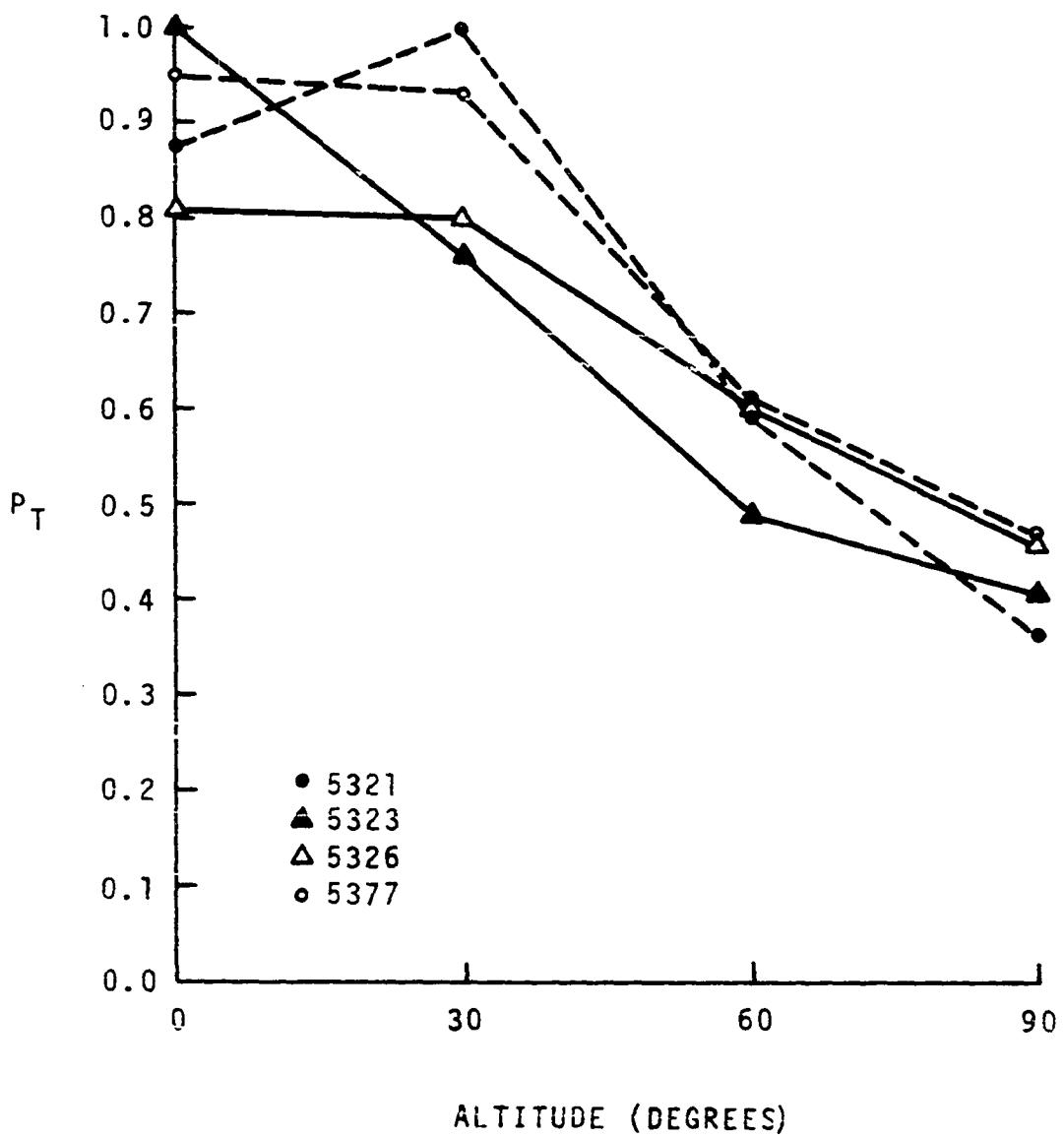


Figure 12. Proportion of the total projected leaf area of the whole crown receiving radiation, P_T , versus altitude of the incident radiation

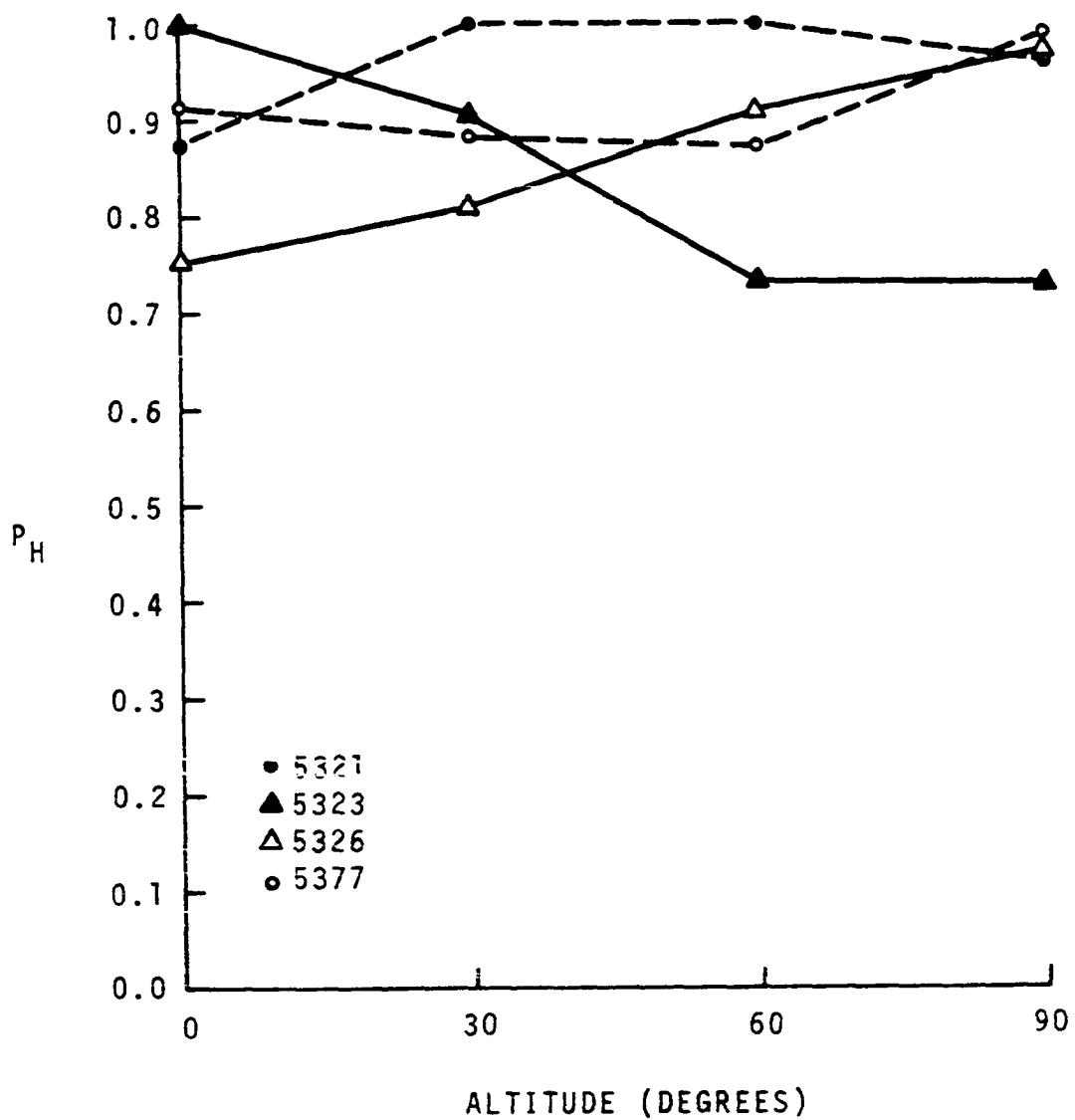


Figure 13. Proportion of the total projected leaf area of the immature section of the crown receiving radiation, P_H , versus altitude of the incident radiation

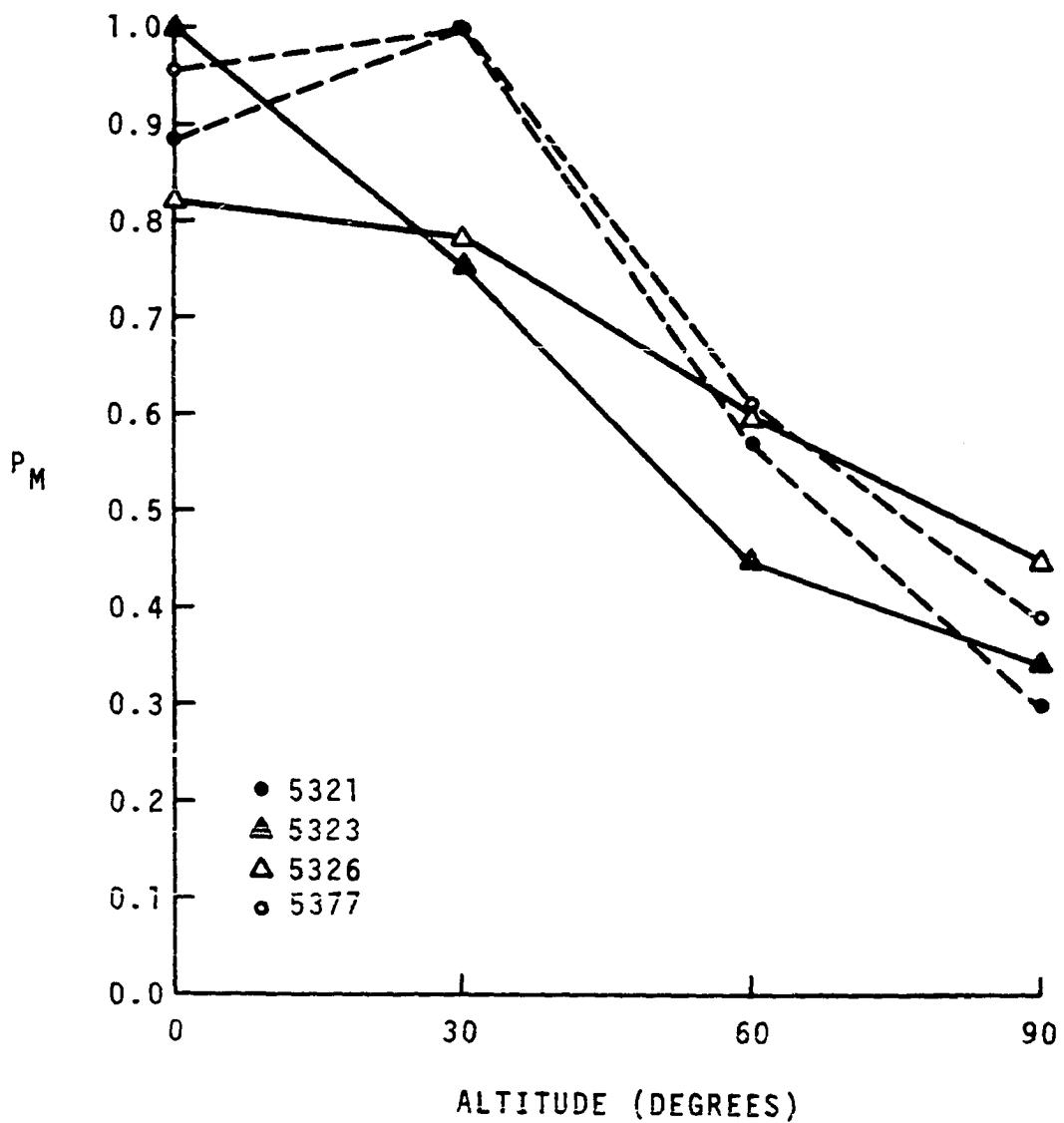


Figure 14. Proportion of the total projected leaf area of the mature section of the crown receiving radiation, P_M , versus altitude of the incident radiation

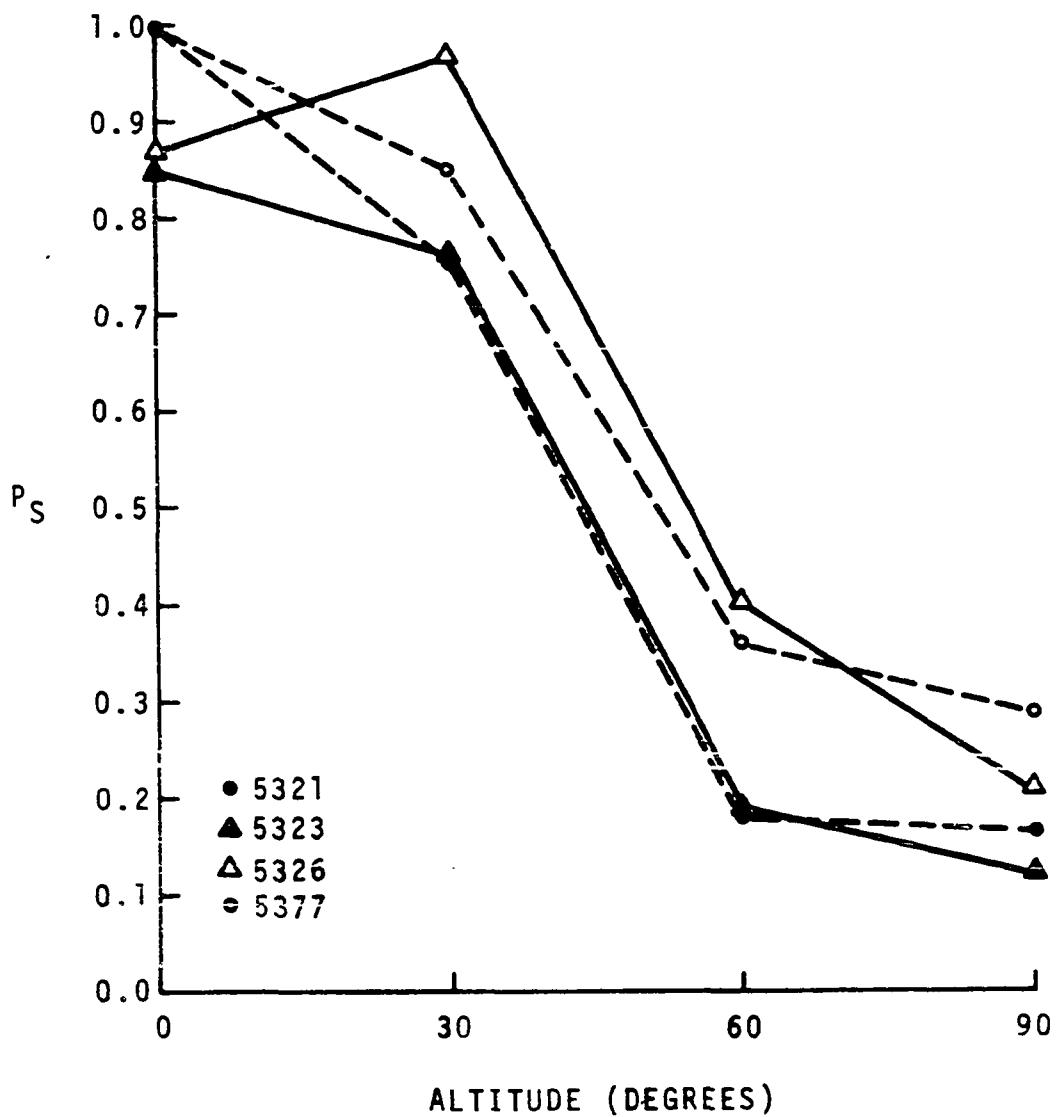


Figure 15. Proportion of the total projected leaf area of the senescent section of the crown receiving radiation, P_S , versus altitude of the incident radiation

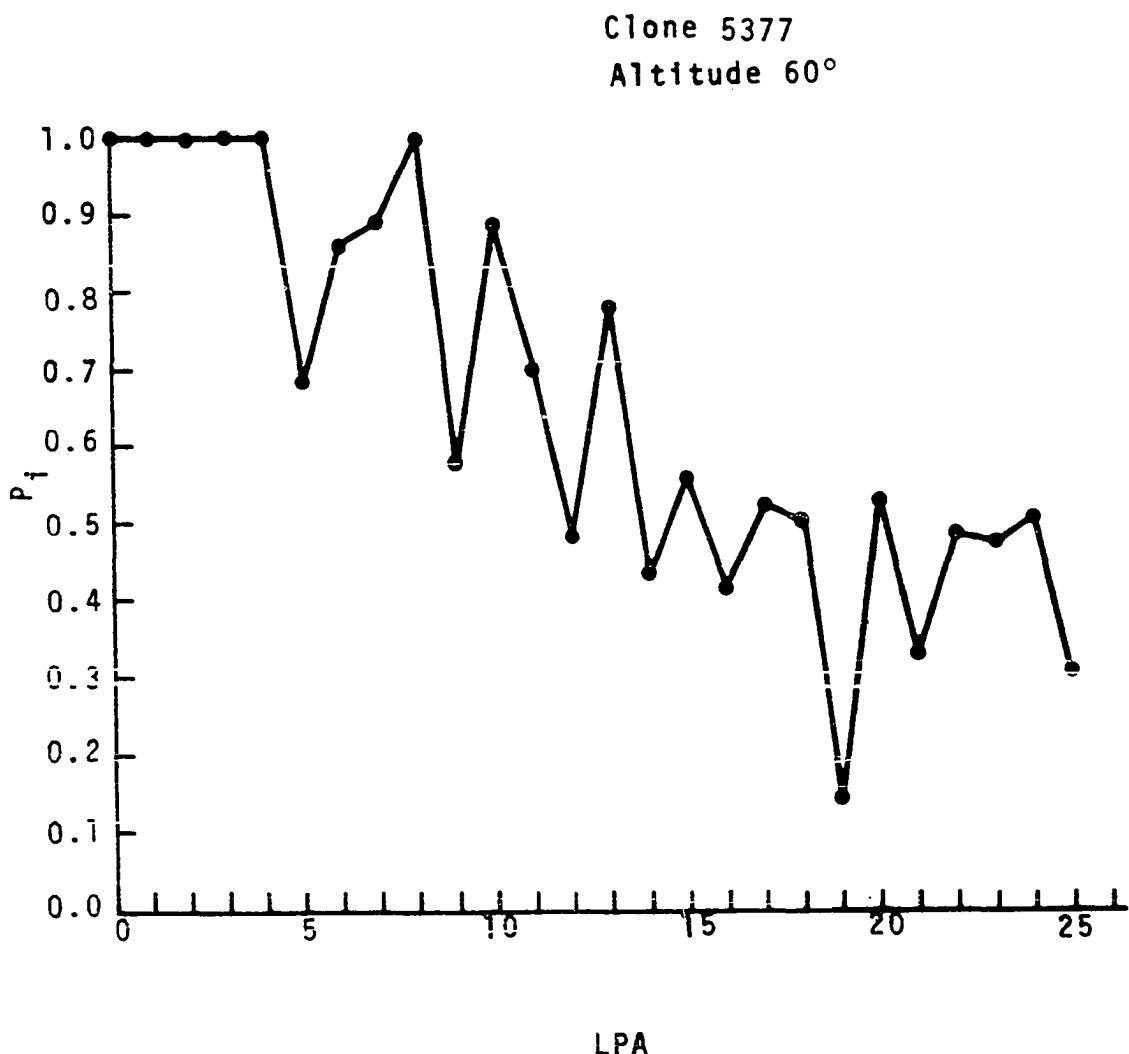


Figure 16. The proportion of an individual leaf exposed to radiation, P_i , versus LPA for clone 5377 and radiation incident from an angular altitude of 60°

In the case when the sun altitude is 90° , the angular displacement of the leaf is not meaningful and depth in the crown as indicated by LPA is the important explanatory variable. The model used for all four clones was of the general form

$$P_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{3i} + e_i \quad (12)$$

where P_i = proportion of the projected leaf area exposed to radiation from this sky position for leaf i

$$x_{1i} = \text{LPA of leaf } i$$

$$x_{2i} = 0 \quad x_{1i} < c_1$$

$$= x_{1i} - c_1 \quad x_{1i} \geq c_1$$

$$x_{3i} = 0 \quad x_{1i} < c_2$$

$$= x_{1i} - c_2 \quad x_{1i} \geq c_2$$

The technique of graphed polynomials (Fuller 1969) was used to fit the relationship. This technique permitted the overall model to consist of three line segments of different slopes; each line segment represented a segment of the crown. With some restrictions the overall model was constrained to be continuous at the join points c_1 and c_2 . These joint points are slightly different for the four clones and identify positions within the crown where changes in the shading regime occur. Values of the join points were determined by the consideration of crown segments based on the physiological development of the leaves in conjunction with plots of the data. The top part of the crown is mostly fully illuminated so the first segment of the curve determined by β_1 and x_1 is slightly decreasing. The middle part of the crown, LPA between c_1 and c_2 , is represented by a sharply decreasing function that indicates the relatively

rapid increase in shaded leaf area when the light source is overhead.

The lower portion of the crown, with LPA greater than c_2 , receives relatively little light and is represented by a slightly decreasing function near zero.

When the sun altitude is 60° , the horizontal angular displacement of leaves from the direction of the incident radiation becomes important (Figure 16). Data were separated by angular displacement into three groups: $0^\circ-45^\circ$, $45^\circ-90^\circ$, $90^\circ-180^\circ$. The general form of the relationship used for the four clones and three groups within each clone was

$$P_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + e_i \quad (13)$$

where P_i = proportion of projected area of leaf i receiving radiation from the designated sky position,

$$x_1 = \text{LPA}$$

$$\begin{array}{ll} x_2 = 0 & x_1 < c_3 \\ = x_1 - c_3 & x_2 \geq c_3 \end{array}$$

Generally the model indicates that for this sun altitude the upper and lower portions of the crown are basically different in their reception of light. In the upper portion of the crown ($\text{LPA} < c_3$), the value of P_i decreases with increasing LPA but decreases more rapidly for the rest of the crown ($\text{LPA} \geq c_3$). This indicates that leaf area exposed to radiation decreases at an increasing rate as a function of depth in the crown for this solar altitude.

When the sun is at an altitude 30° or 0° , depth in the crown as indicated by LPA is of minor importance. Shading of leaves by other leaves higher in the crown is relatively unimportant compared to shading

by leaves at about the same depth in the crown. In this case a simple linear model was used to relate P_i to LPA. The model is

$$P_i = \beta_0 + \beta_1 (LPA)_i + e_i. \quad (14)$$

The model was estimated separately for each clone, each altitude, 30° or 0°, and each set of leaves corresponding to horizontal angular displacement of 0°-45°, 45°-90°, 90°-135° or 135°-180°. The fitted equations were nearly horizontal indicating little change in P_i as a function of LPA for a particular clone and angular displacement. Differences in angular displacement were indicated by different values of the intercept term. The leaves on the part of the plant toward the sun had higher values for the intercept term than the leaves on the plant that were away from the sun, as would be expected. Horizontal angular displacement of the leaf with respect to the sun position is of critical importance whereas depth of the leaf in the crown is relatively unimportant.

The estimated equations discussed in this section were used to simulate photosynthesis. To calculate P_i for any given sun altitude a linear interpolation was used between the appropriate two curves.

SIMULATION OF PHOTOSYNTHESIS

The ultimate goal of the model is to simulate the photosynthesis of an individual tree. These simulations provide a means for assessing some of the many factors which affect photosynthesis. Such simulations can provide realistic estimates of photosynthesis under various light conditions. Parameters describing crown geometry can be varied which could provide estimates of morphological characteristics that are optimal for photosynthesis under specific environmental conditions. The simulations for this study were done for a single day with calculations of the photosynthetic rate made on an hourly basis.

Radiation

The radiation levels used in these simulations were taken from meteorological data for Ames, Iowa, on August 12, 1973. This was a clear day fourteen hours long. The radiation data was converted from the original units to microeinsteins (μE) so that only the PAR was used in the simulations. Figure 17 illustrates the level of radiation in microeinsteins as recorded on a horizontal surface for each hour of the day.

Photosynthetic Response

Photosynthetic response data are not available to fit general photosynthetic response functions for the four clones over a wide range of light intensities and LPA. The most extensive data set available was for clone 5377. Hence the photosynthetic response function for this clone was used for all simulations. This approach facilitated comparing clones for morphological differences since clonal differences in photosynthetic

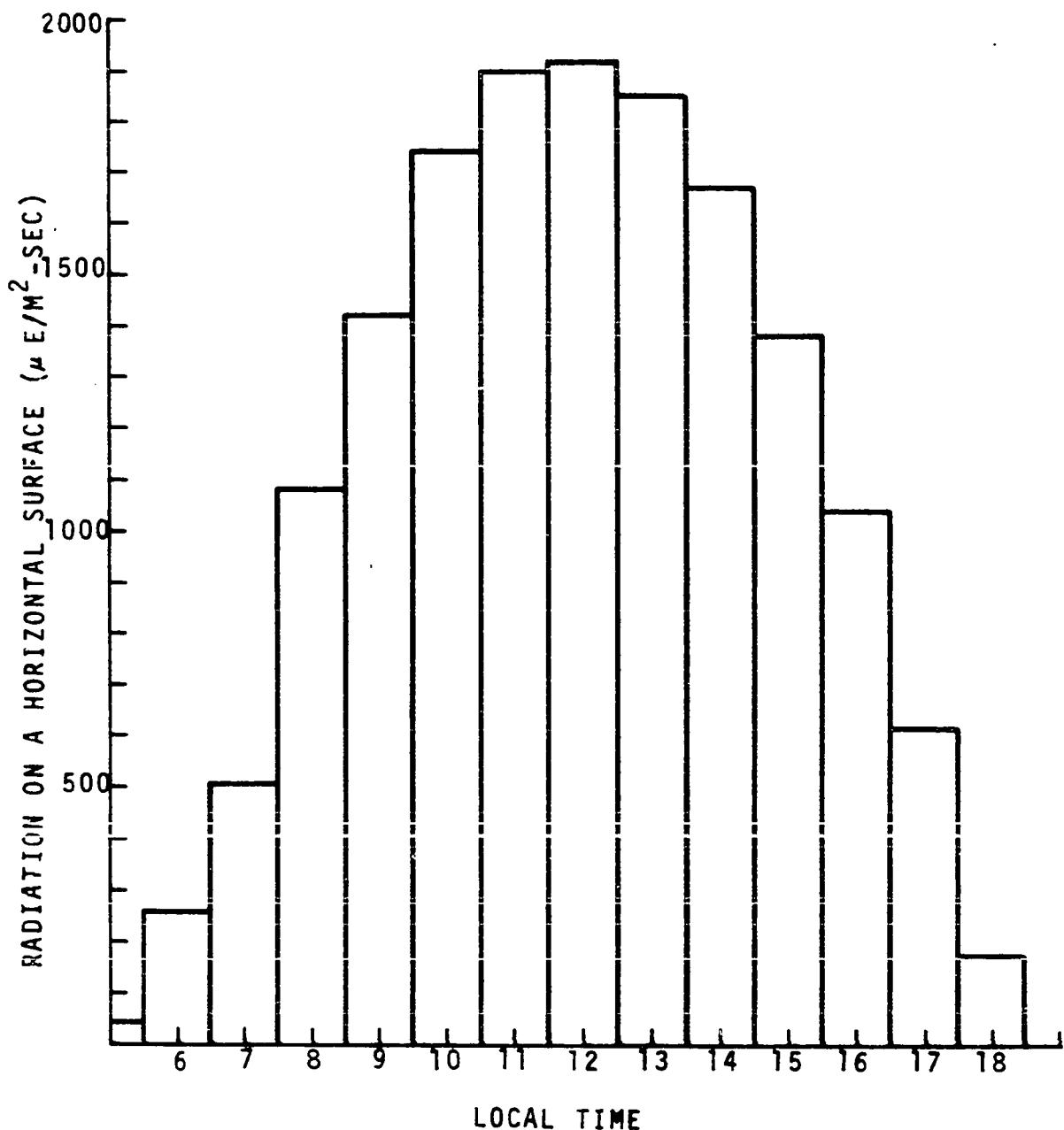


Figure 17. Total radiation recorded at hourly intervals on a horizontal surface at Ames, Iowa on August 12, 1973

response did not enter. When the data become available, however, it would be instructive to rerun the simulations including different photosynthetic response functions for the clones.

The photosynthetic response function used in these simulations is illustrated in Figure 18. The curves for five different LPA are presented over a range of light intensity from $0\mu E$ to $2000\mu E$. Figure 18 illustrates clearly the nonlinearity of photosynthetic response and the dependence of photosynthetic response on LPA.

Simulation Procedure and Results

Introduction

The basic method of simulating photosynthesis is the same for each of the three ways of viewing the crown. This basic procedure is illustrated in Figure 19.

Assumptions must be made in the formulation of any model. One of the most important assumptions necessary in this model concerns the way in which photosynthesis is calculated. Because of the nonlinearity of the photosynthetic response function, ideally, the exact level of radiation received at each point on the leaf's area should be known. This is not possible since different parts of a leaf receive radiation from different parts of the sky, for example, part of a leaf may receive indirect radiation from many sky segments while another part of the leaf may receive radiation from only one sky segment. And no method exists by which a leaf can be partitioned into mutually exclusive parts to avoid this problem. Hence, indirect radiation received by a leaf is assumed to be uniformly spread over the whole leaf's area. Photosynthesis is calculated

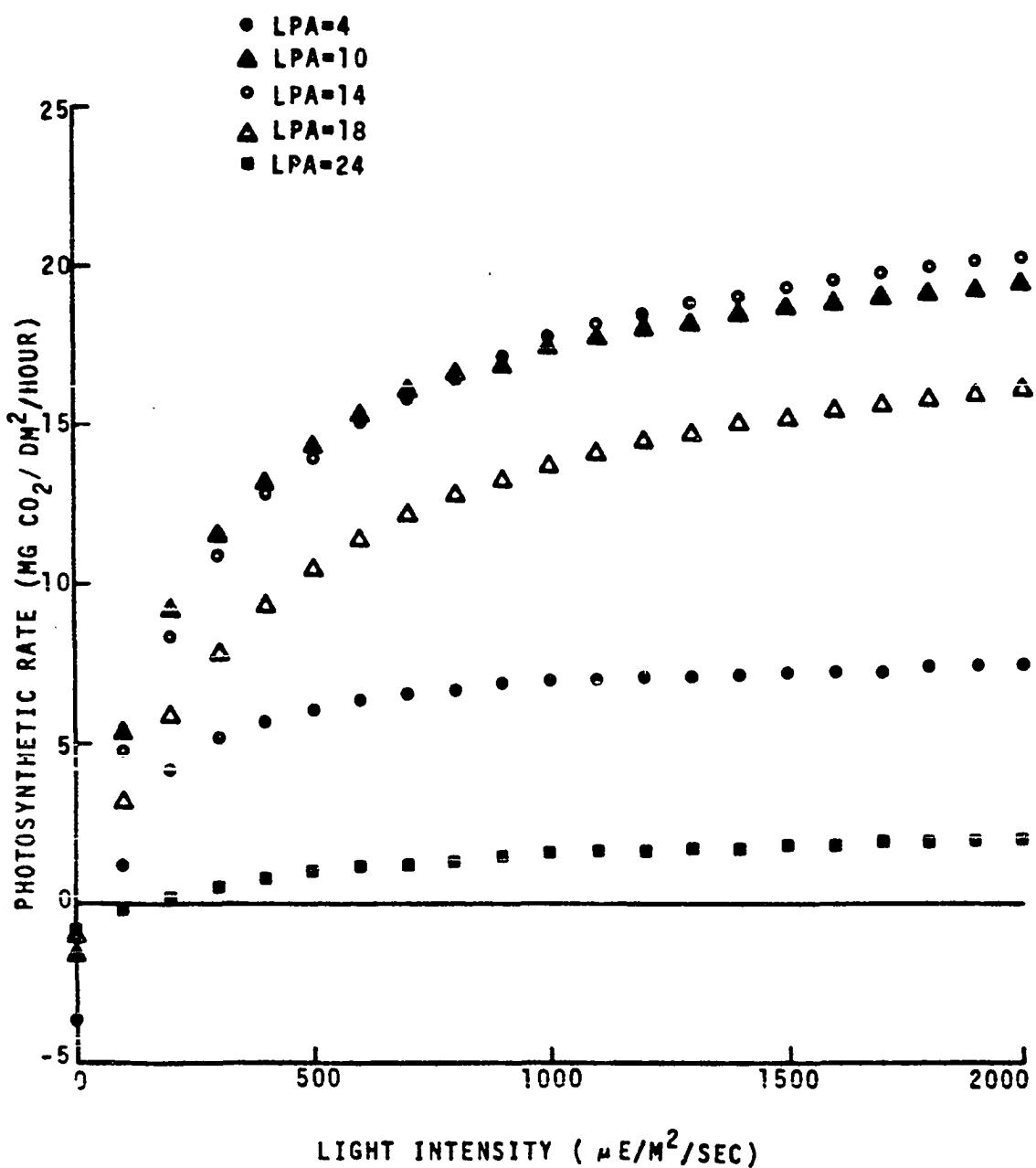


Figure 18. Illustration of photosynthetic response curves for several leaf ages

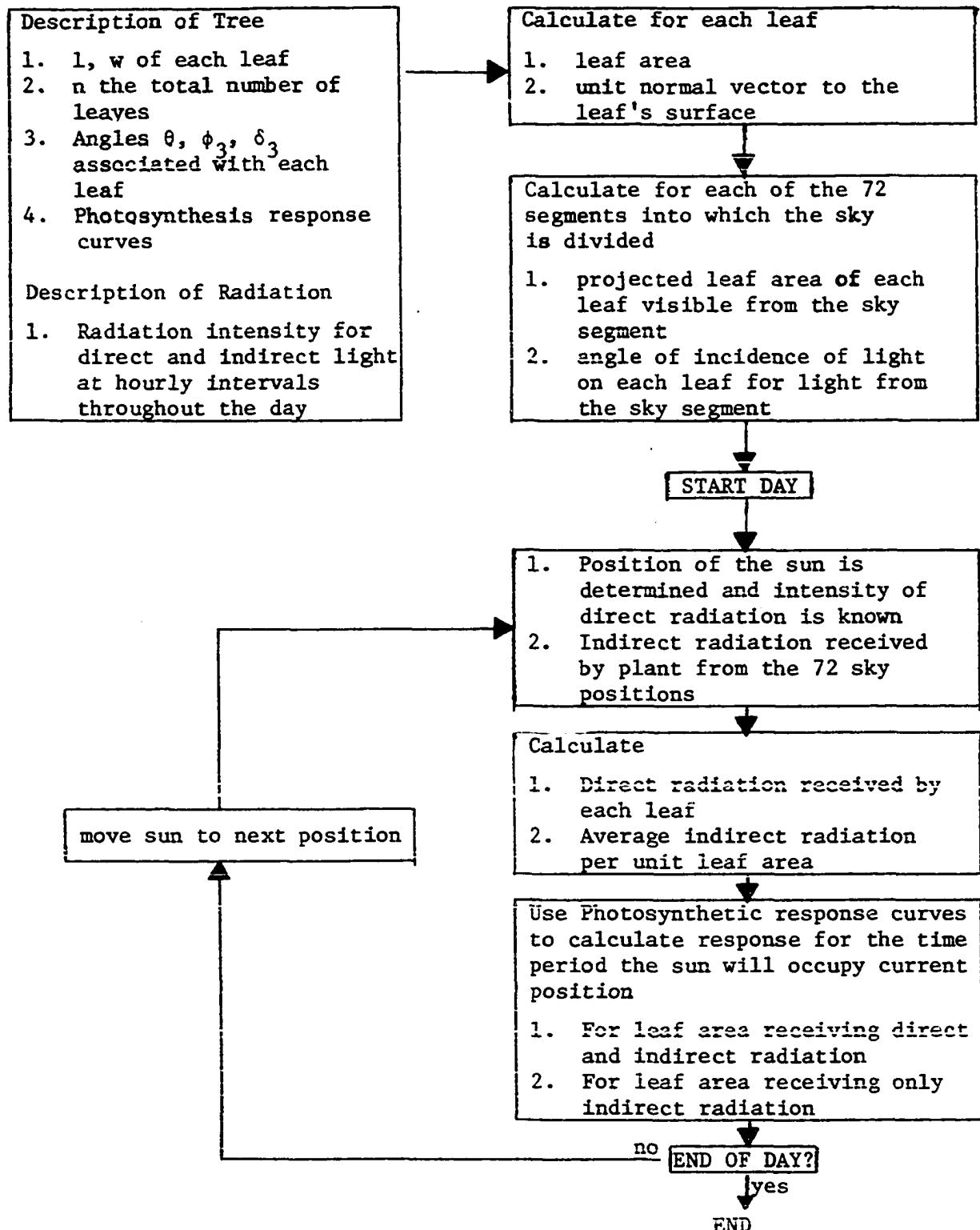


Figure 19. Flow-chart of the photosynthesis simulation procedure

for the leaf area receiving direct radiation using the intensity of direct radiation plus the average intensity of indirect radiation while the rest of the leaf area is assumed to receive indirect radiation at the average intensity. This assumption is more realistic than assumptions used in other similar simulations.

A particular tree was used for all simulation. This tree consisted of twenty-five leaves. The dimensions of the leaves were measurements taken from an actual tree.

Whole-crown method

The whole-crown method assumed that all the leaf area of the crown was identical. For the whole-crown approach the photosynthetic response curve for LPA 14 was used for the entire leaf area of the crown. This resulted in an overestimation of photosynthesis since LPA 14 in this size of plant represents a leaf of about maximum photosynthetic capacity. Results would change considerably if a different photosynthetic response curve were used. This illustrates the problem of using any one photosynthetic response curve to represent the response of widely differing leaves.

Segmented-crown method

The segmented-crown method divided the crown into three segments. Calculations proceed as for the whole-crown approach except that photosynthesis is calculated separately for each crown segment. This entails the calculation of exposed leaf area to the sun and each segment of the sky separately for each segment of the crown. It also permits the use of a different photosynthetic response function and different average angle

of incidence of direct light for each of the three segments of the crown. The photosynthetic response functions for LPA 4, 14 and 23 were used for the immature, mature and senescent zones respectively. This resulted in an underestimate of total photosynthesis because of the underestimate of photosynthesis for both the immature and senescent segments of the crown, illustrating the difficulty in using any particular photosynthetic response curve to represent leaves of even a rather small range of LPA.

Individual-leaf method

The individual-leaf method is basically the same as the other methods except that all calculations are made on the basis of individual leaves. Hence the photosynthetic response function appropriate for each leaf can be used to calculate the photosynthesis of that leaf. The cosine law appropriate for the interception of light is observed exactly since the angle of incidence of the light falling on each leaf is known. Furthermore, diffuse light is averaged only over the area of a single leaf rather than over a part or all of the crown. Errors caused by averaging light reception over leaf area that responds nonlinearly to that radiation are thus reduced. This method predicts photosynthetic rates that fall between the values obtained by the other two methods.

Comparison of methods

Photosynthesis was simulated on an hourly basis by each of the three methods using the radiation data shown in Figure 17. The results were consistent for all four clones. The whole-crown method resulted in the largest estimates of photosynthesis. The segmented-crown method yielded the lowest estimates of photosynthesis while the individual-leaf approach

estimated values of photosynthesis between the two other methods. However, these rankings would change depending upon which photosynthetic response curves were used to represent the leaves in the whole-crown method or to represent segments of the crown in the segmented-crown method. Results of the simulations for clone 5321 are presented in Figure 20. The results were generally as expected because of the response curves chosen to represent the leaf material in the whole-crown and segmented-crown methods. These results demonstrate the need for the individual-leaf method in which the appropriate photosynthetic response curve is used for each leaf. Total photosynthesis for clone 5321 for the simulated day in mg CO₂, calculated by approximating the area under the photosynthetic rate curves shown in Figure 19, were 5263, 4083 and 4555 for the whole-crown, segmented-crown and individual-leaf methods respectively. In this case the whole-crown and segmented-crown methods differed by 1180 mg CO₂, or 28.9% of the segmented-crown value, in their estimate of total photosynthesis for the day. Results for the other three clones were similar.

Contributions of direct and diffuse light

The radiation data used in the simulations are the measured values of radiation falling on a horizontal surface. The measurement includes diffuse radiation from all sky positions plus direct radiation. Diffuse radiation is considered to be a constant proportion of total radiation where the value of the proportion depends only on solar altitude (R. H. Shaw, 1972, personal communication). The source of indirect radiation was assumed to be a uniformly bright sky. Although empirical evidence

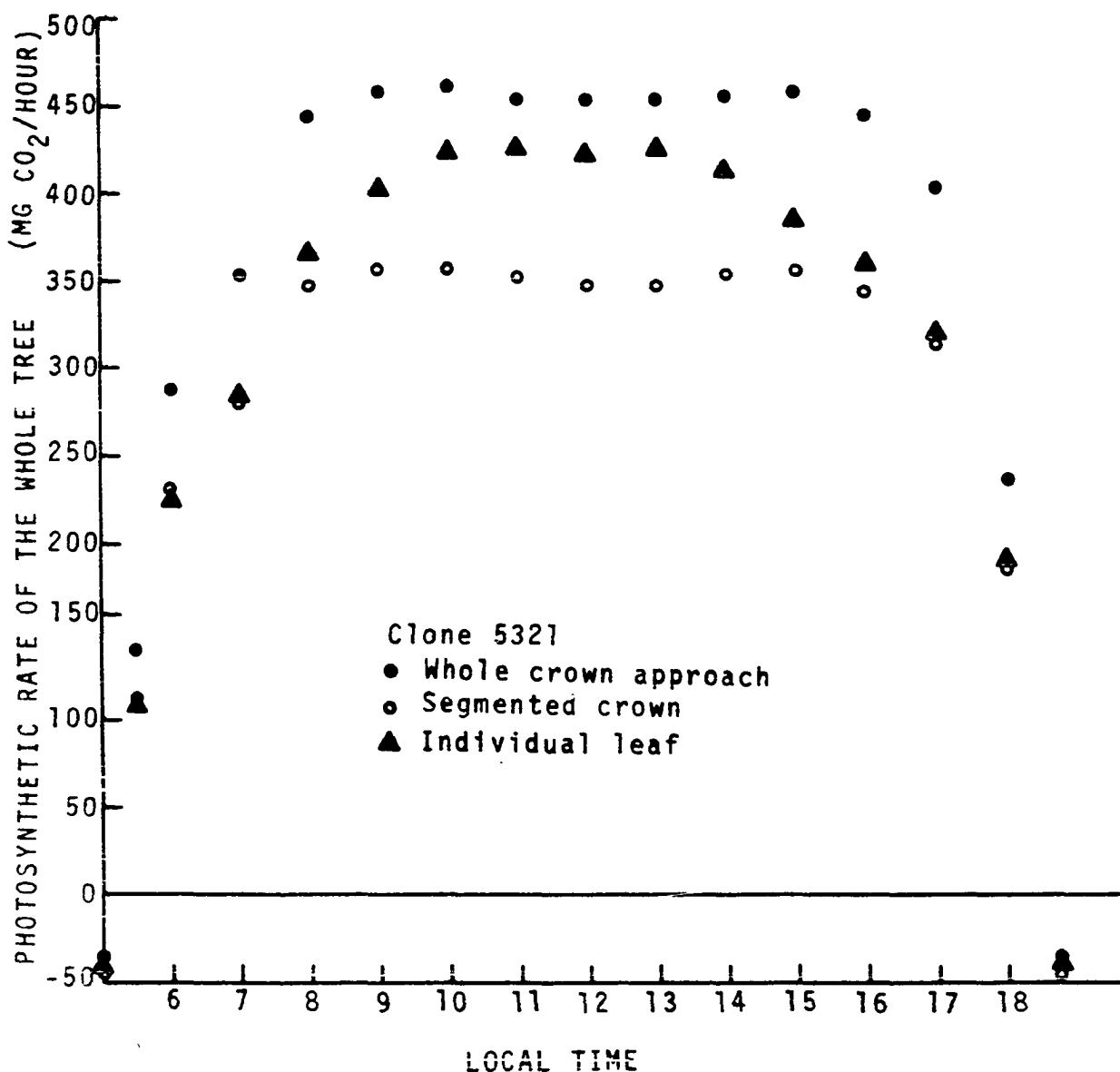


Figure 20. Photosynthetic rate of the whole crown throughout one day calculated by the three methods, the whole-crown method, the segmented-crown method and the individual-leaf method

exists demonstrating that this assumption is not correct, no comprehensive quantitative models have been developed for replacing this assumption. Photosynthetic rates were calculated at hourly intervals for the leaf area receiving only indirect light and for the leaf area receiving simultaneously direct and indirect light. Figure 21 shows the results of such calculations for clone 5323 using the individual-leaf method. Total daily photosynthesis was calculated to be 3059 mg CO₂ and 756 mg CO₂ for the leaf area in direct and indirect light respectively. The segmented-crown method estimated these components to be 2489 mg CO₂ and 1143 mg CO₂ for leaf area in direct and indirect light respectively. The estimates of the same two quantities using the whole-crown method were 3237 mg CO₂ for leaf area in direct light and 1459 mg CO₂ for leaf area receiving only diffuse light. Similar results were obtained for the other clones. Hence diffuse light plays a lesser role in total photosynthesis when using the individual-leaf method than with either of the other two methods. In this respect the individual leaf model corresponds to my expectations as well as to the expectations published by other researchers, although I know of no similar published results.

Clonal comparisons

Photosynthesis was simulated for each of the clones using the three different methods. The same tree, in terms of number of leaves and leaf areas, light intensity data and photosynthetic response curves were used for all of the clones. Therefore the only differences between the simulations were the values of the parameters describing the crown geometry and related light interception. Figure 22 illustrates the results using

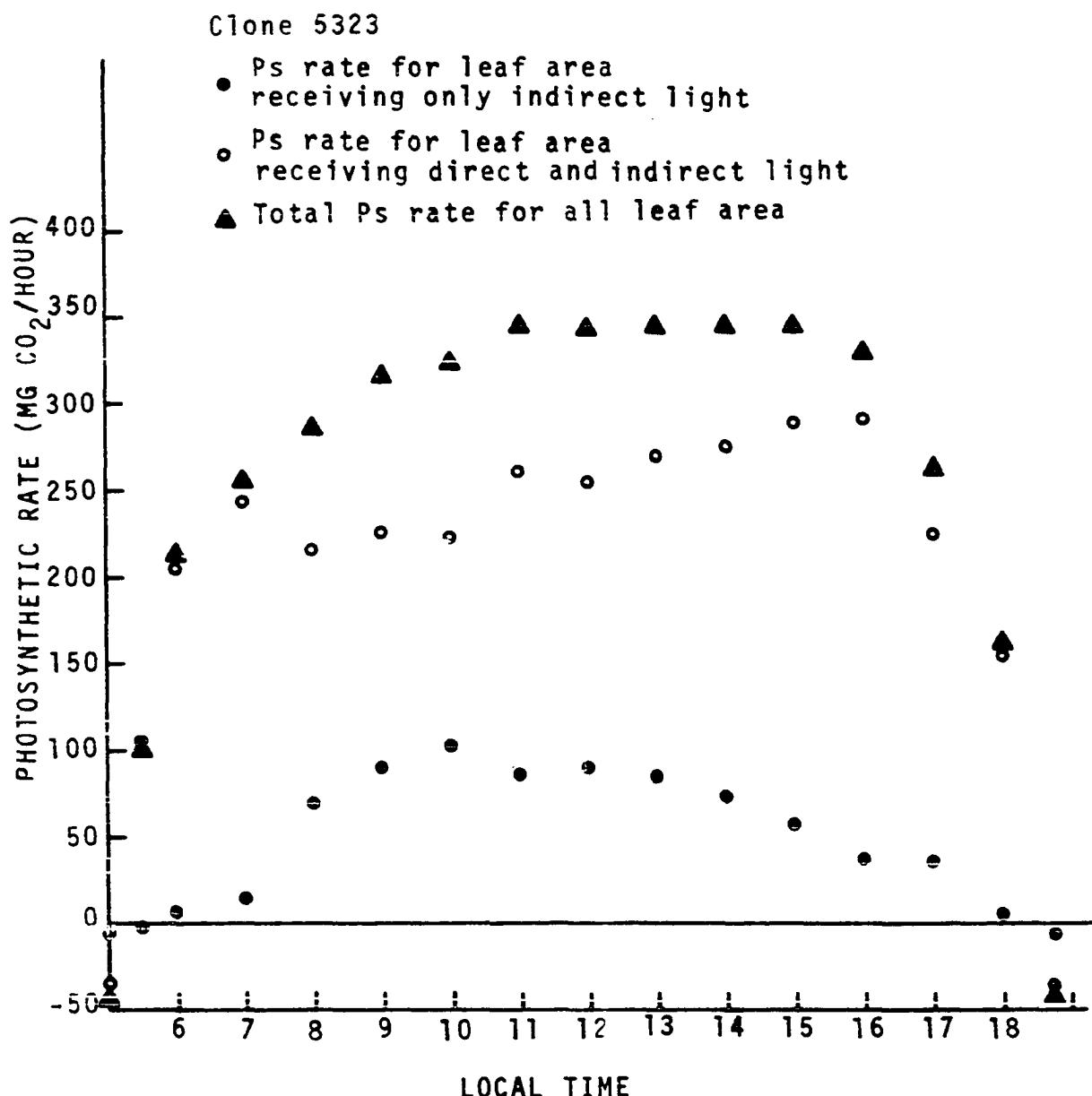


Figure 21. Photosynthetic rates of the whole crown for clone 5321 using the individual-leaf method illustrating the contributions of direct and indirect light to photosynthetic production

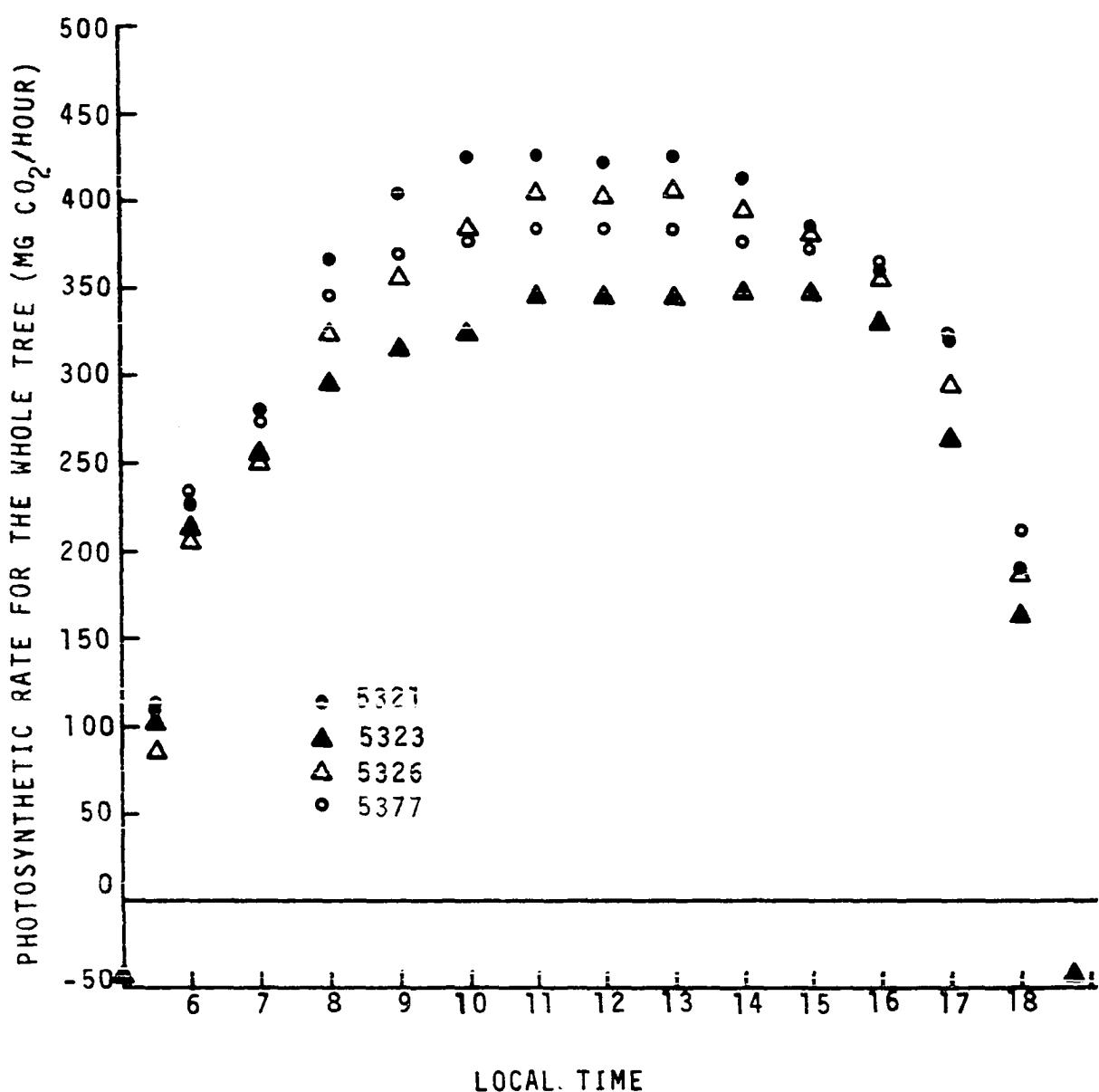


Figure 22. Photosynthetic rate throughout one day as calculated by the individual-leaf method for the four clones used in this study

the individual-leaf method. The values of total photosynthesis in mg CO₂ calculated using the individual-leaf method were 4555, 4305, 4263 and 3816 for clones 5321, 5377, 5326 and 5323 respectively. The clones ranked essentially the same when total photosynthesis was compared using the results from the other two methods of computation. The statistical reliability of these estimates is not known but the difference between the two extreme values is quite large, 739 mg CO₂ or 16.2% of value for clone 5321. Insufficient data were available to estimate complete photosynthetic response functions for each clone. As these data become available the simulations should be rerun incorporating the different photosynthetic response functions for each clone to determine the combined effects of crown geometry and photosynthetic response.

Effect of the angular orientation of leaves

Additional simulations were performed in which the leaf display parameters were changed. In these trials the data for clone 5377 were used. The angular orientations of the leaves were changed and photosynthetic rates were calculated as before. It was assumed that the projected leaf area in direct and indirect light was the same as before even though the angular orientations of the leaves were changed. The changes in the angular orientations of the leaves affected the projected leaf area and the angle of incidence of the intercepted radiation.

The results of some of these simulations are given in Table 3. The angular position of the leaves is described by the values of ϕ_3 and δ_3 as defined in Appendix B. These results indicate that changes in the angular orientation of leaves does not greatly affect total photosynthetic output.

Table 3. Total daily photosynthesis for crowns with leaves arranged by different angular orientation schemes

Angular Position of the Leaves			Total daily photosynthesis (mg CO ₂ fixed) for the three methods		
ϕ_3	δ_3	Description	Whole-Crown	Segmented-Crown	Individual-Leaf
0	90	Vertical leaves	5376	4304	4218
90	0	Vertical leaves	5396	4317	4370
90	45	Leaves at 45°	5143	4097	4300
45	90	Leaves at 45°	5147	4118	4238
90	90	Horizontal leaves	5677	4522	4567
135	90	Leaves at 45°	5207	4142	4303
90	135	Leaves at 45°	5212	4163	4358
Ave.	Ave.	Leaves in average position	5201	4163	4305

This agrees with the results given by Ross (1970) for plants with LAI of about two. Maximum photosynthetic output is obtained when leaves are horizontal, i.e. when $\phi_3=90^\circ$ and $\delta_3=90^\circ$. This result agrees with the results of Duncan et al. (1967) and Ross (1970) because the tree used in these simulations has a LAI of about two. These results in conjunction with the findings of Duncan et al. (1967) indicate that the higher total photosynthetic rates associated with plants with erect leaves is due to the increased penetration of light to lower portions of the crown rather

than a more favorable orientation of leaf material with respect to the sun's rays. As stated by Ross (1970) this is because "The diurnal path of the sun performs an integration over various inclinations and orientations, reducing the difference between the daily totals of photosynthesis in various crop architectures." The conclusions reached by Ross were based on the photosynthetic output of the whole crown and agree with the results presented in Table 3.

The general conclusion is that for low values of LAI leaf orientation has only a minor effect on total crown photosynthesis. With larger values of LAI higher photosynthetic rates for the whole crown are associated with more erect leaves. This is primarily due to increased penetration of light to lower portions of the crown rather than more favorable leaf orientation with respect to the sun. One interesting aspect remains to be considered. Does leaf orientation affect the photosynthetic output of individual leaves? That is, do different orientations of the leaves change the photosynthetic output of individual leaves within the crown while the total crown photosynthetic rate remains unchanged? These questions could not be answered by previously developed models since individual leaves were not explicitly identified. It is possible to consider this question using the individual-leaf model developed here.

The individual-leaf model estimates photosynthetic rate on an hourly basis for each individual leaf in the crown. These figures can be used to calculate the total daily photosynthetic production for each leaf on the tree. This was done for several of the leaf orientation schemes described in Table 3. The results for three such leaf orientation schemes are presented in Table 4. Note that as expected the very immature and

Table 4. Total daily photosynthetic production for each leaf under three different leaf orientation schemes

Leaf	Photosynthetic Output (mg CO ₂ fixed)		
	Scheme 1 ($\phi_3=90^\circ$, $\delta_3=45^\circ$)	Scheme 2 ($\phi_3=135^\circ$, $\delta_3=90^\circ$)	Scheme 3 (ϕ_3 , δ_3 in average position)
1	-3.939	-3.955	-3.940
2	-2.099	-1.778	-1.783
3	6.110	6.014	6.120
4	22.18	20.170	22.290
5	76.429	77.946	76.750
6	126.342	120.273	124.248
7	185.974	221.582	157.173
8	327.907	326.577	325.155
9	309.595	242.862	304.318
10	376.409	408.865	393.198
11	353.754	333.101	351.938
12	344.060	350.920	343.983
13	406.859	419.839	405.620
14	300.544	251.073	298.263
15	257.929	342.455	281.810
16	288.887	277.209	291.125
17	209.408	177.745	207.578
18	253.287	268.020	258.073
19	152.141	134.841	147.693
20	114.934	152.561	133.590
21	99.408	98.253	100.968
22	51.107	32.638	44.295
23	29.696	34.863	33.478
24	7.185	5.945	6.275
25	-4.030	-4.030	-4.030

senescent leaves contribute little to the total production of photosynthate. In fact, some of these leaves have a negative total contribution indicating that they respiration away some of the photosynthate produced by the rest of the crown.

In the three examples of different leaf orientation schemes given in Table 4 the total production of photosynthate was essentially identical as shown in the last column of Table 3. Hence the changes in the photosynthetic production of individual leaves from one scheme to another represent shifts in photosynthetic production within the crown rather than changes in the total photosynthetic production of the whole crown. The orientation scheme changed the productivity of some leaves dramatically but had little effect on other leaves. For example the production of leaf fifteen changed from 257.9 mg CO₂ under scheme 1 to 342.5 mg CO₂ under scheme 2. The production of other leaves, notably those in the top of the crown numbered one through six, changed very little from one scheme to another. These results indicate that crown geometry may affect the way a tree grows. It is known that different sections of the crown support different growth activities within the tree although these translocation patterns are far from well known (Larson and Gordon 1969). Therefore since leaf orientation schemes affect the level of photosynthate production for individual leaves this may well influence growth patterns by this indirect method of photosynthate redistribution. The problem is that photosynthate distribution and the mechanisms regulating this distribution are not well understood. Because of this, it is difficult to say whether changes in the crown geometry would result in a change in

photosynthate distribution, or whether some regulatory mechanism would prevent this from happening. It is, however, an intriguing topic that deserves further research particularly when more is known about photosynthate distribution and its regulation.

Position of the leaves also affects the rate at which photosynthate is produced throughout the day. In many cases where the total daily photosynthetic output of a leaf was not changed under different leaf orientation schemes the photosynthetic rates throughout the day may have changed considerably. For example under one scheme a leaf might have a high photosynthetic rate in the morning and a low photosynthetic rate in the afternoon. Under another scheme the reverse might be true but the total daily output of photosynthate under the two schemes might be about the same. This is not important when trees are considered by themselves as was done in this analysis. In a stand, however, a leaf orientation scheme for individual trees that produces high photosynthetic rates for low solar altitudes would be undesirable, because in a stand the level of shading by neighbors is higher for lower solar altitudes. Hence the most favorable crown geometry would result in the highest photosynthetic rates for high solar altitudes when shading by neighboring trees is minimal.

SUMMARY AND CONCLUSIONS

The objectives of this study were to develop a model for the interception of light by young poplar clones, to collect data and estimate those portions of the model which must be empirically determined and to use the model to simulate photosynthesis of individual trees.

The first model attempted to describe the interception of light on a purely analytical basis. With certain simplifying assumptions such a model was developed for light incident on the plant from directly overhead. Extension of the model to cases where the light source was not directly over the plant could not be made without the introduction of components that had to be empirically determined. However, this initial model did provide insights useful in the subsequent modeling efforts.

The second model was more empirical and was designed to accommodate incident light from any sky position. Empirical portions of the model were fitted using data collected from four hybrid poplar clones. A new photogrammetric technique was developed to measure the proportion of the projected areas of individual leaves exposed to radiation originating from four sky altitudes. This model incorporated several different concepts of light interception modeling. The model is constructed to deal only with the leaf areas rather than light intensities. I thus tried to separate the two complex problems of measuring radiation flux density and measuring the leaf area receiving this radiation. This permits the application of the same basic model to both direct and indirect light. Furthermore I chose as a basic unit the individual leaf, a basic biological unit of all crowns. This permitted realistic treatment of

problems not previously dealt with satisfactorily: the problem of different leaves having different photosynthetic responses, the problem of the nonlinearity of the photosynthetic response functions and the problem of the cosine law which governs radiation incidence and absorption.

The purpose of the model was to simulate photosynthesis. To study this, a crown consisting of twenty-five leaves was used. The dimensions of these leaves were actually measured values taken from one tree. The radiation data were the actual data recorded at Ames, Iowa for August 12, 1973. The model estimated photosynthetic rate on an hourly basis. Separate estimates were made for the leaf area receiving direct and indirect radiation. Thus the relative contributions of direct and indirect light to the production of photosynthate could be evaluated. As expected direct light was responsible for most of the photosynthetic activity. The role of diffuse light, while minor compared to direct light, was important and could not be ignored without the introduction of large errors.

Several problems have always arisen in this type of modeling research. First is the fact that leaves of different ages or positions in the crown have different photosynthetic response functions. Furthermore, these response functions are generally nonlinear. Another problem is that the absorption of radiation is dependent on the angle of incidence of the radiation. To demonstrate the difficulties that arise when these problems are not properly handled, the crown was considered in three ways. The first way treated the crown as a whole unit of identical and nondistinguishable leaf material. The second method viewed the crown as consisting of layers, in this case three layers, an approach often used in the

literature. The third method considered the crown to be an aggregate of individual leaves. Results indicated that sizable errors can be caused by not accounting for the fact that different leaves respond differently to varying light intensities. Furthermore the problems caused by the nonlinearity of the light response curve and the cosine law of radiation absorption could only be satisfactorily solved when the basic modeling unit of leaf area was small, i.e., an individual leaf. This research demonstrated that these problems could be reasonably and realistically solved by using the individual-leaf model.

With the models developed in this study the four clones were compared for photosynthetic productivity. The same photosynthetic response function was used for all clones so that differences between clones would only result from differences in leaf display. The largest difference between two clones was a difference of 739 mg CO₂ in total daily photosynthetic production. These differences may be increased or decreased when the simulations are rerun using photosynthetic response functions that properly reflect clonal differences.

The individual leaf model was used to simulate photosynthesis under various assumptions about crown geometry. Results indicated that for this amount of leaf area leaf orientation had little effect on total photosynthesis. In these simulations the shading regime was assumed not to change with changes in leaf orientation. In the model used by Duncan et al. (1967) changes in leaf orientation changed both the angle of light reception and the shading regime. In reviewing their results I found that their model predicted small differences in photosynthetic rates for various leaf angles when LAI was small. Large differences were predicted

for various leaf angles when the LAI was large. These results in conjunction with the results of my study indicate that erect leaves are important because they allow the penetration of light to lower portions of the crown, not because erect leaves are more efficient receptors of radiation. This is probably because of the physical integration performed by the diurnal path of the sun over various leaf orientations as stated by Ross (1970). These results indicate that clonal differences in photosynthetic rate due to leaf display can only be detected on larger plants, i.e., high values of LAI. Clonal differences in photosynthetic response were not included in these results. These should be included at a time when complete photosynthetic response curves are available for the clones.

Leaf orientation did affect the photosynthetic rate of individual leaves within the crown. This might result in different growth characteristics because of the redistribution of photosynthate resulting from shifts in the production of photosynthate between leaves within the crown. In most cases changes in leaf orientations did cause shifts in the time of day when high and low photosynthetic rates occurred.

The main criticism of this modeling research is the totally empirical estimation of the leaf area exposed to radiation. This empirical approach to the shading regime limits the model to the crown geometry configurations used in the estimation of the parameters. The model cannot be used to represent realistically the shading regimes of tree crowns with a different leaf display. The model would be significantly improved if the mutual shading of leaves could be assessed using an analytical approach.

The model as presented here could be extended in several ways. It could be extended to predict photosynthesis on successive days or for a whole growing season. Stochastic elements could be introduced in the model, particularly in determining leaf angle or radiation levels to correspond more closely with what may actually happen in a real biological system. Inclusion of reasonable stochastic elements coupled with numerous computer trials could provide valuable information on the variability of photosynthetic production.

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APPENDIX A. TECHNICAL DEVELOPMENT OF MODEL I

The crown of a very simple tree is assumed to consist of n identical leaves attached to a straight vertical stem of specified height. The leaves are attached to the stem by petioles of specified length. The phyllotactic characteristics of the tree are described by the fraction e/f . Leaves are assumed to be horizontal and irradiated by direct light which is incident in a direction parallel to the vertical stem. Leaf shape is assumed to be an isosceles triangle with base w and length l as illustrated in Figure 23.

The angle between any two adjacent petioles is α_1 where $\alpha_1 = (360^\circ)e/f$. The angles between petioles of leaves that are not adjacent can also be calculated on the basis of phyllotactic characteristics. If petiole length is constant, say r_1 , then a relationship can be derived between the dimensions of the leaves and the angle between petioles which will discriminate whether or not one leaf will shade another leaf. Figure 24 shows the critical angle for which there occurs no shading of leaf 2 by leaf 1, shading would only occur if α_1 was less than the critical angle shown.

The derivation of this critical angle follows.

$$\tan\left(\frac{\alpha_2}{2}\right) = \frac{w/2}{r_1}$$

Hence the critical angle, denoted α_2^* , is given by

$$\alpha_2^* = 2\tan^{-1}\left(\frac{w}{2r_1}\right) \quad (15)$$

So if $\alpha_2 < 2\tan^{-1}\left(\frac{w}{2r_1}\right)$ then leaf 1 will shade leaf 2. If $\alpha_2 \geq 2\tan^{-1}\left(\frac{w}{2r_1}\right)$ then leaf 1 will not shade leaf 2.

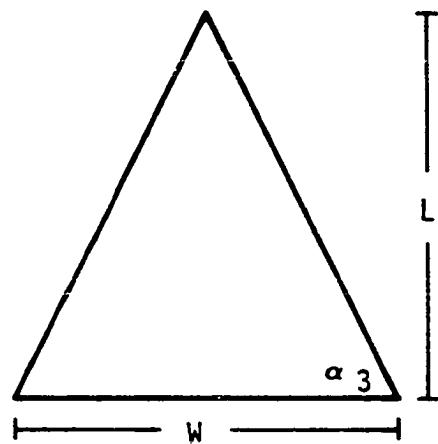


Figure 23. Assumed shape of an ideal leaf

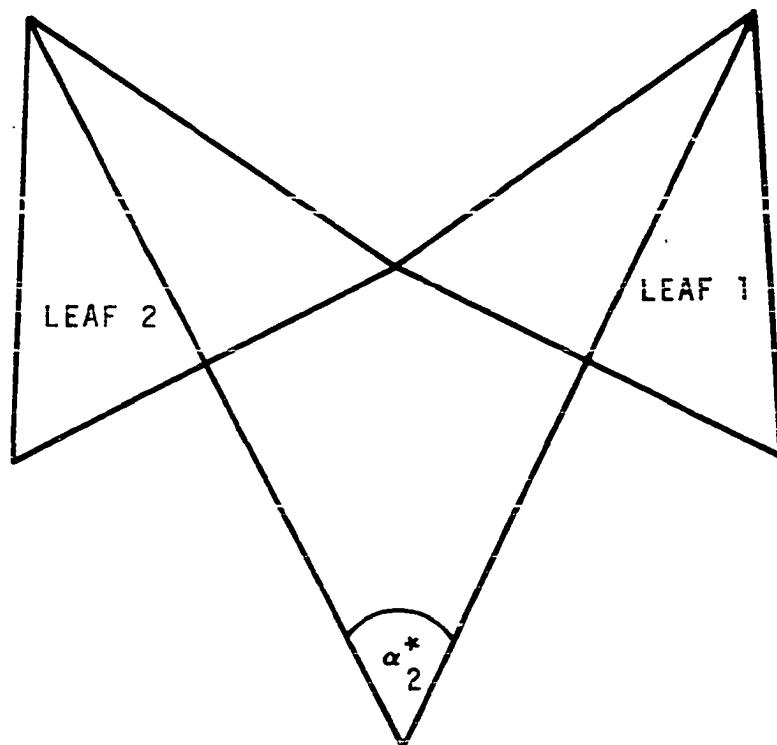


Figure 24. Two ideal leaves separated by the critical angle α_2^*

If $\alpha_2 < 2\tan^{-1}(\frac{w}{2r_1})$ then the area of shade on leaf 2 caused by leaf 1 is in the shape of a quadrilateral as illustrated in Figure 25. The area of shade is equal to the area that the two leaves overlap. This is the area of the quadrilateral, denoted A_1 , which is

$$A_1 = 1/2 (c_1 + c_2) (d_1 + d_2).$$

This area is calculated as follows.

Triangle (Tr) OAB is similar to Tr ABD.

Tr ABD is similar to Tr DEF.

Tr OAB is similar to Tr DEF.

$$\text{Now } \overline{OB} = r_1 \cos (\alpha_2/2)$$

$$\text{and } \overline{DE} = w/2 - AD$$

$$\text{and } \overline{AB} = r_1 \sin (\alpha_2/2).$$

By similarity, angle BAD equals $\alpha_2/2$ and hence

$$\overline{AD} = \overline{AB}/\cos(\alpha_2/2).$$

Also

$$\overline{AD} = r_1 \frac{\sin (\alpha_2/2)}{\cos (\alpha_2/2)}$$

so

$$\overline{DE} = w/2 - r_1 \tan (\alpha_2/2) \text{ by substitution.}$$

$$\text{Now } c_1 = \overline{DE} \sin (\frac{\alpha_2}{2}).$$

$$\text{Hence } c_1 = [\frac{w}{2} - r_1 \tan(\frac{\alpha_2}{2})] \sin (\frac{\alpha_2}{2}).$$

$$\begin{aligned} \text{Also } d_1 &= d_2 = \overline{DE} \cos (\frac{\alpha_2}{2}) \\ &= [\frac{w}{2} - r_1 \tan(\frac{\alpha_2}{2})] \cos (\frac{\alpha_2}{2}). \end{aligned}$$

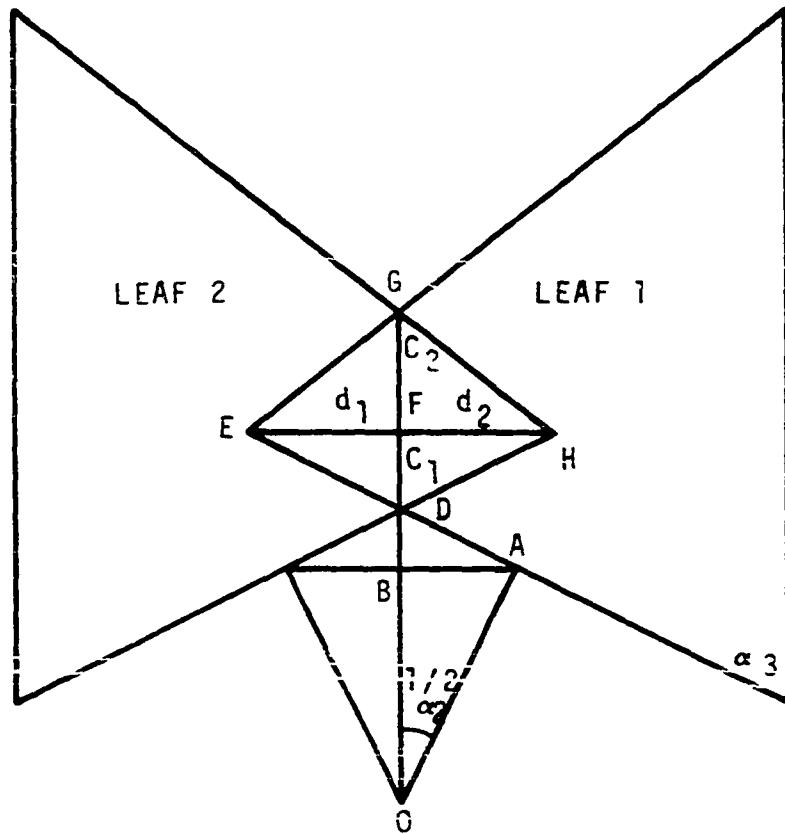


Figure 25. Illustration of the area of leaf 2 shaded by leaf 1 when the angular separation of the leaves is less than the critical angle

$$\text{Now } \tan(\alpha_3 - \frac{\alpha_2}{2}) = \frac{c_2}{d_1}$$

$$\text{so } c_2 = d_1 \tan(\alpha_3 - \frac{\alpha_2}{2}).$$

$$\begin{aligned} \text{Now } d_1 + d_2 &= 2[\frac{w}{2} - r_1 \tan(\frac{\alpha_2}{2})] \cos(\frac{\alpha_2}{2}) \\ &= [w - 2r_1 \tan(\frac{\alpha_2}{2})] \cos(\frac{\alpha_2}{2}) \\ &= w \cos(\frac{\alpha_2}{2}) - 2r_1 \sin(\frac{\alpha_2}{2}). \end{aligned}$$

$$\begin{aligned} \text{And } c_1 + c_2 &= [\frac{w}{2} - r_1 \tan(\frac{\alpha_2}{2})] \sin(\frac{\alpha_2}{2}) \\ &\quad + [\frac{w}{2} - r_1 \tan(\frac{\alpha_2}{2})] \cos(\frac{\alpha_2}{2}) \tan(\alpha_3 - \frac{\alpha_2}{2}) \\ &= [\frac{w}{2} - r_1 \tan(\frac{\alpha_2}{2})] [\sin(\frac{\alpha_2}{2}) + \cos(\frac{\alpha_2}{2}) \tan(\alpha_3 - \frac{\alpha_2}{2})]. \end{aligned}$$

So the area of the quadrilateral $= A_1 = 1/2(c_1 + c_2)(d_1 + d_2)$.

$$\begin{aligned} A_1 &= 1/2[\frac{w}{2} - r_1 \tan(\frac{\alpha_2}{2})][\sin(\frac{\alpha_2}{2}) + \cos(\frac{\alpha_2}{2}) \tan(\alpha_3 - \frac{\alpha_2}{2})] \\ &\quad \cdot 2[\frac{w}{2} - r_1 \tan(\frac{\alpha_2}{2})] \cos(\frac{\alpha_2}{2}) \\ A_1 &= [\frac{w}{2} - r_1 \tan(\frac{\alpha_2}{2})]^2 [\sin(\frac{\alpha_2}{2}) \cos(\frac{\alpha_2}{2}) + \cos^2(\frac{\alpha_2}{2}) \tan(\alpha_3 - \frac{\alpha_2}{2})] \quad (16) \end{aligned}$$

Assuming direct overhead light the maximum number of leaves that can receive direct radiation is f . The calculation of the angle between any two leaves is possible if e/f is known. Using Equation 16, the area of shade for those leaves whose angular separation is less than the critical angle α_2^* can be calculated. Hence, the area of leaves receiving direct radiation can be calculated.

For example, for Populus $e/f = 2/5$. Ideally, the angle between successive petioles is $360^\circ (2/5) = 144^\circ$. Suppose for convenience that the 0° is taken as the direction in which the first leaf is pointed. Moving in a counter-clockwise direction, leaf two lies at 144° , leaf three at 288° , leaf four at 72° , leaf five at 216° and leaf six at 0° , directly beneath leaf 1. So the smallest angle between any two leaves can be calculated. These angles can be compared to the critical angle to determine which leaves are shaded and this shaded area can be calculated using Equation 16. Hence, the total leaf area receiving direct radiation can be calculated.

In general, of course, leaves will not be horizontal. Leaves are usually tilted at some characteristic angle. Relaxing the assumption of horizontal leaves, it is now assumed that all leaves are tilted from the horizontal by an angle denoted by γ . All leaves are tilted in the same direction and the rotation occurs on leaf axis 1. Under this assumption, the shape of the projected area of any individual leaf onto a horizontal plane is an isosceles triangle. The dimensions of the projected leaf area are l , w' and α_3' where $w' = w \cos \gamma$ and $\alpha_3' = \tan^{-1} (2(1/w'))$.

The theory developed before now applies to this case. The angles between petioles have not changed, however the critical angle for shading of leaves has changed. This new critical angle is used to determine which leaves are shaded. After it is determined that one leaf shades another, the area of this shade must be calculated. If we assume that both leaves are projected onto a horizontal plane that lies between the two leaves then we have essentially the same problem as was dealt with earlier. The

intersection of the projected leaf areas will be a quadrilateral whose area can be calculated using Equation 16 after w and α_3 have been replaced by w' and α_3' respectively. The actual area on the leaf that is in shade is $A_{ACT} = A_1 / \cos \gamma$ where A_1 is the result of Equation 16 using w' and α_3' instead of w and α_3 . So again we can calculate the leaf area that receives direct solar radiation from overhead.

Other assumptions could be relaxed and the model would still be solvable. For example, petiole length could be allowed to be different for different sets of leaves. Then portions of leaves below the first two spirals would be exposed to direct sunlight. This area of exposure to direct light could be calculated by finding the difference in areas of two superimposed triangles. It may also be possible to allow leaf size to change for different parts of the crown.

One interesting extension of the model is to allow the leaf shape to be a quadrilateral. This is illustrated in Figure 26. Derivation of the critical angle for determining whether two leaves shade one another is similar to the derivation appropriate for triangular leaves. The area of leaf 2 shaded by leaf 1 as shown in Figure 26 can be calculated. The following angles are assumed known:

$$\text{angle } AOB = 1/2 \alpha_2,$$

$$\text{angle } DEH = \text{angle } EGH = \alpha_3 \text{ and}$$

$$\text{angle } DAK = \delta_1.$$

Also known are the lengths of line segments $\overline{QA} = r_1$ and $\overline{EK} = 1/2 w$.

Then

$$\overline{OB} = r_1 \cos (1/2 \alpha_2).$$

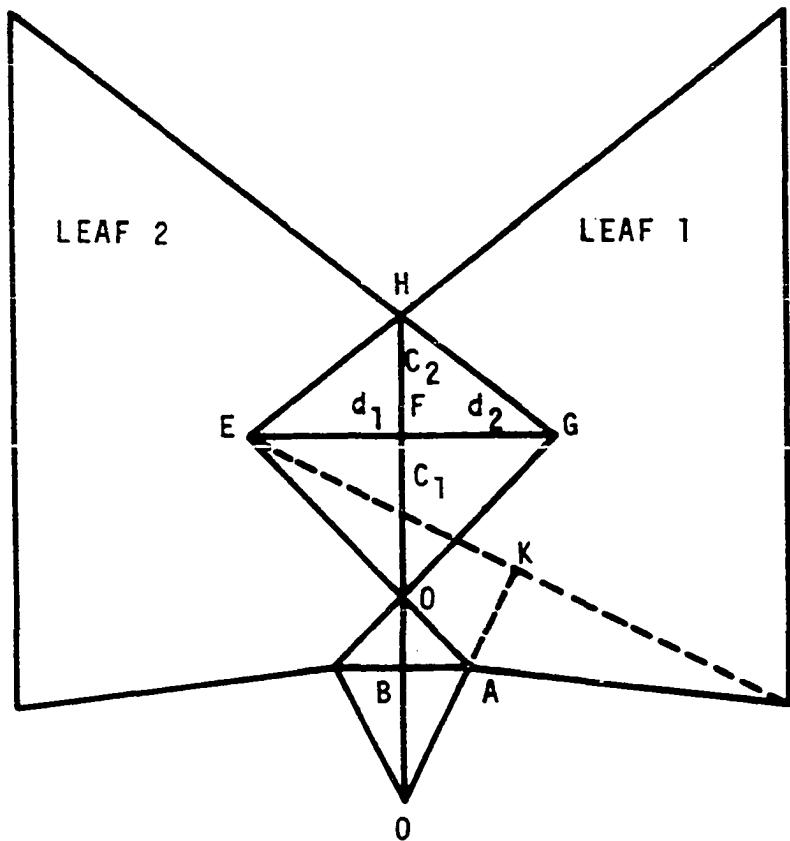


Figure 26. Area of leaf 2 shaded by leaf 1 under the more general assumption of quadrilateral leaf shape

$$\overline{AB} = r_1 \sin (1/2 \alpha_2).$$

$$\begin{aligned} \text{Now } \text{angle } BAD &= \delta_2 = 180^\circ - \delta_1 - (90^\circ - 1/2 \alpha_2) \\ &= 90^\circ - \delta_1 + 1/2 \alpha_2. \end{aligned}$$

$$\text{And } \overline{AD} = \overline{AB}/\cos \delta_2.$$

$$\text{Angle } BDA = \delta_3 = 90^\circ - \delta_2 = \delta_1 - 1/2 \alpha_2. \quad (17)$$

$$\overline{DE} = \overline{AE} - \overline{AD}$$

$$= (w/2 \sin \delta_1) - r_1 \sin (1/2 \alpha_2)/\cos \delta_2. \quad (18)$$

Then $d_1 = d_2 = \overline{DE} \sin \delta_3$ (19)

where δ_3 and \overline{DE} are given by Equations 17 and 18 respectively.

Also $c_1 = \overline{DE} \cos \delta_3$, (20)

angle HEF = $\alpha_3 - \delta_2$ and

$$\tan(\alpha_3 - \delta_2) = c_2/d_1.$$

So $c_2 = d_1 \tan(\alpha_3 - \delta_2)$. (21)

The area of shading on leaf 2 by leaf 1 is then

$$A = 1/2 (d_1 + d_2) (c_1 + c_2)$$

where d_1 and d_2 are given by Equation 19 and c_1 and c_2 are given by Equations 20 and 21 respectively.

Thus it is possible to relax some of the restrictive assumptions without complicating the results beyond solvability.

APPENDIX B. TECHNICAL DEVELOPMENT OF MODEL II

Consider a leaf of LPA i. Consider, also the two vectors

$$\mathbf{v}_1 = \cos \phi_1 \mathbf{i} + \cos \phi_2 \mathbf{j} + \cos \phi_3 \mathbf{k}$$

and

$$\mathbf{v}_2 = \cos \delta_1 \mathbf{i} + \cos \delta_2 \mathbf{j} + \cos \delta_3 \mathbf{k}.$$

\mathbf{v}_1 is directed outward from the plant along leaf axis 1. ϕ_1 , ϕ_2 and ϕ_3 are the angles between \mathbf{v}_1 and the positive x-, y- and z-axes respectively.

Note that the tree's main stem is coincident with the positive z-axis.

\mathbf{v}_2 lies in the plane of the leaf and is directed in the general direction of leaf axis 2. In particular \mathbf{v}_2 is directed such that the projection of \mathbf{v}_2 in the x-y plane is perpendicular to the projection of \mathbf{v}_1 in the x-y plane. δ_1 , δ_2 and δ_3 are the angles between \mathbf{v}_2 and the positive x-, y- and z-axes respectively. \mathbf{v}_1 and \mathbf{v}_2 are important since they are used to construct a normal vector to the leaf's surface.

First consider the case where the leaf is horizontal along the leaf axis 2. This is the case considered by Reeve (1960). This case is considered here since the results I obtained are slightly different from those obtained by Reeve (1960). The results obtained by Reeve (1960) were also reprinted by Duncan et al. (1967). Consider the coordinate system GXYZ where GX is due east, OY is due south and OZ is vertically upward. It is assumed that axis 1 of the leaf being considered makes an angle ϕ_3 with the positive z-axis and that this axis 1 is point θ degrees south of east, where θ can have any value between 0° and 360° . It is also assumed that axis 2 of the leaf being considered makes an angle of

90° with the positive z-axis, that is $\delta_3 = 90^\circ$. Hence,

$$\cos \delta_3 = \cos 90^\circ = 0$$

The angle θ is determined in the case of Populus by phyllotaxy and the LPA of the leaf under consideration in conjunction with the orientation of the plant with respect to the coordinate system.

Now $V_1 = \cos \theta \sin \phi_3 i + \sin \theta \sin \phi_3 j + \cos \phi_3 k$. In this case V_2 is perpendicular to the positive z-axis and V_1 . Hence, $V_2 = k \times V_1$, where \times represents the vector product, so that $V_2 = -\sin \theta \sin \phi_3 i + \cos \theta \sin \phi_3 j + 0 k$. Normalizing vector V_2 to unit length results in

$$V_2 = -\sin \theta i + \cos \theta j + 0 k$$

A vector normal to the leaf's surface area can be calculated as

$$\begin{aligned} N_1 &= V_2 \times V_1 \\ &= \cos \theta \cos \phi_3 i + \sin \theta \cos \phi_3 j - \sin \phi_3 k \end{aligned}$$

In Reeve's notation $\theta = \alpha$

$$\phi_3 = 90 - \alpha \quad \sin \phi_3 = \sin (90 - \alpha) = \cos \alpha$$

$$\cos \phi_3 = \cos (90 - \alpha) = \sin \alpha$$

so for comparison I get

$$N_1 = \cos \theta \sin \alpha i + \sin \theta \sin \alpha j = \cos \alpha k$$

whereas Reeve calculated as the direction cosines of a normal vector to the leaf ($\sin \alpha \sin \theta, -\sin \alpha \cos \theta, \cos \alpha$), which differs from my result by a minus sign on one term.

The more general case is when leaf axis 2 is not assumed to be horizontal. The leaf is allowed to be rotated on axis 1 through some specified angle. In this case V_1 is the same as calculated in the simpler case just previously considered. So

$$\mathbf{v}_1 = \cos \theta \sin \phi_3 \mathbf{i} + \sin \theta \sin \phi_3 \mathbf{j} + \cos \phi_3 \mathbf{k}.$$

Now assuming that the vector \mathbf{v}_2 makes an angle δ_3 with the positive z-axis. So \mathbf{v}_2 lies in the plane of the leaf and makes an angle δ_3 with the positive z-axis. The projections of \mathbf{v}_1 and \mathbf{v}_2 onto the x-y plane are at right angles. Similar to the derivation for \mathbf{v}_1 we derive

$$\mathbf{v}_2 = \sin \theta \sin \delta_3 \mathbf{i} - \cos \theta \sin \delta_3 \mathbf{j} + \cos \delta_3 \mathbf{k}$$

a normal vector to the leaf is

$$\begin{aligned} \mathbf{N} = \mathbf{v}_1 \times \mathbf{v}_2 &= (\sin \theta \sin \phi_3 \cos \delta_3 + \cos \theta \cos \phi_3 \sin \delta_3) \mathbf{i} \\ &\quad + (\sin \theta \cos \phi_3 \sin \delta_3 - \cos \theta \sin \phi_3 \cos \delta_3) \mathbf{j} \\ &\quad - (\sin \phi_3 \sin \delta_3) \mathbf{k} \end{aligned}$$

The magnitude of both vectors \mathbf{v}_1 and \mathbf{v}_2 are one. Hence the angle, θ_3 , between \mathbf{v}_1 and \mathbf{v}_2 in the plane of the leaf can be calculated as

$$\theta_3 = \cos^{-1} (\cos \phi_3 \cos \delta_3)$$

or

$$\theta_3 = \sin^{-1} (1 - \cos^2 \phi_3 \cos^2 \delta_3)^{1/2}.$$

Now the quantity of ultimate interest is the projection of the leaf area in question onto a plane normal to the sun's rays. So \mathbf{N} is normalized to unit length. Next a unit vector, \mathbf{N}_s , is constructed directed toward the sun, parallel to the sun's rays. The projected leaf area in which we are interested is the positive value of

$$A \mathbf{N} \cdot \mathbf{N}_s$$

where A is the area of the leaf. This is the area of the leaf projected onto a plane normal to the sun's rays. The actual leaf area receiving radiation is $A \mathbf{N} \cdot \mathbf{N}_s \cos \theta_4$ where θ_4 is the angle between \mathbf{N} , the normal

to the leaf's surface and N_s , the vector representing the sun's rays. The angle of this incident radiation is then θ_4 , where θ_4 is determined by

$$\theta_4 = \cos^{-1} (N \cdot N_s)$$

since both N and N_s have magnitudes equal to one.

APPENDIX C. NAME, PARENTAGE, SOURCES AND REFERENCE NUMBERS FOR THE HYBRID
POPLAR CLONES INCLUDED IN THIS STUDY

North Central For. Expt. Station number	Name and Parentage	Common name or local identification name	Recent source (Original source)
5321	<u>Populus x euramericana</u> (Dode) Guinier ¹	"Negrito de Granada"	Maple, Ontario (Spain)
5323	<u>Populus x euramericana</u> (Dode) Guinier	"Canada Blanc"	Maple, Ontario (Italy)
5326	<u>Populus x euramericana</u> (Dode) Guinier	"Eugenii"	Maple, Ontario (France)
5377	<u>Populus x euramericana</u> (Dode) Guinier	"Wisconsin No. 5"	Rhinelander, Wisconsin

¹ Populus x euramericana (Dode) Guinier = Populus deltoides Marsh. x Populus nigra L.

APPENDIX D. DESCRIPTION OF METHODS

This appendix describes the methods developed for obtaining the data used in this study. The main method developed was a photographic technique used to assess the amount of leaf area receiving radiation for a given sky position. In this technique photographs are taken of the individual trees with the camera placed to simulate the view from a specified sky position. The film then acts as a reference plane for this sky position and records the projected leaf area that is visible from this position. The projected leaf area of individual leaves receiving radiation from this sky position can be determined from the photograph.

To estimate the proportions of interest, P_T , P_I , P_M , P_S and the P_i 's, the area of each leaf must be known or estimated. To this end the length and width of each leaf was measured to the nearest one-tenth cm. The area of each leaf was determined by indirect estimation using a prediction equation of the form

$$\hat{A} = \hat{\beta}_0 + \hat{\beta}_1 LW + \hat{\beta}_2 W^2 \quad (22)$$

where \hat{A} is the predicted area of the leaf in cm^2 ,

L is the length of the leaf in cm and

W is the width of the leaf in cm.

Table 5 gives the parameter estimates, the standard errors of the estimated parameters and the R^2 statistics for the fitted equations for each of the four clones. The parameters were estimated using data from plants grown in controlled environment chambers and were tested for suitability for use as prediction equations for plant material grown in the greenhouse.

Table 5. Coefficients, standard errors of the coefficients, number of observations and values of R^2 for fitting the model given by Equation 22

Clone	Coefficient	SE ^a	n ^b	R^2
5321	0.50868	0.52286	37	0.9972
	0.54004	0.03319		
	0.09037	0.03587		
5323	0.43073	1.05231	40	0.9977
	0.52406	0.05146		
	0.14628	0.04666		
5236	-0.07917	1.32275	39	0.9953
	0.27336	0.04602		
	0.38605	0.04257		
5377	1.26054	0.64691	50	0.9975
	0.29245	0.02778		
	0.36252	0.02795		

^aSE = Standard error of the coefficient.

^b n = Number of observations.

Four photographs, each at a different angular altitude, were taken of each tree. Each photograph was taken with the tree at the same orientation with respect to the direction of the camera. Photograph type 1 was taken with the camera directly over the plant and corresponds to the case when the sun is directly over the tree. Photograph type 2 was taken with the line of sight of the camera making an angle of 30° with the main stem of the plant and corresponds to a sun altitude of 60° . Photograph type 3 was taken so that the angle between the main stem of the plant and the

line of sight of the camera was 60° and corresponds to a sun altitude of 30°. Photograph type 4 was taken from the horizontal and corresponds to a sun altitude of 0°.

A background marked with a standard grid, placed at the base of each tree, facilitated the determination of the scale of the photographs. For use in interpreting the photographs, vertical distance from the background to each leaf was measured to the nearest cm.

Photographs were taken using a 35 mm Pentax camera with black and white film. Negatives were used to make eight by ten inch positive prints. Each leaf was labeled by LPA on the enlarged prints and the area of each leaf visible in the photograph was measured by planimetry to the nearest one-tenth cm^2 . Measured leaf area was converted to actual leaf area using the scale appropriate for the photograph and leaf under consideration.

Analysis of Photographs

Photograph types 1 and 4

Photograph types 1 and 4 can be analyzed using the methods appropriate for standard vertical photography. The only problem is the determination of scale of each leaf as related to the height of the leaf from the background. The standard formula for determination of scale is

$$RF = 1/x_n = id/(H-h) \quad (23)$$

where RF is the representative fraction which is the ratio of distance as measured in the photograph to actual distance,
 x_n is the actual distance associated with one unit of distance in the photograph,

id is the image distance,

H is the height of the lens above the background and

h is the height of the leaf above the background.

Solving for x_n in Equation 23 yields

$$x_n = (H-h)/id. \quad (24)$$

The image distance can be calculated using the thin lens formula which is

$$1/id = (od - f)/(od)(f) \quad (25)$$

where id is image distance,

od is object distance and

f is the focal length of the camera.

Now let $x_{B(neg)}$ denote the value of x_n at the base of the tree in the actual film negative. $x_{B(neg)}$ is calculated by setting $od = H$ in Equation 25 and substituting into Equation 24 with $h = 0$. This yields

$$x_{B(neg)} = (H-f)/f. \quad (26)$$

Let $x_{B(enl)}$ denote the value of x_n at the base of the tree in the enlarged photograph. This is determined empirically from measurements in the photograph of the grid in the background. Then, taking into account the enlargement, the value of x_n for leaf i , denoted x_i , if that leaf is at the height h_i above the background is

$$x_i = \frac{H-h_i}{id} \cdot \frac{x_{B(enl)}}{x_{B(neg)}} \quad (27)$$

Substituting into Equation 27 for id , from Equation 25 with $od = H-h_1$, and $x_{B(neg)}$ from Equation 26 yields

$$x_i = \frac{(H-h_i-f) x_{B(enl)}}{(H-f)} \quad (28)$$

So if M_i is the leaf area measured on the photograph for leaf i then the actual area is

$$AC_i = M_i x_i^2 . \quad (29)$$

Type 4 photographs are taken with the line of sight of the camera horizontal. In this case the formulas for vertical photography are valid since the photographed plant is parallel to the film and lens. The scale was determined empirically from each enlarged photograph by measuring a standard length that was placed at the base of the plant when the photograph was taken. Minor changes in scale caused by a leaf being nearer or farther away from the camera than the main stem were ignored.

Photograph types 2 and 3

Since photographs of type 2 and 3 are oblique photographs, determination of scale is difficult for objects at varying heights. Hence, the scale for these photographs was determined empirically. Each photograph was taken with the camera at exactly the same horizontal and vertical position with respect to the plant. A different position was required for trees of height 90 cm. as opposed to trees of height 60 cm. and 75 cm. This insured that the film negative was the same scale for all photographs within a given height class. A standard photograph was used to determine the change in scale as a function of height along the stem of the plant. The standard consisted of a thin board positioned in place of the stem with cross pieces placed at heights of 0 cm, 20 cm, 40 cm, 60 cm and 80 cm. Twenty cm lengths were marked on each cross piece. Simple linear regression was used to relate the length of the cross pieces as measured from

the photograph to height in the photograph. The regressions were of the form

$$MD_i = \alpha_0 + \alpha_1 h_i + e_i \quad (30)$$

where MD_i is the length as measured from the photograph of the 20 cm long cross piece at height h_i and h_i is the height of the cross piece.

By simple proportionality the scale at height h in any photograph can be determined given the scale at the base of the tree. So

$$x_{ph} = (x_{p0})(x_{sh})/x_{s0} \quad (31)$$

where x_{ph} is the scale at height h in photograph p ,
 x_{p0} is the scale at base ($h=0$) in photograph p ,
 x_{sh} is the scale at height h in the standard photograph and
 x_{s0} is the scale at base ($h=0$) in the standard photograph.

Now scale is just the ratio of actual distance to photograph distance, so using the fitted form of Equation 30

$$x_{ph} = (x_{p0})(\hat{\alpha}_0)/(\hat{\alpha}_0 + \hat{\alpha}_1 h) \quad (32)$$

since the actual distance in the standard photographs were all 20 cm. If M_i is the measured area from the photograph for leaf i then the actual area is

$$AC_i = M_i x_{ph_i}^2. \quad (33)$$

where h_i is the height of leaf i .