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A photosynthate allocation model for tree growth

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A photosynthate allocation model

for tree growth

by

Lawrence Charles Promnitz

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INTRODUCTION

Currently, much attention is being given to the concept of intensive silvicultural systems as a means for attaining high production rates of wood fiber. The concept usually includes management practices such as the fertilization and irrigation of densely spaced, rapidly growing hardwood species for coppice rotations of three to seven years (McAlpine et al., 1966).

Little is known, however, about the economic feasibility of such systems or the biological responses of trees grown under them. Traditionally, growth and yield models of forest stands have placed primary emphasis on predictive capabilities for older stands through the use of variables such as site index and basal area to describe site quality and stand density. Definitions of growth generally have been restricted to changes in bole volume while other aspects of tree growth have been slighted or ignored.

If intensive silvicultural systems are to be analyzed, complete response functions for young stands will be needed. It will be necessary to define variables that will accurately describe the environment in enough detail so that effects of changes in nutrient and moisture regimes on growth can be analyzed and evaluated. In addition, the variables and resulting response functions should be based on biological principles rather than empirical relationships to accurately predict the effects of stand treatment and manipulation.

If the stand is the system to be dealt with, it will be necessary to define the components of this system so that the economic questions of production can be answered without compromising the biological identity and significance of growth variables. Crop systems have been viewed in many ways, and each viewpoint has its own shortcomings and advantages with regard to economic usefulness and biological accuracy. For example, the modeling efforts of Duncan et al. (1967) have led to the conceptualization of the principal components of a crop system as the various levels of the foliage canopy. Thus, the action and interaction of these levels in the interception of light and the production of photosynthate lead to the end results of growth and yield as defined by total dry-matter production.

In a crop of trees, however, growth of the stem, crown, and roots have differing degrees of physiological importance and economic impact. Thus, the individual tree can be visualized as being a logical and biologically significant subsystem, and the components of this subsystem could be the aspects of individual tree growth (Figure 1). Many of the previous workers using this type of conceptualization based their examination of growth on strictly empirical relationships. For example, Mitchell (1969) simulated the growth of even-aged stands of white spruce by considering the individual trees and the relationships that exist among

Figure 1. A stand viewed in a system context.

```
                            Stand


      Other Trees      Individual Tree      Other Factors



         Crown                Bole                Roots


Branch Growth          Stem Elongation      Root Elongation
Leaf Development        Stem Thickening      Root Thickening
Competitive Status     Competitive Status   Competitive Status
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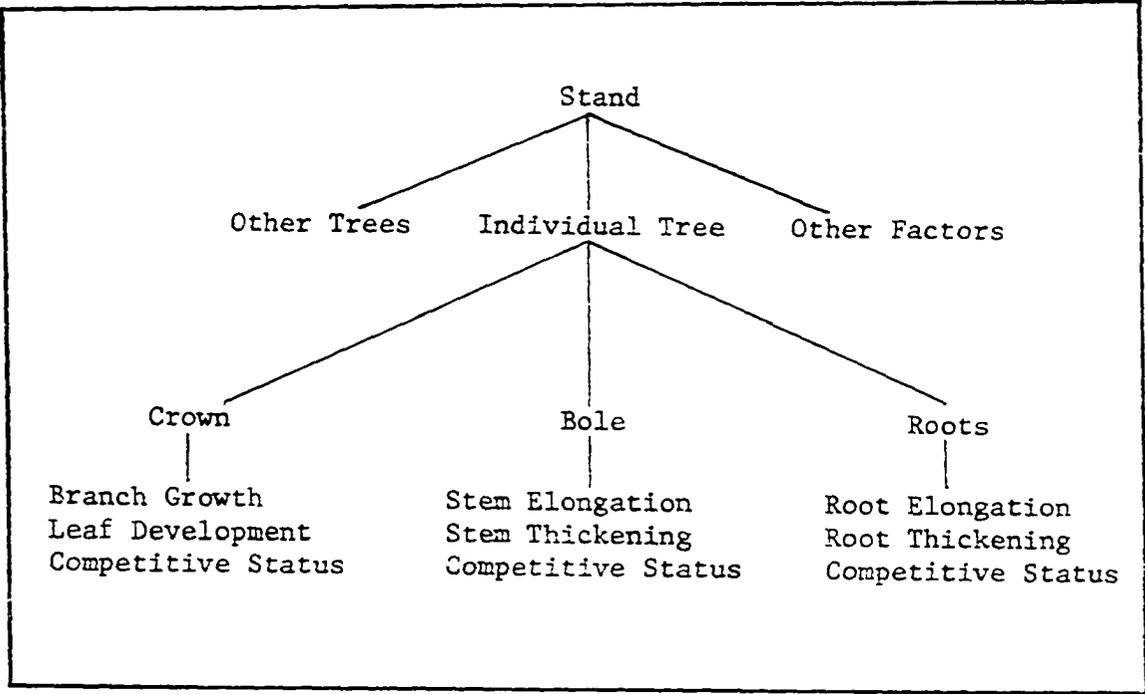
the individuals. In contrast to Duncan et al. (1967), the growth of the stand is then the summation of growth of individual trees, plus their interaction effects. Shortcomings of Mitchell's approach lie in absence of complete biologically derived causal relationships for growth. Growth is defined as change in bole volume and related to variables such as time, site index, and spatial relationships of the crown canopy.

Growth in a physiological sense, however, is the formation of cellular structure. The raw materials for this process are ultimately derived from the interception of solar energy by the canopy and the reduction of carbon dioxide in photosynthesis. Therefore, concepts concerning the production of photosynthate by layers of the crown canopy, as expressed by Duncan, seem the logical driving force for growth. These concepts could be incorporated in a model, such as Mitchell's, in which there is detailed crown description. This would lend a degree of realism to the total structure of the system because growth would then be described as the result of an actual physiological process.

However, growth will depend, not only on the rate of photosynthate production, but also upon its use. Within the individual tree, a particular growth area will receive an income from photosynthesis, and this income will be expended in assimilation and respiration, with a possible balance accumulated as a metabolic substrate for use

at a later date (Figure 2). It is this budgeting of photosynthate
that can be used to describe the actual process of growth, with the
resulting net assimilation rate being one definition of growth.

When viewed as net assimilation rate, growth could roughly be
considered to be changes in dry weight because this would be approxi-
mately a measure of the increase in the amount of cell structure.
Changes in the number and size of cells, as reflected by volume or
dimensional aspects of the tree, however, must also be considered as
important components of growth. Not only is size important from an
economic viewpoint, but also, the spacial relationships among trees
in a stand will determine the competitive status of an individual
tree and, therefore, its growth rate.

Although there have been many empirical studies concerning
dimensional growth of trees and relationships among tree dimensions,
models that could be classified as describing the process of cell
formation have been limited primarily to cambial-activity models.
An example of this is the model derived by Wilson and Howard (1967),
which simulates the cell-by-cell changes that occur through cambial
activity for the growing season. The result is a model that can be
used to describe the dimensional aspects of cambial growth. But,
the inputs to the model include variables to describe the rates of
cell division, cell elongation, and cell thickening. These inputs
would largely be determined by the availability of physiologically

Figure 2. An individual tree viewed in a system context.

Stem Elongation Stem Thickening Roots

  Structure   Structure   Structure

Respiration   Respiration   Respiration

  Substrate   Substrate   Substrate

Photosynthate

Leaf Tissue

  Structure

  Respiration

  Substrate
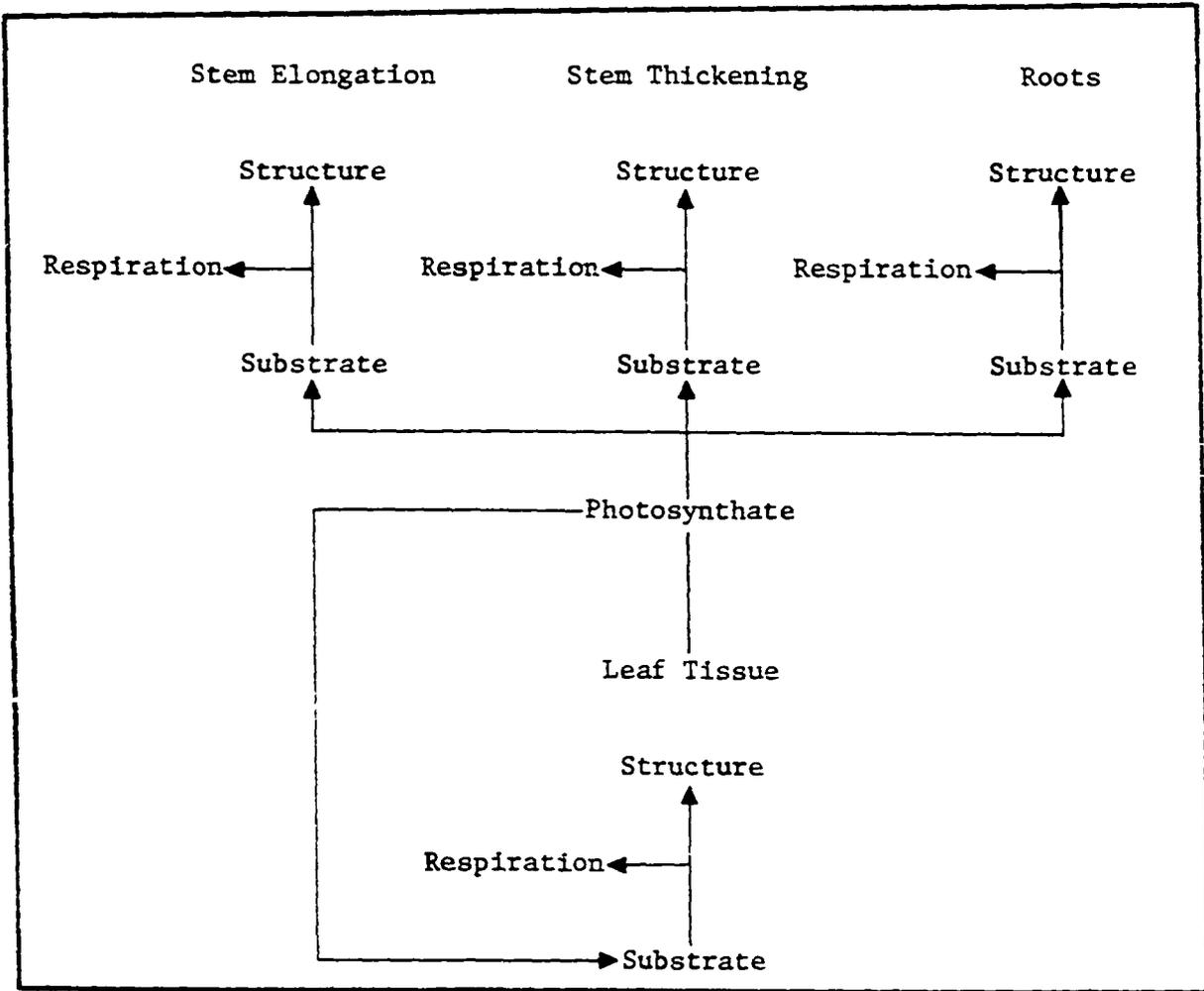
active compounds. Therefore, the entire model could be considered as a detailed description of a single growth area, or component, as illustrated in Figure 2.

Although not all components have been adequately modeled with respect to cellular growth and development, it may eventually be possible to relate assimilation rates to dimensional growth through the actual physiological processes of cell formation. It is the process of photosynthesis, however, that provides the necessary linkage between incoming solar radiation and resulting net assimilation rates of growth. With this link, a fairly complete model of individual tree growth would be attainable that would be based primarily on biological principle rather than empirical relationships. The objective of this study was to develop such a model.

TREE GROWTH AS A SYSTEM

Development of the Model

A model developed by Ledig (1969) is an attempt to describe seedling growth through the use of photosynthetic rates, but falls short of including a complete description of the distribution of photosynthate.

The initial model is stated as:

$$dY(t)/dt = k\ P(t)\ L(t)$$

where:

$Y(t)$ = total dry weight of the plant.

$P(t)$ = net assimilation rate per unit of leaf dry weight.

$L(t)$ = leaf dry weight.

k = constant.

t = time in days

In words then, this model simply states that the growth rate of the total plant is proportional to the product of the net assimilation rate per unit of leaf dry weight and the amount of photosynthetic tissue as measured by leaf dry weight. For a complete description of growth, however, it is necessary to consider the plant as a system. It is the components of this system (i.e., plant parts or growth areas) that interact in the budgeting of available photosynthate in assimilation and respiration and result in the total growth of the plant as illustrated in Figure 3.

Figure 3. Diagramatic representation of a model
for individual tree growth.
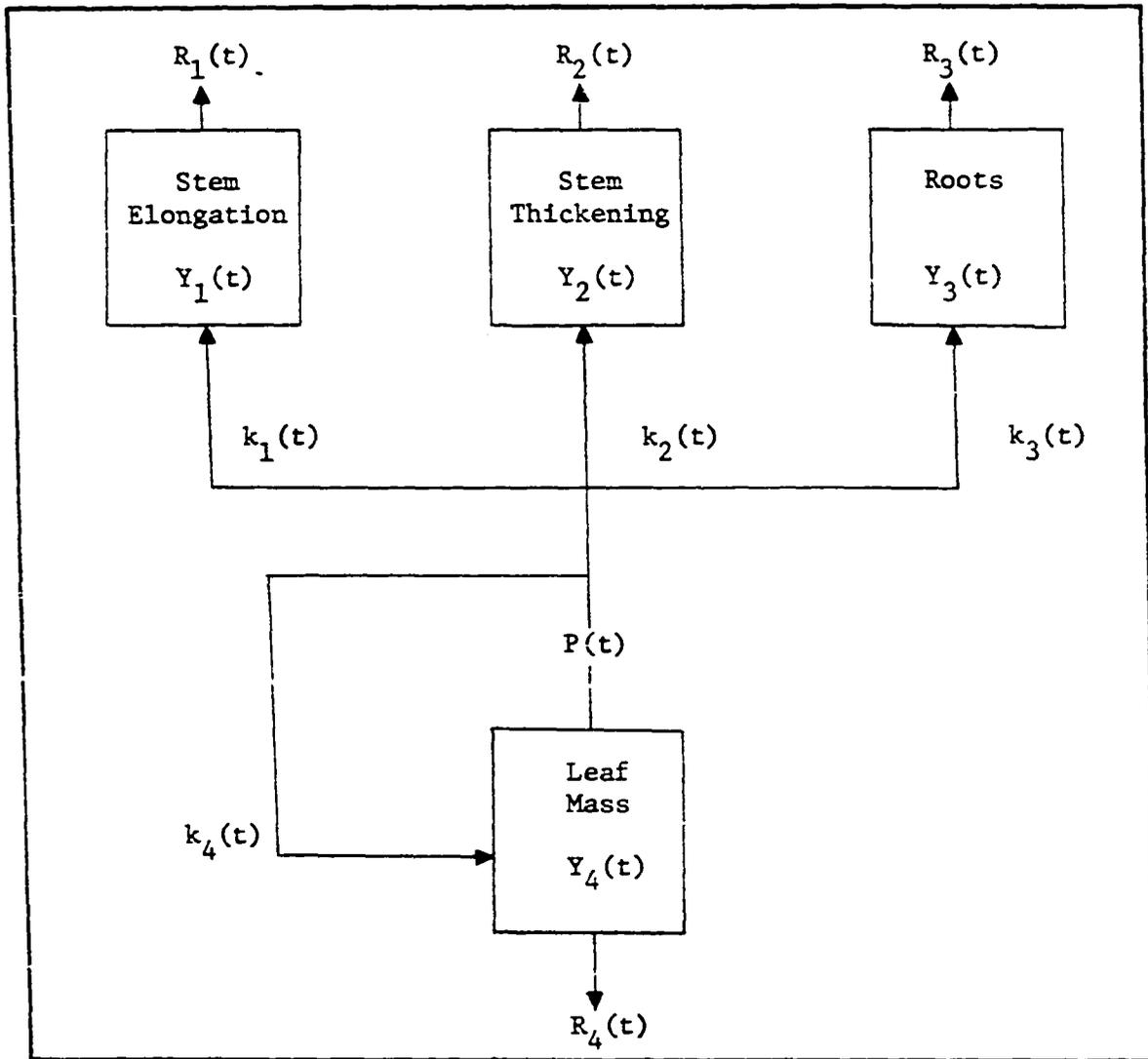
The first step in expanding a model such as Ledig's would be to consider the plant as a system and deal with the rates of change exhibited by the various parts of the system. We would then have:

$$dY_1(t)/dt = k_1(t) \, P(t) \, Y_4(t) - R_1(t) \qquad (1)$$

$$dY_2(t)/dt = k_2(t) \, P(t) \, Y_4(t) - R_2(t) \qquad (2)$$

$$dY_3(t)/dt = k_3(t) \, P(t) \, Y_4(t) - R_3(t) \qquad (3)$$

$$dY_4(t)/dt = k_4(t) \, P(t) \, Y_4(t) - R_4(t) \qquad (4)$$

Definition of variables:

$dY_i(t)/dt$ = net assimilation rate of part i.

$Y_i(t)$ = dry weight of part i at time t where $Y_4(t)$ would be the dry weight of the leaves.

$P(t)$ = gross photosynthetic rate per unit of leaf dry weight.

$k_i(t)$ = proportion of the currently produced photosynthate directed to part i.

$R_i(t)$ = respiration rate of plant part i.

t = time in days.

Implications of the Model

In words, the model states that the growth rate of any plant part is proportional to the current photosynthetic rate, minus the

respiration rate. At this point, the basic formulation of the model is complete, but several problems remain about the correctness of the structure.

Growth has been cast as a one-way relationship with photosynthesis, although there is evidence to suggest that the gross photosynthetic rate is also a function of growth (Sweet and Wareing, 1966). That is, if the magnitude of the sinks for assimilation are changed, the photosynthetic rate may be changed.

One possible way to restructure the model to incorporate this two-way relationship between photosynthetic rate and growth would be to consider P(t) as the maximum photosynthetic rate attainable when there is no associated build-up of photosynthate in the leaves. Then, an element could be included to indicate the amount of photosynthate retained in the leaves, and the realized photosynthetic rate could be modeled in a manner similar to Mitsherlich's description of the action of limiting factors.

An additional, and possibly critical shortcoming of the model as it currently stands, is that the aspect of storage of photosynthate is largely ignored. The model states that current growth rate is based solely on current photosynthetic rate. In most temperate zone tree species, however, this is not the case. Storage of photosynthate and lags in assimilation play an important role in growth when daily changes in plant size are considered. Since stored photosynthate would be included in the dry weight of a plant part, it would be

possible to have a negative growth rate if the photosynthate trans-
located out of a plant part (say, the root system) would be greater
than the incoming photosynthate.

However, the simplifying assumption of positive growth rates may
not greatly affect the seasonal course of growth. The problem would
be of primary importance when attempting to operate the model for more
than one growing season. This could be circumvented by considering
the model as operational for only one season. The initial conditions,
or sizes of the plant parts, could be the dry weights for the plant
parts at the end of the preceding season adjusted for the transloca-
tion of photosynthate from storage to establish a new leaf mass. In
this manner, the model could then be made operational over several
growing seasons.

Specification of Model Components

In the general construction of the model, four components have
been identified, but the number of dimensions of the model can be
altered without changing the basic structure or concepts. For
example, as stated in the initial model, only the total leaf mass was
considered. This could be further subdivided, however, into leaves
in the expanding stage of developing as a primary sink, leaves in the
mature stage as a primary source, and leaves in the senescenting stage
as a nonproductive part of the leaf mass. To do this would simply
require that the system be expanded to include these extra dimensions.

For example, letting equations 8, 9, 10 represent the growth rates of leaves in the stages of expanding, mature, and senescenting respectively, the system would appear as:

$$dY_1(t)/dt = k_1(t) \; P(t) \; Y_5(t) - R_1(t) \qquad (5)$$

$$dY_2(t)/dt = k_2(t) \; P(t) \; Y_5(t) - R_2(t) \qquad (6)$$

$$dY_3(t)/dt = k_3(t) \; P(t) \; Y_5(t) - R_3(t) \qquad (7)$$

$$dY_4(t)/dt = k_4(t) \; P(t) \; Y_5(t) - R_4(t) \qquad (8)$$

$$dY_5(t)/dt = h_1(t) - h_2(t) \qquad (9)$$

$$dY_6(t)/dt = h_2(t) \qquad (10)$$

where $h_1(t)$ would be the maturation rate of the expanding leaves and $h_2(t)$ would be the rate of senescence of mature leaves.

Also, the stem can be considered to be composed of an apical section where cell division, cell elongation, and primary wall formation are occurring and a section where cambial activity, secondary wall formation, and lignification are occurring. Subdivided in this fashion, the stem comprises a region primarily responsible for stem elongation and a region primarily responsible for stem thickening as outlined in the initial model and represented by equations 5, 6.

In essence then, the components of the system will have to
describe in some detail the activity of the apical zone, which would
include both expanding leaves and stem. Although this zone accounts
for only a small portion of a plant of a given size (Figure 4), its
inclusion in a growth model is critical because it is within the
apical zone that the actual growth of the leaves occurs, and thus, the
growth of the total leaf mass is primarily governed by the activity
of this zone.

Also, the apical zone is responsible for the height growth of
the plant and thereby largely determines its competitive status.
Although height has not been previously conceived of in terms of dry-
weight accumulation, it will be necessary to include this dimension
of growth if the model is to describe the changes in a tree in both
weight and space.

Once the components of the system are specified, the primary
information needs for such a model are:

1) Photosynthetic rates per unit of leaf dry weight $(P(t))$.

2) Respiration rates of the various plant parts $(R_i(t))$.

3) Distribution functions for photosynthate $(k_i(t))$.

With this information, the model would then be functional, and the
resultant output would be a vector of dependent variables describing
the total dry weight of, say, the stem, the roots, and the leaves.

Figure 4. Dry weight distribution of young _Populus_
trees as a function of total tree height.
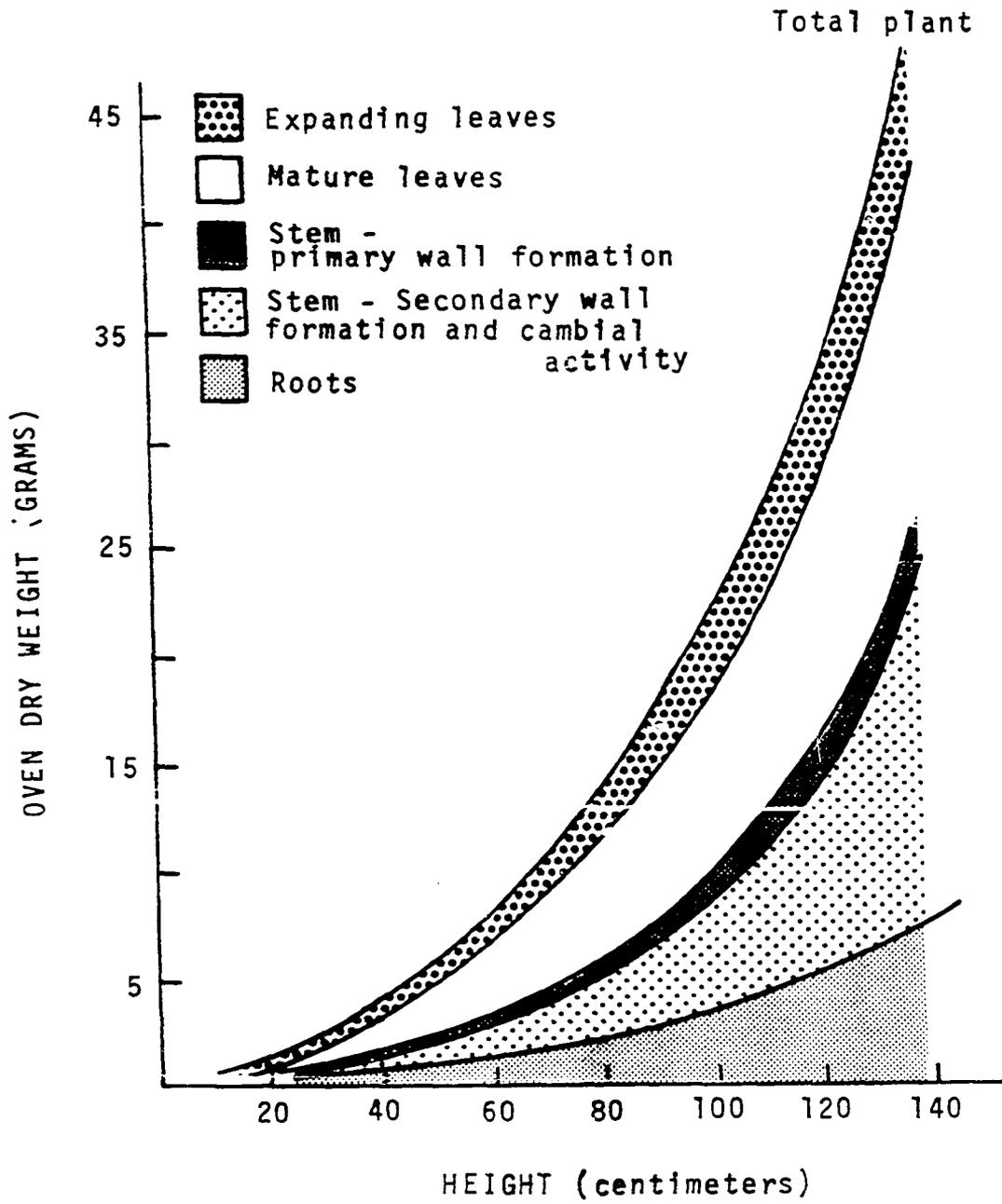
There have been numerous studies involving the measurement of photosynthetic rates of leaf tissues of Populus species (e.g., Dickmann, 1971; Gatherum et al., 1967) and several attempts at modeling photosynthesis.

Not all these models, however, would be compatible with the system as presently developed. For example, the model used by Ledig (1969) is not the result of actual observation of photosynthetic rates, but rather, results from the fitting of dry-weight growth functions. This is consistent with the concept of modeling net assimilation rate, but does not allow the processes of photosynthesis and respiration to be separated. The ability to incorporate laboratory studies conducted to observe actual realized photosynthetic rates as related to selected independent variables should be one of the advantages of the model developed here.

A model developed by Waggoner (1969) predicts the effects on net photosynthesis of changes in light, temperature, CO_2 concentration, and certain physical characteristics of the leaf. However, the model is an analog simulation model for an individual leaf and could not be directly incorporated into the tree model as it currently stands. This would require the subdivision of the leaf-mass component in a way that could account for the activity of individual leaves or the activity of an "average" leaf.

If how an individual tree behaves in a stand is to be described, however, the spatial relationships of the crown will have to be

accounted for. When considering the output of an individual leaf
(or leaf layer) functioning under optimal conditions, the most
important variable to consider would be the density of the photo-
synthetically active radiation (PAR) reaching the specific leaf. The
vertical distribution of PAR has been expressed as an exponential
function (Monsi and Saeki, 1953; Saeki, 1960; Ross and Nilson, 1965):

$$\phi_i = \alpha \; \phi_o \; \exp \; \{-\alpha L\}$$

where L is the leaf area index (i.e., that is, leaf area divided by
land area) (Watson, 1958), α is a function characterizing leaf arrange-
ment or geometrical structure of the plant community, and ϕ_o is the
density of the incident PAR. The functions α and L would allow for the
effects of different stand densities when attempting to combine the
individual trees into a stand model. This concept has been incor-
porated into a photosynthate model by Tooming (1967). But, the
problem of expressing the relationships in terms of dry weight
instead of area would remain.

If we consider the problem of simulating trees grown in growth
chambers or greenhouses, the function to describe the photosynthetic
rate can be considered approximately constant because growing condi-
tions would be nearly constant. Changing light regimes caused by
changes in the total size of the leaf mass, however, must still be
accounted for.

According to Thornley (1971), utilization of photosynthate by a plant part can be represented as the subdivision of a substrate pool:

Substrate Pool

Growth   Maintenance   Wastage

Plant Material   Energy Loss
and storage

Essentially, the growth-component energy loss can be considered simply as a conversion efficiency and is a function of the substrate pool or the amount of photosynthate available. The specific maintenance rate generally is not assumed to be dependent on the substrate pool, but rather, the total amount of living tissue present in the plant part.

McCree (1969), studying respiration in white clover plants, found that respiration had only two components, one proportional to the gross supply of substrate and, the other, proportional to the dry weight of the plant. It would seem that the wastage component behaved similarly to the growth rate and (or) the maintenance component. For macroscopic purposes, wastage can be included in either or both of these processes.

If this is true, and we can assume constant environmental conditions, then we have a possible formulation for the respiration-rate functions $(R_i(t))$ if we consider the initial model (as represented by equations 1, 2, 3, 4).

Consider first the respiration rate of the plant part $Y_1(t)$ as representing stem elongation. Since the total structure involved is small, the respiration rate will be primarily a function of the gross substrate supply or:

$$R_1(t) = C_1 \{k_1(t) \ P(t)Y_4(t)\}$$

where C_1 would represent the energy conversion factor of photosynthate into plant structure.

The respiration rate for the bole or the component to describe stem thickening becomes a slightly more complex problem. The growth component of respiration would be proportional to the gross substrate supply, but, as a first approximation, the maintenance component would be proportional to the total dry weight of the stem. Therefore:

$$R_2(t) = C_2 \{k_2(t) \ P(t) \ Y_4(t)\} + C_2 ' \{Y_1(t) + Y_2(t)\}$$

Although McCree determined that the maintenance component of growth as proportional to the dry weight, the plants he dealt with were nearly all living tissue, in contrast to the bole of a tree, which contains a large proportion of dead xylem. The maintenance component should be directly related to the amount of living tissue, and this would imply that, for a tree stem, surface area should be considered since this is more closely related to the living part of the stem than to total dry weight.

If we assume that the volume of the bole could be expressed as:

$$V = a_1 \{Y_1(t) + Y_2(t)\}$$

and the height as:

$$H = a_2 \, Y_1(t)$$

then, assuming a conical form for the stem, the surface area at any given time would be:

$$\pi \{ \{3a_1/\pi a_2 \, (1 + Y_2(t)/Y_1(t))\} \, \{3a_1/\pi a_2 \, (1 + Y_2(t)/Y_1(t))$$

$$+ a_2^2 \, Y_2^2 \, (t)\}\}^{\frac{1}{2}}$$

For simplicity, however, it may be adequate to assume that the maintenance component is directly proportional to the square root of stem dry weight or, for small trees, simply proportional to the dry weight as initially stated.

When considering the respiration rate of the root system, we may also want to consider the surface area. But, since no geo-metric model exists, we may use dry weight as a first approximation:

$$R_3(t) = C_3 \{k_3(t) \, P(t) \, Y_4(t)\} + C_3' \, Y_3(t)$$

We may also assume a similar situation for the leaf mass where:

$$R_4(t) = C_4 \{k_4(t) \, P(t) \, Y_4(t)\} + C_4' \, Y_4(t)$$

At the present stage of development, the initial system can be rewritten as:

$$dY_1(t)/dt = (1 - C_1) \, k_1(t) \, P(t) \, Y_4(t)$$

$$dY_2(t)/dt = (1 - C_2)\ k_2(t)\ P(t)\ Y_4(t) - C_2{'}\ (Y_1(t) + Y_2(t))$$

$$dY_3(t)/dt = (1 - C_3)\ k_3(t)\ P(t)\ Y_4(t) - C_3{'}\ Y_3(t)$$

$$dY_4(t)/dt = (1 - C_4)\ k_4(t)\ P(t)\ Y_4(t) - C_4{'}\ Y_4(t)$$

The most critical aspects of the model as presently developed
are the functions describing the net movement of photosynthate from
one plant part to another. Experiments have shown definite patterns
of distribution that seem to change continuously during the growth
of the plant. Much work has been done on this subject for crop
plants, such as soybean, tobacco, sugar beat, etc. (e.g., Thrower,
1962; Jones, et al., 1959; Belikol and Yakostetskii, 1964). Also,
some work has been done in forest tree seedlings (e.g., Gordon and
Larson, 1968, 1970; Larson and Gordon, 1969). Patterns of distribu-
tion have not been found uniform, but rather, are affected by
many different conditions, such as position of the leaf, absorption
of ions by the roots, temperature, water supply, etc.

The answer to how the flow of photosynthate is regulated, finds
little agreement among plant physiologists. Theories on the action
of growth hormones have been postulated and others on the idea of
passive mass flow have been rejected, but the basic mechanism is
not known with certainty.

Since the functions are possibly the result of unknown, complex
hormonal systems, immediate attention should be given simply to
describing photosynthetic flows rather than to attempts to describe

the underlying physiological processes. With the present formulation of the model, we are concerned with the functions:

$$k_1(t), \ldots, k_n(t)$$

where $k_i(t)$ is the proportion of photosynthate directed to plant part i at time t and n is the number of plant parts under consideration.

Generally, experiments conducted to study translocation patterns have dealt with either gross assimilation by plant parts through the tracing of ^{14}C (e.g., Gordon and Larson, 1968; Dickmann and Kozlowski, 1968) or net assimilation through the examination of relative dry weight changes (Ledig and Perry, 1965). The model was specifically developed to consider gross assimilation of photosynthate by a plant part, and tracer studies would yield information directly on the translocation of current photosynthates. Also, tracer studies could yield information on the mobilization of reserves to meet post-dormancy growth and respiratory demands (Gordon and Larson, 1970).

This latter point would be of prime importance in attempts to extend the model over several growing seasons. Dry-weight techniques would not be adequate for this type of analysis since the measurements would not indicate whether weight loss was due to redistribution within the tree or to changes in respiration and photosynthesis.

Tracer studies of woody species, however, still are relatively few, and currently available studies are not complete enough to yield

a detailed formulation for seasonal growth patterns. In contrast, dry-weight relative growth rates have been studied extensively for many crop plants (e.g., Huxley, 1932; Throughton, 1955) and for some tree species (Ledig and Perry, 1965; 1969). In most instances, presentation of the data is in terms of allometric growth constants or shoot-root ratios. The critical nature of the distribution of photosynthate has long been recognized, and plant physiologists have hypothesized that there should be an optimal balance or proportion between the shoot system and the root system. However, this concept of a balanced system should extend to all plant parts. Meyer et al. (1960) and Kramer and Kozlowski (1960) present the idea that best growth requires a balance between the root and shoot size. Beyond this, Huber and Polster (1955) have hypothesized that better growth rates of some poplar clones may be due to differences in the relative efficiency of shoot and root systems in their reallocation of photo-synthate to new leaves.

Analyses of this type, however, have been limited primarily to dry-weight studies and have, therefore, dealt with net assimilation rates. Exactly how this net assimilation rate differs from the gross assimilation rate as indicated by tracer studies can be shown through the use of previous model developments.

Measurements used in a dry-weight study would consider the change in dry weight of a plant part relative to the change in dry weight of the total plant. Estimates would be made at two points in time, and

$(\Delta\ Y_i / \Delta\ Y)$ would be used to approximate (dY_i/dY). If we were to express the entire model in discrete terms, then these dry-weight observations would be measurements of the following[1]:

$$\{Y_i(t_j) - Y_i(t_{j-1})\} / \{\sum^n Y_i(t_j) - \sum^n Y_i(t_{j-1})\} = K_i(t_j) +$$

$$\{K_i(t_j) \sum^n R_i(t_j) - R_i(t_j)\} / \{P(t_j) - \sum^n R_i(t_j)\}$$

where there would be n parts in the system, and $Y_i(t_j)$ would represent the dry weight of part i at time t_j. $P(t_j)$ would represent the total amount of photosynthate produced on, say, day t_j, and $R_i(t_j)$ would represent the total loss in respiration by part i on day t_j.

The factor $k_i(t)$ would be the gross assimilation rate of plant part i or the proportion of the total current photosynthate production being translocated to part i. This would be the factor measured by a tracer study, and the remaining terms in the equation would indicate the bias involved if dry-weight measurements were used as measures of gross assimilation rates. This bias would be greatest for plant parts receiving a large proportion of the photosynthate but having a low respiration rate. If the respiration rate for the entire plant is small relative to the photosynthetic rate, this bias should be small. The bias will be zero if:

---

[1] Derivation available from the author upon request.

$$k_i(t_j) = R_i(t_j)/\Sigma \; R_i(t_j)$$

That is, if the respiration rate of the i^{th} plant part relative to the respiration rate of the entire plant is equal to the proportion of the gross assimilation rate attributable to part i.

Consequently, within the limits of the bias involved, examination of relative dry-weight changes can be considered as a first approximation to measurements of gross assimilation rate. Because of the importance of the timing of the translocation of photosynthates, it would be necessary to consider a detailed description of the translocation process within a growing season. To use seasonal averages for individual plant parts would alter greatly the total distribution of dry weight because of the changing amount of photosynthate produced.

ESTIMATION OF PHOTOSYNTHATE DISTRIBUTION FUNCTIONS

Materials and Methods

Data were collected for purposes of estimating the distribution

functions, based on the assumption that the initial conceptualization

of the individual tree model was correct. Dry-weight measurements

were chosen as a source for data because they are more simply made

than measurements of ^{14}C distribution.

Only the first 12 weeks of growth were observed so that growth

rates were assumed to be strictly positive and any translocation

of stored photosynthates negligible. Because of the rapid growth

rates encountered, photosynthetic rates were assumed to be high, and,

therefore, the bias involved in using dry weight to estimate gross

assimilation rate was probably small.

The rapidly growing Populus clone, Wisconsin #5, was selected,

and 72 cuttings were chosen for uniformity in number of leaves and

length. These plants were then randomly assigned locations in a

greenhouse bay and randomly assinged to 1 of 12 harvest times at

1-week intervals. Photoperiod was maintained at 18 hours, and all

plants received consistent and identical watering and fertilizer

applications in an attempt to maintain optimum growth conditions

throughout the sampling time.

Records of leaf production rates and height growth were main-

tained on each plant and at each harvest the following measurements

were made on each of six sample trees:

1. Oven-dry weight of the total root system with the stem being cut at the root collar.

2. Oven-dry weight of the total leaf mass.

3. Oven-dry weight of the y_1 (cell division) stem section as illustrated in Figure 5.

4. Oven-dry weight of the y_2 (cell elongation) stem section as illustrated in Figure 5.

5. Oven-dry weight of the remainder of the stem.

Analysis of Data

The data were collected so that the five growth areas or sinks for photosynthates could be separately identified. These represent: (1) root growth, (2) leaf growth, (3) cell division by the apical zone, (4) cell elongation and primary wall formation, and (5) secondary wall formation, lignification, and stem thickening. Accordingly, the dry-weight data can then be used as observations of a system of five equations to represent photosynthate distribution.

Because it was necessary to consider independent samples of trees over time, and these samples were taken to indicate the growth of an individual the problems of sample variability become acute. Some samples indicated a decrease in dry weight of some plant parts over a given time. Because the initial assumptions considered mobilization of photosynthate out of storage as insignificant, such points are regarded as solely the result of sample variability.

Figure 5. Definition of variables to describe
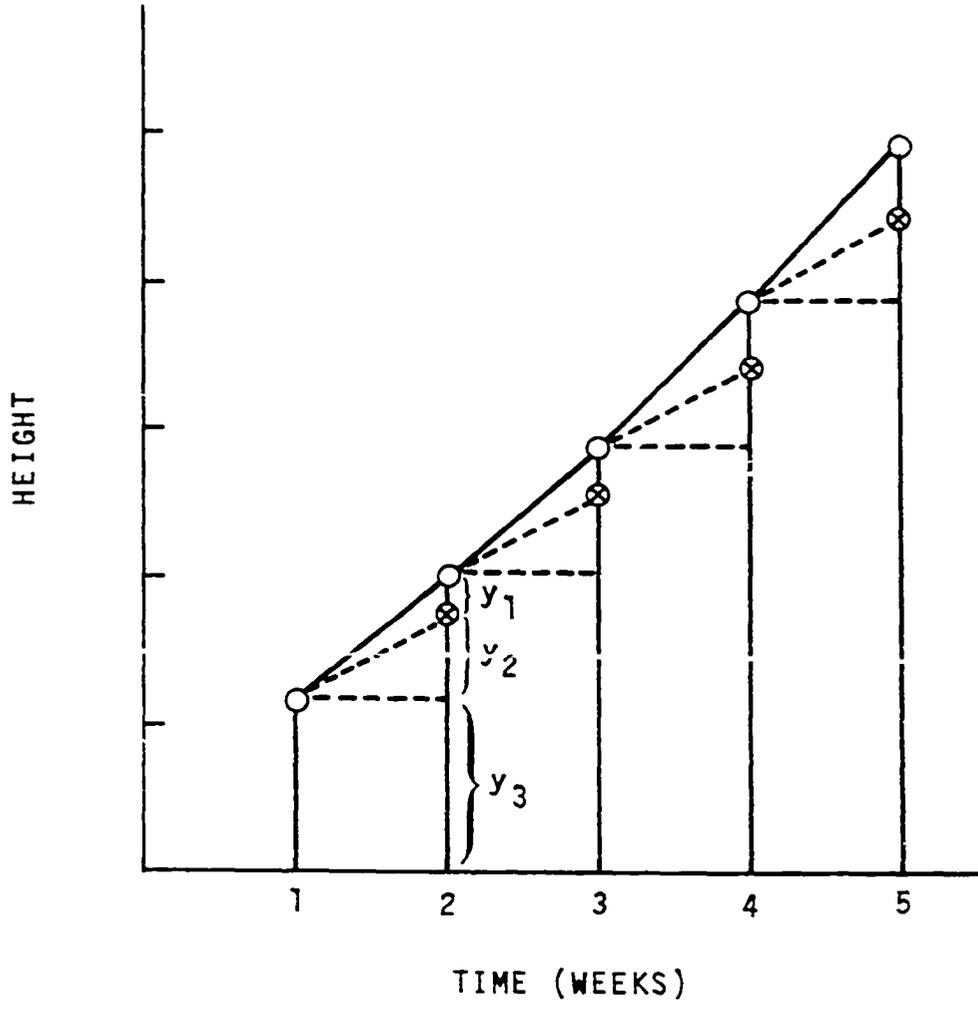aspects of stem growth.

y_1 = cell division

y_2 = cell elongation

y_3 = stem thickening

O : plant height at time t_j

$\otimes$: position of leaf that was the
first leaf at time t_{j-1}

HEIGHT

TIME (WEEKS)

Hughes and Freeman (1967) suggest that, for analyzing growth rates using frequent small harvests, to avoid the problem of negative growth rates, cumulative dry weight versus time curves should first be fitted to all the data. Growth analysis can then proceed from considering the first derivatives of these estimated functions.

The data were first analyzed through the fitting of cumulative growth curves. The ratios of the first derivatives of these cumulative growth curves were calculated, and the distribution of photosynthate was estimated.

In contrast to Hughes and Freeman's (1967) technique, however, adjustment of sample average dry weights by the covariate of height, gave estimates of growth that were positive for all time intervals. These points, when used to estimate values of $k_i(t)$, did not yield smooth trends (Figure 6); it was possible, however, to estimate the variance-covariance structure from individual tree data.[2] The system of functions were then fitted to the data points by using single-equation techniques, first, by simple least squares with no adjustments for the error structure and, then, by generalized least squares where statistical bias in the observations, variance of the data points, and autocorrelation between data points were accounted for. The estimated distribution functions are shown in Figure 7.

_____

[2] Technique available from author upon request.

Figure 6. Distribution of current photosynthate: data points.
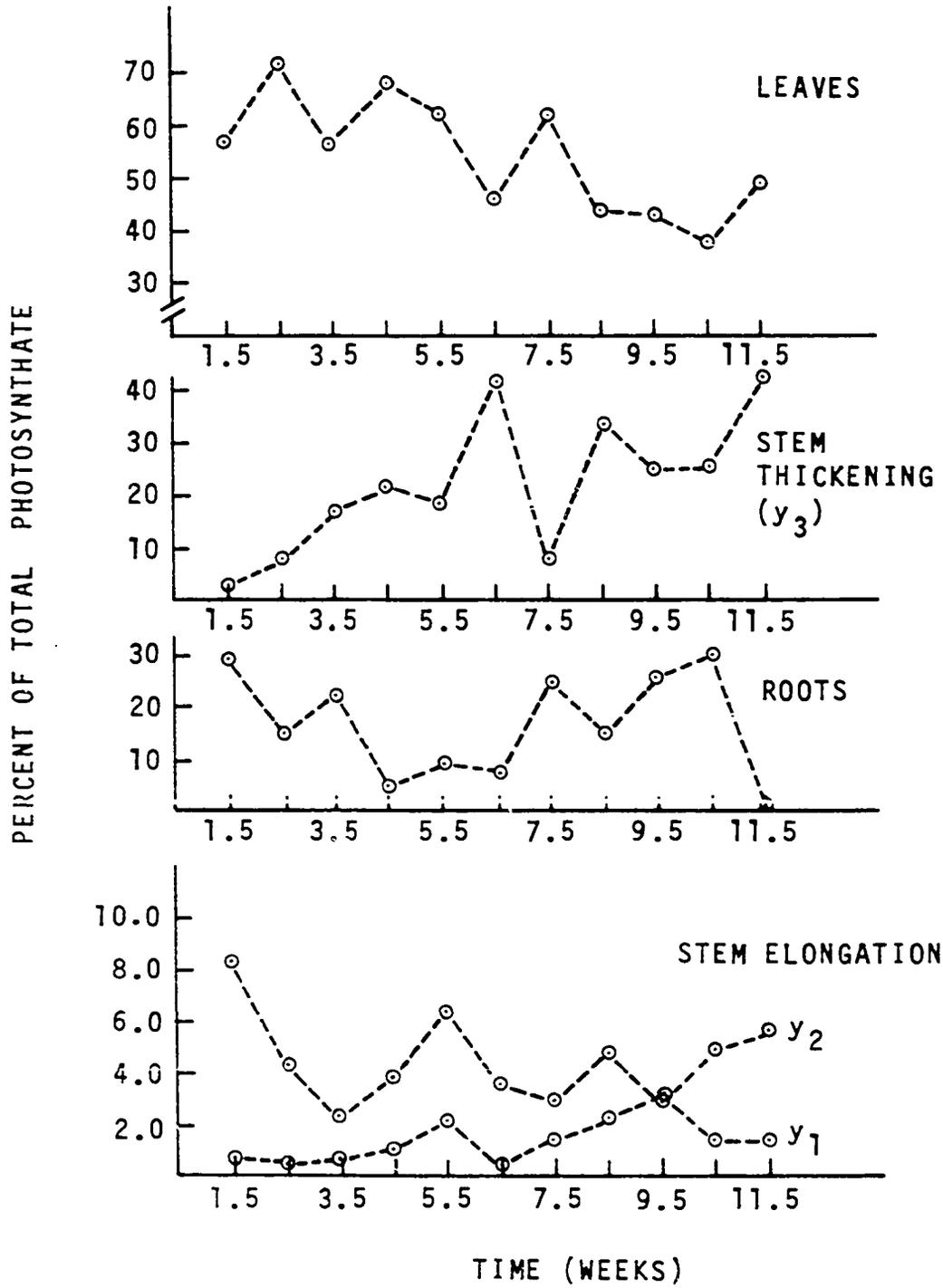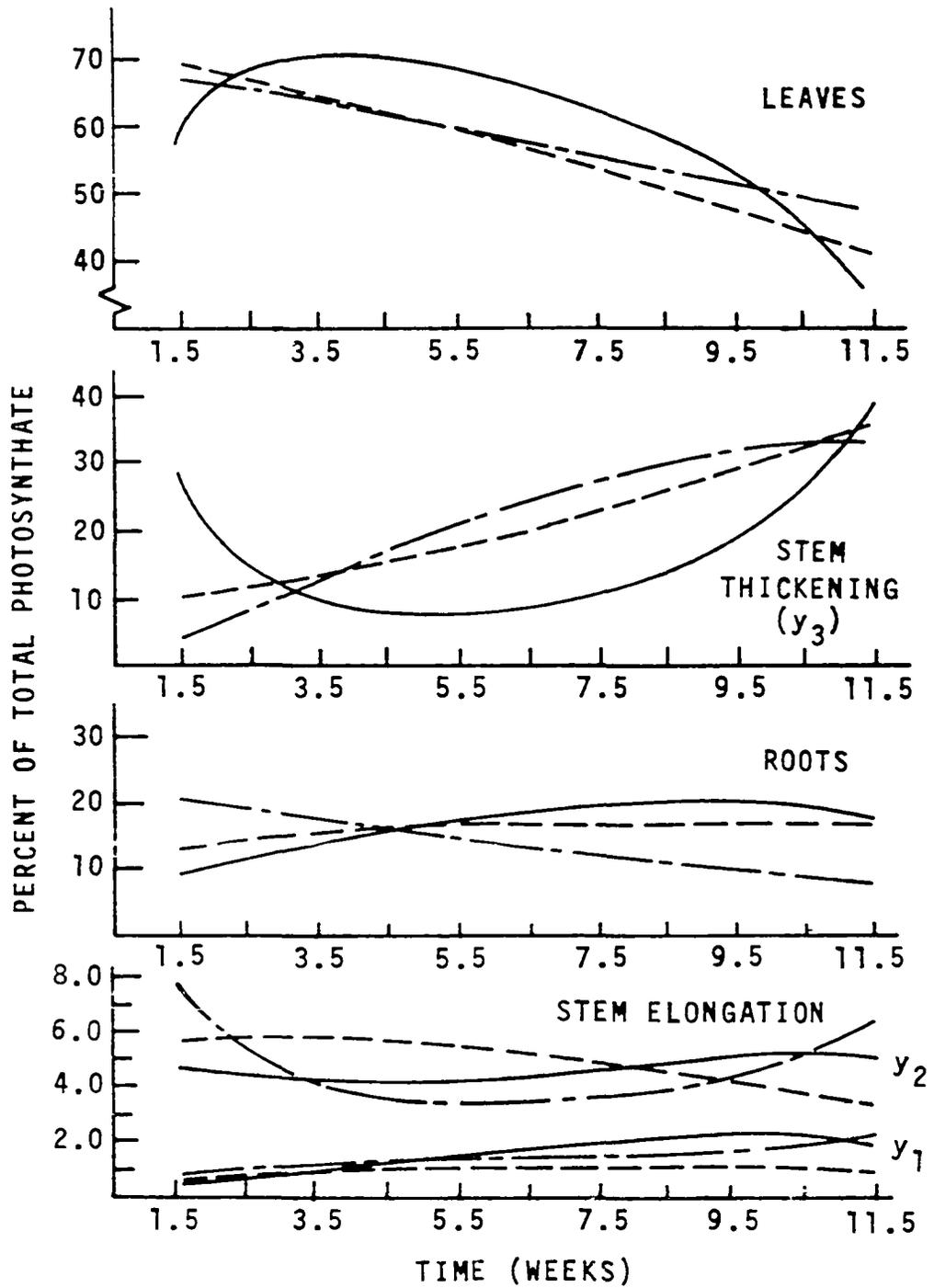
Figure 7. Distribution of current photosynthate: results
of different analytical techniques.

------ Ratio of derivatives.

— - —- Simple least squares.

———— Generalized least squares

When considering the estimates of the parameters resulting from these three methods of analysis, the technique using the ratio of first derivatives of growth functions would, at best, result in a biased estimation procedure, with little known about other statistical properties. The simple least-squares techniques, since additive errors were assumed and logarithmic transformations used, would result in biased and inefficient estimation, but the estimators should be consistent. The generalized least-squares technique, with corrections for bias and autocorrelation, should reduce the magnitude of the bias and improve the efficiency of the estimators.

The important question, however, pertains more to whether or not the results are intuitively reasonable for the set of data rather than for the general statistical properties of the procedures. When considering the distribution function for the leaves, roots and stem thickening, the three procedures yielded different results, none of which was biologically inconsistent. For example, the analysis using the ratio of derivatives shown about a constant proportion of photosynthate allocated to the root system while generalized least squares showed a slightly increasing trend and simple least squares showed a slightly decreasing trend.

To discern which method of analysis gave the most reasonable results, the performance of the three sets of distribution functions were examined in the complete model. However, photosynthetic-rate data and respiration-rate data were not collected for the sample

plants, and these values had to be obtained from previous experiments. According to an experiment by Domingo (1971) a different _Populus_ clone had a maximum net photosynthetic rate of about 15 mg CO_2 hr^{-1} g^{-1} of leaf dry weight, with a dark respiration rate of 2 mg CO_2 hr^{-1} g^{-1}. These values were assumed approximately correct for the sample trees where there would be about 16 hours per day of photosynthetic activity at this rate. Values for the respiration rates of the root system were assumed similar to those for the stem since no applicable data were available for _Populus_.

Using these values and assuming that photosynthetic rates would not change over the time considered, the system of differential equations was then solved by Hamming's modified predictor-corrector method: IBM scientific subroutine package. The results are shown in Figures 8, 9, 10. As could be expected, the results did not fit the original data exactly, but the general curve forms were similar.

The important aspect to note is the positioning of the curves. In all cases, the generalized least-squares technique resulted in distribution functions that underestimated the original data, indicating that the values used for photosynthetic and respiration rates were not correct for the sample trees but that the distribution functions were consistent with the data. However, the other two techniques of analysis resulted in underestimation for the leaf and root curves while the total stem curve was fairly consistent with

Figure 8. Model simulation using different distribution
           functions: cumulative leaf dry weight.

SAMPLE AVERAGES

GENERALIZED
LEAST SQUARES

SIMPLE LEAST
SQUARES

RATIO OF DERIVATIVES

OVEN DRY WEIGHT (GRAMS)

15.0

10.0

5.0

TIME (WEEKS)

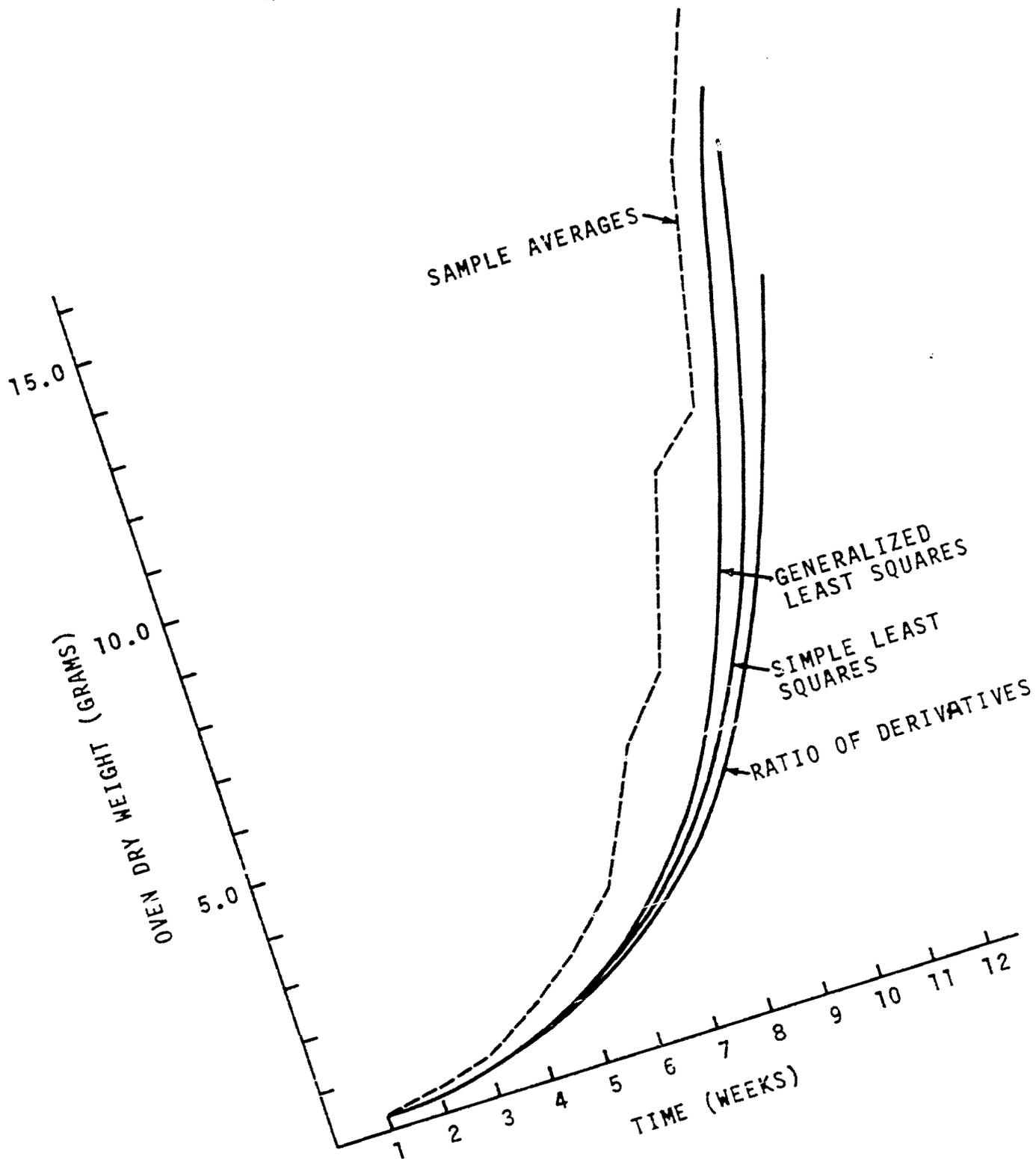1 2 3 4 5 6 7 8 9 10 11 12

Figure 9. Model simulation using different distribution
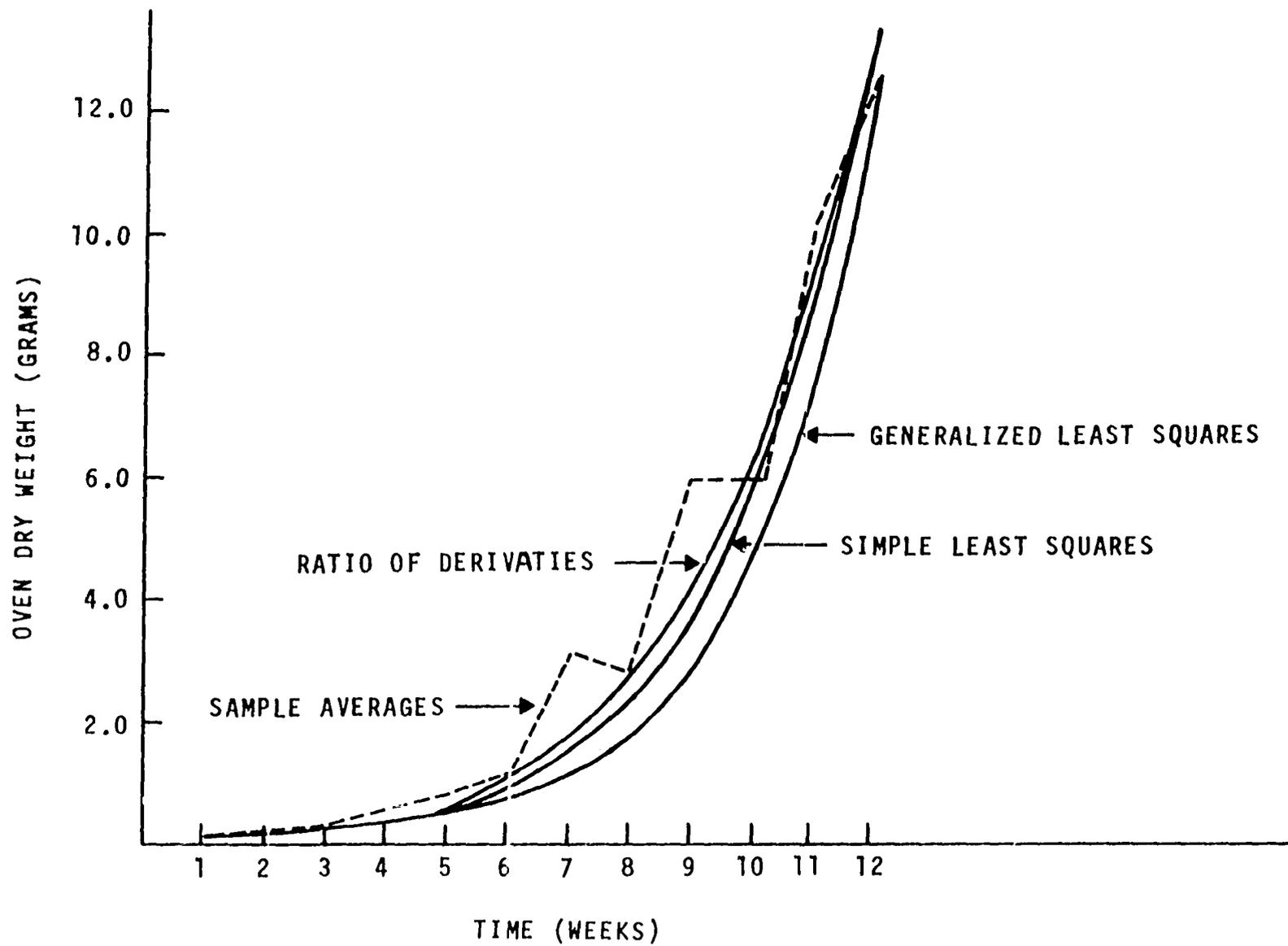   functions: cumulative total stem dry weight.

Figure 10. Model simulation using different distribution
functions: cumulative root dry weight
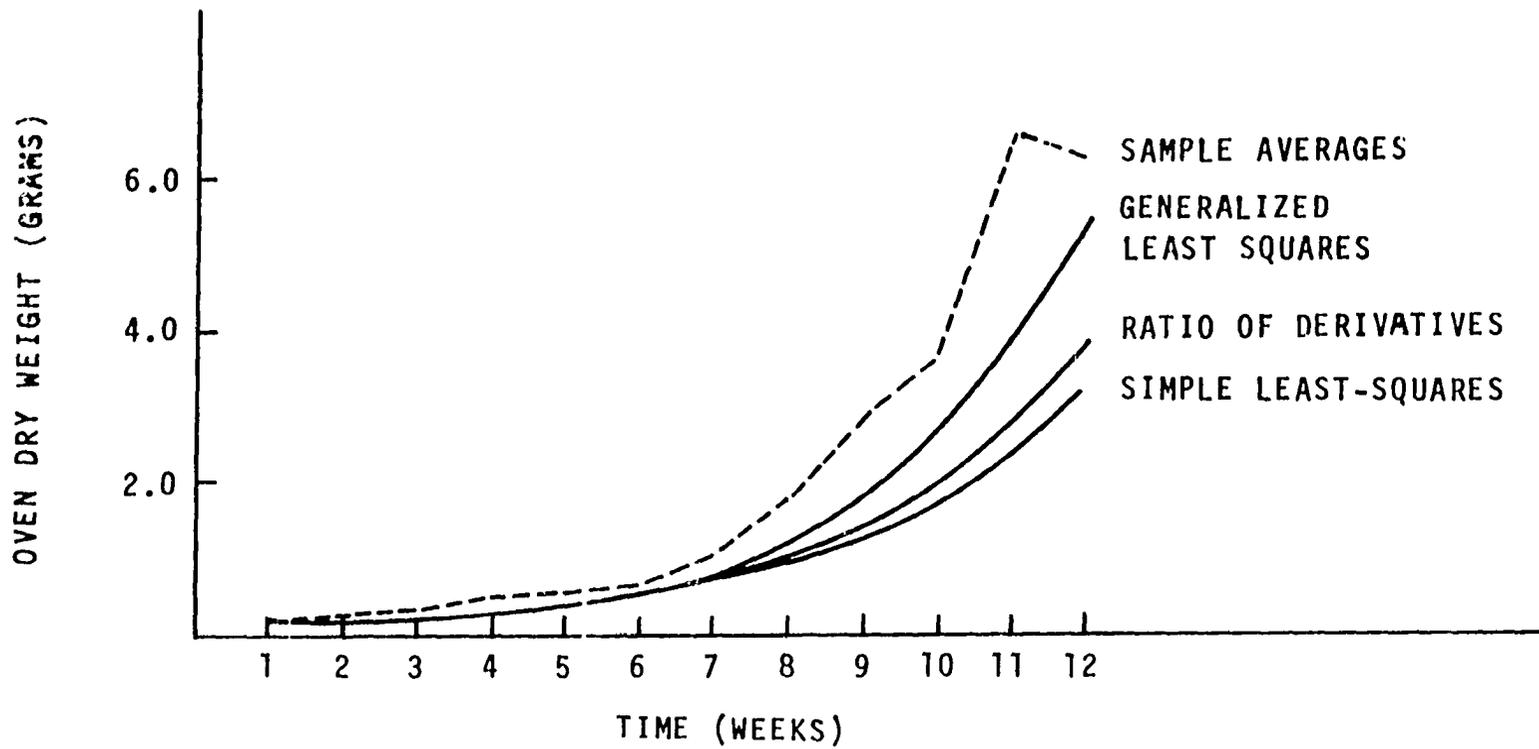
the data. This would indicate that there was an overdistribution of photosynthate to the stem while there was an underdistribution to the roots and leaves.

The additional aspect of the sensitivity of the model to the data inputs should be noted. There was about a 13% difference in the total dry weight of the plant at the 12-week point, depending on which set of distribution functions was used. Increasing the dark respiration rate by 1 mg CO_2 hr^{-1} g^{-1}, however, resulted in a 31% decrease in total plant dry weight (Figures 11, 12, 13).

This sensitivity to data inputs indicates the value of a model of this form in simulation studies of plant growth. It also indicates that a high degree of accuracy will be needed in the collection and measurement procedures used in obtaining the data to be used.

Figure 11. Model simulation using different dark respiration
           rates: cumulative leaf dry weight.
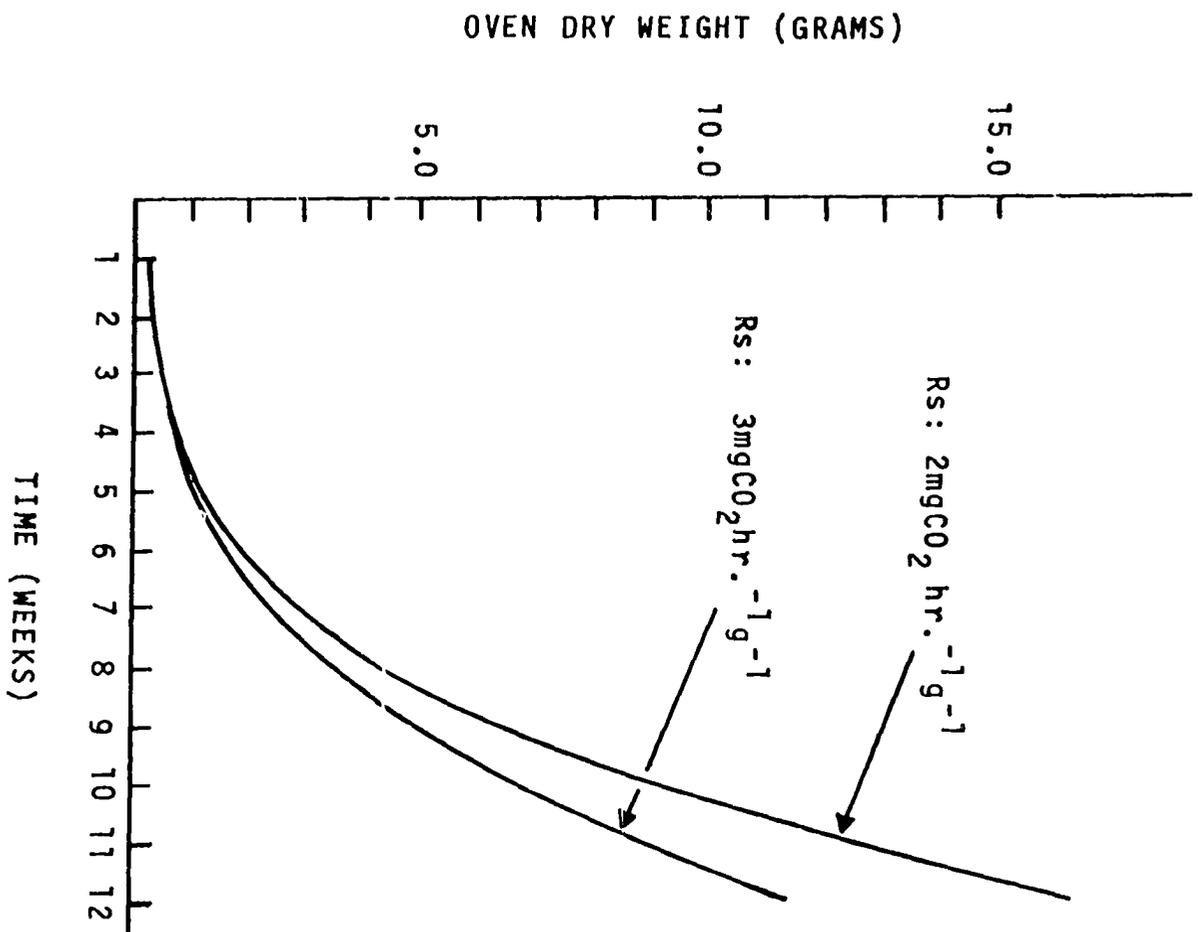
Figure 12.   Model simulation using different dark respiration
             rates: cumulative stem dry weight.

OVEN DRY WEIGHT (GRAMS)

Rs: 2 mg.CO$_2$ hr.$^{-1}$g^{-1}

Rs: 3 mg CO$_2$hr.$^{-1}$g^{-1}

10.0

5.0

TIME (WEEKS)

1 2 3 4 5 6 7 8 9 10 11 12
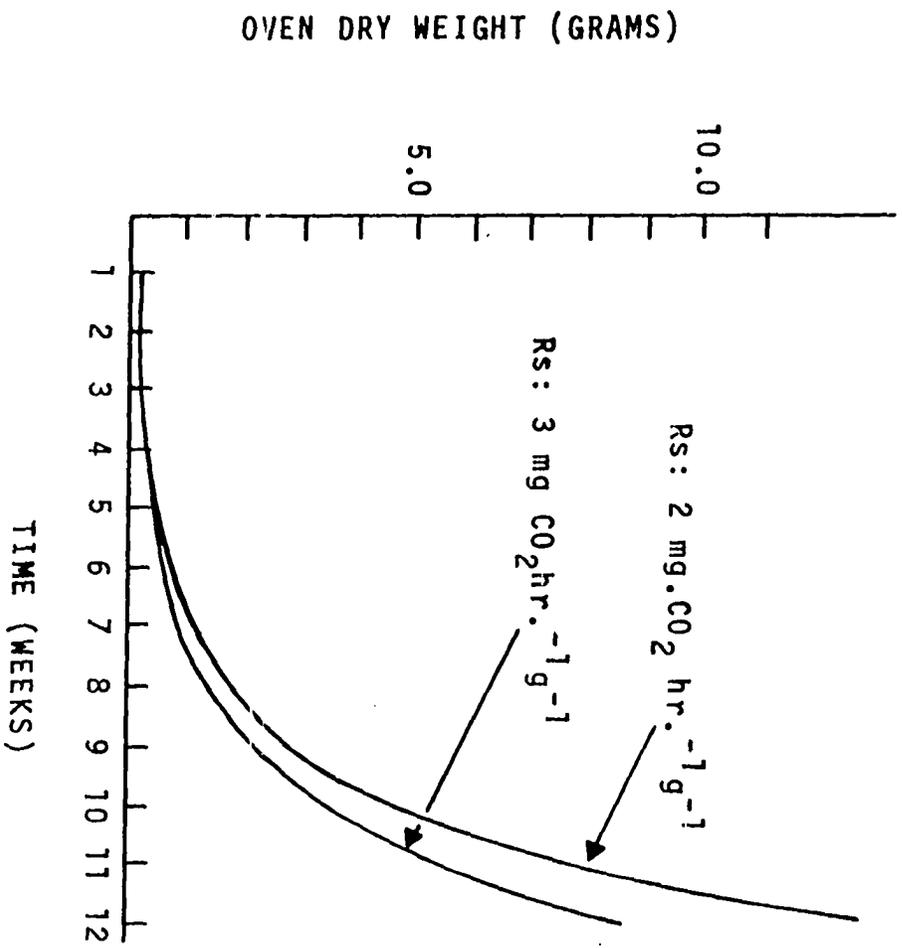
Figure 13. Model simulation using different dark respiration
            rates: cumulative root dry weight.

OVEN DRY WEIGHT (GRAMS)

TIME (WEEKS)

Rs: 2mgCO$_2$hr.$^{-1}$g^{-1}

Rs: 3mgCO$_2$hr.$^{-1}$g^{-1}
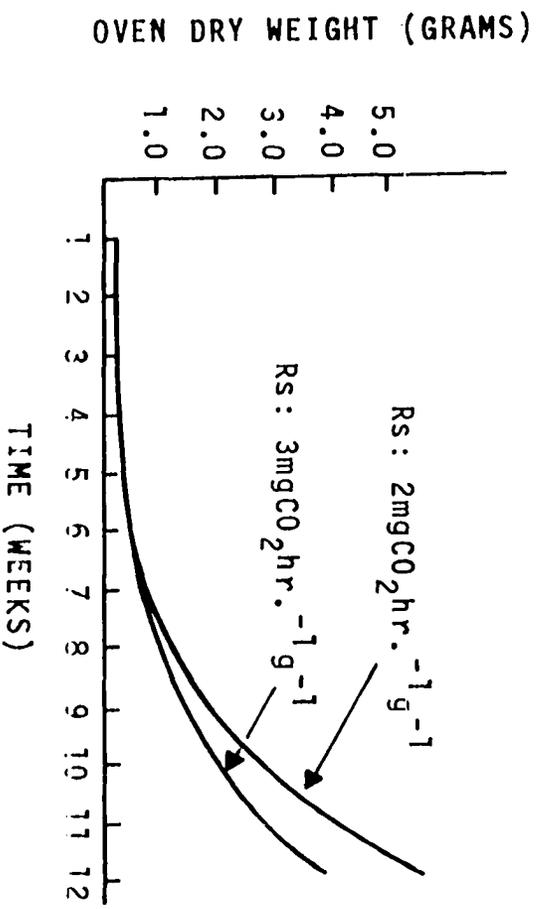
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APPENDIX

The general model form suggested for the photosynthate distribution functions was the following system of five equations:

$$k_i(t) = \frac{f_i(t)}{\sum\limits_{j=1}^{5} f_j(t)} \qquad i = 1, \cdots, 5$$

where

$k_1(t)$ = distribution of photosynthate to the apical zone for cell division.

$k_2(t)$ = distribution of photosynthate to cell elongation and primary wall formation.

$k_3(t)$ = distribution of photosynthate to secondary wall formation, lignification and stem thickening.

$k_4(t)$ = distribution of photosynthate to root growth.

$k_5(t)$ = distribution of photosynthate to leaf growth.

However, by specification:

$$\sum_{i=1}^{5} k_i(t) = 1$$

Therefore the system is under identifical and not all functions are estimable. However, if we consider the ratio of two distribution functions, say $k_i(t)/k_5(t)$, the system will be reduced by one equation and the ratios will then be estimable. We can then return to the initial system by considering:

$$k_i(t) = \{k_i(t)/k_5(t)\} / \{\sum_{j=1}^{5} k_i(t)/k_5(t)\}$$

Accordingly, observations on changes in dry weight of a given tree can be used as a first approximation to the distribution functions. Using the definition of the stem sections and one week time intervals for twelve weeks we would have:

$$k_1(t + .5) / k_2(t + .5) \doteq y_{1t} / (y_{5t} - y_{5t-1})$$

$$k_3(t + .5) / k_2(t + .5) \doteq y_2t / (y_{5t} - y_{5t-1})$$

$$k_3(t + .5) / k_2(t + .5) \doteq (y_{3t} - (y_{3t-1} + y_{1t-1} + y_{2t-1})) /$$

$$(y_{5t} - y_{5t-1})$$

$$k_4(t + .5) / k_2(t + .5) \doteq (y_{4t} - y_{4t-1}) / (y_{5t} - y_{5t-1})$$

When attempting to use sample averages of dry weights to estimate the ratios, problems with negative values are encountered.

A negative value would indicate that photosynthate is being translocated out of a plant part. This, however, would not be the case since all sample trees were undergoing rapid growth and any negative values are simply the results of sampling error. If negative estimates of the distribution functions are admitted as valid data points, this will result in not only an under estimate of the distribution of photosynthate to a particular plant part but also over estimates for the remainder of the parts in the system.

Hughes and Freeman (1967) suggest that for analyzing growth

rates using frequent small harvests that, to avoid the problem of

negative estimates of growth rates, cumulative dry weight versus

time curves should first be fitted to all of the data. Growth

analysis can then proceed from considering the first derivatives

of these estimated functions. However, to consider the ratios of

derivatives as the estimated photosynthate distribution functions

is not directly possible because of the definition of variables to

describe stem growth and the dependence of the measurements on the

one-week measurement period involved. As a modification of Hughes

and Freeman's technique the following functions were fitted to the

individual dry weight observations:

$$y_{itj} = a_i \, b_i^{\,t} \, t^{c_i}$$

i = plant part 1, --- ,5

t = time 1, --- ,12

j = sample unit

The resulting regression equations are given in Table 1. These func-

tions were then used to estimate the dry weights of the plant parts

for each of the twelve harvest times.

However, the standard statistical techniques to increase the

precision of the estimated average dry weight at each time would be

to consider initial size as a covariate and adjust all dry weight

data to an average initial size. But the cuttings selected for the

Table 1. Regression fit of the functions $\ln y_{itj} = \ln a_i$

+ $t \ln b_i + c_i \ln t$

Plant Part	$\ln a_i$	$\ln b_i$	c	Sy.x	R^2
y_1	-6.8671	.5398	.3086.5398	.6536	.98
y_2	-4.6067	.3501	.2520.3501	.7269	.93
y_3	-3.0307	.1076	.4512	.5747	.89
y_4	-2.3383	-.1416	.3883	.3962	.91
y_5	-1.5747	.5689	.2630	.4208	.94

experiment were chosen to minimize initial differences in length and number of leaves. This resulted in poor correlations of these variables with dry weights at time of harvest. For this reason plant part dry weights were related to several aspects of plant height as discussed in the main text and adjusted to the average value for all trees. The variables y_1, y_2 were related to height growth during the week prior to harvest; y_3 was related to total height at the week prior to harvest; y_4, y_5 were related to total current height.

The results of these adjustments essentially gave two data sets, one from considering the approximations to the derivatives of the cumulative dry weight versus time curves and the other from considering the dry weight values as adjusted for aspects of plant height.

The model form chosen for the right hand sides of the system was:

$$f_i(t) = \begin{cases} \alpha_i (t/T)^{\beta_i} (1-t/T)^{\gamma_i} & 0 < t < T \\ 0 & \text{otherwise} \end{cases}$$

With a logarithmic transformation this will appear as a linear function. This form was chosen because the system was designed to operate within a given growing season $(0,T)$, and also because the distribution functions are approximately equal to the relative growth of a particular plant part. Although the integrated form of $f_i(t)$ is not available in a close expression, the function is flexible enough to allow for a cumulative growth curve to range from linear to symmetric or asymmetric sigmoid shaped curves.

However, the first problem encountered is the estimation of T
or the length of the growing season. Since greenhouse grown Populus
is indeterminant in growth there is no fixed value for T. An attempt
was made to estimate this parameter from the data. The distribution
functions were fitted for a range of T values and for each value
the sum of the residual sum of squares from each regression was
computed. However the data were essentially exponential. Altering
T values had little effect on the total residual sum of squares
however, it affects the parameter estimates. For this reason, T was
set at twenty weeks for all methods of analysis.

Using this value of T, the distribution functions were then
fitted to the ratios of the estimated derivatives of the dry weight
versus time curves. Also, the distribution functions were fitted
using simple least squares with the data as adjusted by aspects of
plant height. These results are shown in Table 2.

However, the use of simple least squares implies the assumption
of additive error to the observations. Since dry weights were
adjusted by simple linear regression, the most realistic error struc-
ture would be to maintain the assumption of additive error to each
of the dry weight observations. Let the change in dry weight of
plant part j at time i be represented by the following:

$$y_{ji} = (\mu_{ji} - \mu_{ji-1}) + (\varepsilon_{ji} - \varepsilon_{ji-1})$$

Table 2. Results of analytical techniques for fitting distribution functions.

I: Ratio of derivatives

II: Simple least squares

III: Generalized least squares

	$y_1/\Delta y_5$	$y_2/\Delta y_5$	$\Delta y_3/\Delta y_5$	$\Delta y_4/\Delta y_5$
	$\ln \alpha_1/\alpha_5$	$\ln \alpha_2/\alpha_5$	$\ln \alpha_3/\alpha_5$	$\ln \alpha_4/\alpha_5$
I	-3.3603	-1.9178	-1.1515	-1.2490
II	-3.7855	-5.1531	1.1581	-1.3811
III	-3.2500	-4.4167	-8.0000	-1.4568
	$\beta_1 - \beta_5$	$\beta_2 - \beta_5$	$\beta_3 - \beta_5$	$\beta_4 - \beta_5$
I	.4366	.1915	.2089	.1642
II	.3005	-1.0780	1.4728	- .0930
III	.6797	- .6458	-2.5948	.1758
	$\gamma_1 - \gamma_5$	$\gamma_2 - \gamma_5$	$\gamma_3 - \gamma_5$	$\gamma_4 - \gamma_5$
I	- .1122	.6732	1.4677	.5402
II	-1.0644	-2.9949	.7444	.4300
III	-1.0066	-2.5149	-7.7649	-1.0227

With this as the case, then the observation's appeared for analysis as:

$$\ln (y_{ji}/y_{1i}) = \ln \left(\frac{(\mu_{ji} - \mu_{ji-1}) + (\varepsilon_{ji} - \varepsilon_{ji-1})}{(\mu_{1i} - \mu_{1i-1}) + (\varepsilon_{1i} - \varepsilon_{1i-1})}\right)$$

These observations were then fitted to the function:

$$\ln (y_{ji}/y_{1i}) = \beta^{o}_{j1} + \beta^{1}_{j1} \, z_1 + \beta^{2}_{j1} \, z_2$$

for $j = 1, \cdots, 4$ $i = 1, \cdots, 12$

where $\beta^{o}_{j1} = \ln (\alpha_i/\alpha_1)$

$\beta^{1}_{j1} = (\beta_j - \beta_1)$

$\beta^{2}_{j1} = (\gamma_i - \gamma_1)$

$z_1 = \ln (t/20)$

$z_2 = \ln (1 - t/20)$

However, using the Taylor's series expansion, the error structure would appear as follows:

$$\ln (y_{ji}/y_{1i}) \doteq \ln \left(\frac{\mu_{ji} - \mu_{ji-1}}{\mu_{1i} - \mu_{1i-1}}\right) + \left\{\left(\frac{\varepsilon_{ji} - \varepsilon_{ji-1}}{\mu_{ji} - \mu_{ji-1}}\right) - \right.$$

$$\left(\frac{\varepsilon_{1i} - \varepsilon_{1i-1}}{\mu_{1i} - \mu_{1i-1}}\right) \left. \right\} - \frac{1}{2} \left\{\frac{(\varepsilon_{ji} - _{ji-1})^2}{(\mu_{ji} - \mu_{ji-1})^2} - \right.$$

$$\frac{(\epsilon_{1i} - \epsilon_{1i-1})^2}{(\mu_{1i} - \mu_{1i-1})^2} \} + \ldots$$

Since samples are independent, we would then have:

$$E (\ln (y_{ji}/y_{1i})) \doteq \ln \left(\frac{\mu_{ii} - \mu_{ii-1}}{\mu_{1i} - \mu_{1i-1}} \right) - \tfrac{1}{2} \{ \frac{\sigma_{ji}^{i} + \sigma_{ji}^{i-1}}{(\mu_{ji} - \mu_{ji-1})^2} -$$

$$\frac{\sigma_{11}^{i} + \sigma_{11}^{i-1}}{(\mu_{1i} - \mu_{1i-1})^2} \}$$

However, if we just consider the first two terms of the Taylor's series expansion we have:

$$E (\ln (y_{ji}/y_{1i})) \doteq \ln \{ \frac{\mu_{ji} - \mu_{ji-1}}{\mu_{1i} - \mu_{1i-1}} \}$$

The covariance between any two variables (j, k) at a given time would be:

$$Cov (\ln (y_{ji}/y_{1i}), \ln (y_{ki}/y_{1i})) \doteq$$

$$\frac{(\sigma_{jk}^{i} + \sigma_{jk}^{i-1})}{(\mu_{ji} - \mu_{ji-1}) (\mu_{ki} - \mu_{ki-1})} - \frac{(\sigma_{k1}^{i} + \sigma_{k1}^{i-1})}{(\mu_{ki} - \mu_{ki-1}) (\mu_{1i} - \mu_{1i-1})}$$

$$\frac{(\sigma_{j1}^{i} + \sigma_{j1}^{i-1})}{(\mu_{ji} - \mu_{ji-1}) (\mu_{1i} - \mu_{1i-1})} + \frac{(\sigma_{11}^{i} + \sigma_{11}^{i-1})}{(\mu_{1i} - \mu_{1i-1})^2}$$

And the covariance between any two parts (j, k) at succeeding times (i - 1, i) would be: Cov $(\ln (\hat{y}_{ji}/\hat{y}_{1i})$, $\ln (\hat{y}_{ki-1}/\hat{y}_{1i-1}) \doteq$

$$\frac{\sigma_{kl}^{i-1}}{(\mu_{ki} - \mu_{ki-2})(\mu_{1i} - \mu_{1i-1})} - \frac{\sigma_{jk}^{i-1}}{(\mu_{ji} - \mu_{ji-1})(\mu_{ki-1} - \mu_{ki-2})}$$

$$- \frac{\sigma_{1l}^{i-1}}{(\mu_{1i} - \mu_{1i-1})(\mu_{1i-1}\ \mu_{1i-2})} + \frac{\sigma_{jl}^{i-1}}{(\mu_{ji} - \mu_{ji-1})(\mu_{1i-1} - \mu_{1i-2})}$$

The variance and covariance terms can be estimated by considering that for each time and plant part we have conducted a simple linear regression of dry weight (y_{ijk}) on some aspect of height (x_{ijk}) where:

$$y_{ijk} = \alpha_{ij} + \beta_{ij}x_{ijk} + \Sigma_{ijk}$$

If we then use simple least squares analysis to estimate $\hat{\alpha}_{ij}$, $\hat{\beta}_{ij}$, we can then predict for some index value $(x_{i'j})$ an adjusted dry weight $(\hat{y}_{ij})$.

Then:

$$\text{Cov}\ (y_{ij}, y_{i'j}) = \sigma_{ii'j}$$

$$= \text{Cov}\ (y_{ijk}\ y_{i'jk})\ \{\ 1 + \frac{\text{Cov}\ (x_{ijk}\ x_{i'jk'})}{V\ (x_{ijk})\ V\ (x_{i'jk'})}\ (x_{i'j} - \bar{x}_{ij})$$

$$(x_{i'j} - \bar{x}_{ij})\}\ \frac{1}{n}$$

The covariance matrix for plant parts at a specified time can be estimated by considering the residuals for each set of tree measurements $(\hat{\underset{\sim}{\varepsilon}}_{i.})$

$$\text{Cov } (y_{ijk} \; y_{i'jk'}) = \sum_{j=1}^{n} (\hat{\underset{\sim}{\varepsilon}}_{i'.} \; \hat{\underset{\sim}{\varepsilon}}_{i'.}) \, / \, n - 2$$

We can then proceed to estimate the bias and the complete variance-covariance structure for the observations. This information can be incorporated into the model as a transformation to eliminate the effects of changes in variance and autocorrelation through the use of generalized least squares. The results of this analysis are given in table 2.