

GENETIC VARIATION IN GROWTH AND YIELD COMPONENTS  
OF JUVENILE BALSAM POPLAR (Populus balsamifera L.)  
GROWING IN NORTHWESTERN ONTARIO

by

Frank Schnekenburger ©

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## ABSTRACT

A nursery and greenhouse study of balsam poplar (Populus balsamifera L.) were carried out in Thunder Bay, Ontario, to study the extent and nature of variation in growth and its relation to the following yield components: phenology, assimilation rate, leaf morphology, and assimilate distribution. The studies involved clones of four sources of balsam poplar selected along an approximate latitudinal gradient: N. Wisconsin (45-46°N), Thunder Bay (48-49°N), Pickle Lake (51-52°N), and Severn River (53-54°N). As part of the greenhouse study, the effects of a reduction in the daily period of photosynthate production were studied. For this purpose, plants were grown under either a normal or reduced photosynthetic period of approximately 16 or 8 hours per day, respectively. The reduced photosynthetic period was achieved by covering plants with opaque shade cloth from 4:00 p.m. of one day until 8:00 a.m. of the next day. Low-level incandescent lighting provided an 18-hour photoperiod that prevented height growth cessation under both photosynthetic periods.

The nursery study demonstrated significant variation among clones of the Thunder Bay and Pickle Lake sources, in terms of date of bud break and growth cessation, initial plant height, and total shoot elongation. Date of growth cessation differed significantly between sources, occurring eight days earlier for the Pickle Lake source than for the Thunder Bay source; source differences in date of bud break were not significant. Total shoot elongation was moderately correlated with date of growth cessation, but not with date of bud break.

The greenhouse study entailed assessment of clones from all four sources. Clonal variation was significant in terms of leaf, stem, and root dry weight; leaf area and number; shoot length; and root number. Relative growth rate (RGR) differed significantly among sources; clonal variation in RGR and in relative leaf weight growth rate (RLwGR) and relative leaf area growth rate (RLaGR) was significant for some sources, but not others. Differences in RGR were closely linked to differences in unit leaf rate, but not to leaf growth characteristics. Plants under the reduced photosynthetic period produced less dry weight and leaf area, fewer leaves, and less shoot growth than those under the normal photosynthetic period. Relative growth rate, unit leaf rate, and the allometric constant relating the relative rate of shoot growth to that of root growth were also lower under the reduced photosynthetic period. Leaf area ratio was greater under the reduced photosynthetic period, largely due to greater specific leaf area. Marked changes in clonal rankings based on relative growth rates suggest that differences exist among the clones studied in their response to the reduced photosynthetic period. In general, the reduced photosynthetic period affected the southern sources to a lesser degree than the northern sources.

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## 1 INTRODUCTION

An important consideration in the development of tree improvement programs is the level and distribution of genetic variation of the species of interest. This factor will have a profound effect on the potential for tree improvement and the manner in which improvement activities are carried out.

Genetic variation within a species may be distributed among various levels of species organization: 1) widely separated geographic populations, 2) local populations, 3) families within populations, and 4) individuals within families. The distribution of the total variation within and among these levels will vary with species and the traits of interest. Knowledge of the distribution is essential for the genetic improvement of a species (Zobel and Talbert, 1984).

Genetic tests may be used to define the level and distribution of variation for various traits of interest. Traits most often studied are those of direct economic significance such as growth and yield. It is also of interest and importance, however, to understand the physiological basis of observed variation in growth and yield.

Many studies have been carried out in efforts to examine the physiological basis of genetic variation in growth and

yield of species of the genus Populus L. , but little of this work has been applied to balsam poplar (P. balsamifera L.). The range of balsam poplar extends through the Boreal, Great Lakes-St. Lawrence, and Acadian Forest regions of Canada. It grows well on a wide range of sites, exhibiting very rapid height and diameter growth. Balsam poplar is suitable for several products, including production timber, pulpwood, plywood, wafer-board, and particle-board. It can be vegetatively propagated, coppices readily, is easy to breed, and hybridizes readily with other poplars. Thus, balsam poplar may be well suited for fast growth, short rotation plantation culture. Its potential in tree improvement programs will depend in part on the level and nature of genetic variation that exists in the species.

The current work entailed a nursery and greenhouse study of balsam poplar, designed to examine the nature and extent of variation in growth and its relation to specific yield components. Clones of four sources of balsam poplar were utilized: N. Wisconsin (45-46° N), Thunder Bay (48-49° N), Pickle Lake (51-52° N), and Severn River (53-54° N). The purpose of the nursery study was to examine variation in height growth and phenology. The purpose of the greenhouse study was to examine variation in growth and specific yield components: assimilation rate, leaf morphology, and assimilate distribution.

As part of the greenhouse study, the effect of reducing the daily period of photosynthate production, i.e. the photosynthetic period, was also explored. While the photoperiodic response of Populus has been well demonstrated in several species, little work has dealt with the effects of changes in photosynthetic period independently of changes in photoperiod. The aim here was to study the growth response to a reduced photosynthetic period, and to determine whether variation exists in the degree of the response.

## 2 LITERATURE REVIEW

The purpose of this literature review is two-fold. The first section of the review examines studies of genetic variation in growth, yield, morphology, phenology, and physiology within the genus Populus. Emphasis is placed on the relationships observed among these variables, which will here be termed plant yield components. The purpose is to identify and quantify potential causal relationships between growth and other yield components.

The second section of the review provides an introduction into the theory and techniques of plant growth analysis. Growth analysis is an effective method for studying genetic and environmental variation in plant growth over time. It can be used to study the physiological basis of observed variation in growth and yield.

### VARIATION IN YIELD COMPONENTS WITHIN THE GENUS POPULUS

Variation in the growth and yield of forest trees is largely determined by the following factors: 1) the seasonal pattern and duration of growth, 2) the rate of photosynthesis and its relation to respiration, 3) the distribution and allocation of photosynthate, and 4) general plant morphology (Ledig, 1969; Luukkanen and Kozlowski, 1972; Farmer, 1978).

The extent to which tree growth of a species can be enhanced through selective breeding and genetic manipulation depends largely on the magnitude and nature of genetic variation in these factors.

Relatively little work has been done in the study of genetic variation in the growth and yield of P. balsamifera L. Several other species and hybrids of Populus, however, have been the focus of studies of variation in (and relationships among) growth, phenology, morphology, and physiology.

The following subsections will serve to describe observed genetic variation in yield components. Each subsection deals with one factor, defined as follows: growth, phenology, assimilate distribution, leaf morphology, and photosynthesis and respiration.

### Variation In Growth

Phenotypic variation has been observed within and among naturally occurring stands of Populus species. For example, Einspahr and Benson (1967), working with naturally occurring clones of P. tremuloides Michx., observed considerable variation due to clones, stands, and geographic location, in terms of height, diameter, tree volume, and crown volume growth. Barnes (1969) studied the natural variation among clones of P. tremuloides and P. grandidentata Michx. on two sites of distinct soil characteristics. He observed differences in phenology, and in height and diameter growth,

both among sites and among clones within sites. On a given site, phenological differences also existed between the two species.

Phenotypic variation reflects the effects of environmental and genetic factors. These two components of variance can be delineated and estimated through controlled experiments of appropriate design. Using this strategy, several workers have demonstrated the presence of significant genetic variation in height, diameter and volume growth within species and hybrids of Populus (e.g., Curlin, 1967; Farmer and Wilcox, 1968; Cannell and Willett, 1976). Using provenance trials, Ying and Bagley (1976) and Kelly et al. (1978) demonstrated variation in height and diameter growth due to provenances, families within provenances and clones within families of P. deltoides. In these two studies, each of the three variance sources (provenances, families, and clones) accounted for comparable proportions of variation, ranging from 8 to 18 percent of total variation. Error or ramet-within-clone variance accounted for 53 to 72 percent. Also working with P. deltoides, Mohn and Randall (1971) determined that clonal variation accounted for 30 to 50 percent and 20 to 35 percent of the total variation in height and diameter growth, respectively. Variation among half-sib families of the same species accounted for 6 to 10 percent and 13 percent of the variation in height and diameter growth,

respectively (Farmer, 1970a).

While genetic variation in growth is in itself of importance to the tree breeder, genotype by environment interaction is also important. The presence of an interaction implies that the relative growth response of clones differs in different environments. This may mean a change in the ranking of clones and/or changes in the magnitude of the differences among them. If interaction is significant, consideration must be given to the site on which various clones will be grown. Significant clone by site interactions in height and diameter growth of P. deltoides were observed by Randall and Mohn (1969), Mohn and Randall (1973), and Randall and Cooper (1973).

Certain silvicultural treatments may also interact with genotype, and therefore require consideration in their application. For example, a significant clone by fertilizer treatment interaction was observed in the height, diameter, and volume growth of 22 clones of P. deltoides by Curlin (1967). He noted that several clones, exhibiting relatively poor growth when unfertilized, had superior growth when fertilized; the reverse was also true.

### Variation In Phenology

The presence of genetic variation within a species is the result of one or more of several mechanisms that can affect gene and genotypic frequencies of a population. One

such mechanism is natural selection, which leads to the development of individuals that are generally well adapted to a given set of environmental factors.

One important environmental factor affecting genetic differentiation within Populus is the variation in photoperiod and temperature associated with latitude. Adaptation to local photoperiodic and temperature regimes associated with latitude results in individuals which vary in their phenological and growth responses to these environmental factors.

#### Date of Growth Cessation

Negative correlations between source latitude and date of growth cessation have been observed in provenance trials of P. tremula L., P. trichocarpa Torr. & Gray, P. balsamifera, P. deltoides, and P. tremuloides (Sylvén, 1940; Pauley and Perry, 1954; Cannell and Willett, 1976; Brissette and Barnes, 1984). These works suggest that there is a clinal trend in the variation in date of growth cessation resulting from adaptation to photoperiod. Pauley and Perry (1954) noted that genetic variation in the photoperiodic response occurred locally, even among sources from areas of uniform photoperiod. They offered the following explanation:

Through the selective pressure exerted by the first killing frosts of autumn, only those genotypes capable of terminating height growth at a sufficiently early date to escape such frosts are capable of survival. Within any uniform day-length zone, therefore, where the growing season varies considerably in length, due to topography or other factors, the hypothesis may be made

that adaptation to any particular length of growing season is effected through the selection of those genotypes having a suitable photoperiodic response to the prevailing day-length regime of that latitude.

This hypothesis was supported by positive correlations between the length of the growing season associated with the source location and the date of growth cessation of the source in a provenance trial.

Avanzo (1969) and Eldridge et al. (1972), working with P. deltoides, attributed the superior height growth of southern provenances, relative to northern provenances, to the earlier growth cessation of the latter. The provenances exhibited comparable growth rates during the main part of the growing season. In a study with P. tremuloides, Hoffmann (1953) observed that the height growth of half-sib progeny, differing in paternal origin, was strongly affected by the latitude of the pollen source.

Departures from a negative correlation between height growth and latitude have also been observed. Ying and Bagley (1976) and Kelly et al. (1978) reported that some southern sources of P. deltoides suffered greater mortality and winter die back than the northern sources. Apparently the southern sources, adapted to shorter photoperiods, continued growth through the end of the local growing seasons and were adversely affected by the first fall frosts.

Evidence that hybridization may lead to clones exhibiting delayed growth cessation and increased yield was suggested by Nelson et al. (1982). These workers studied the

growth of certain exotic hybrids which maintained leaves for a period of several weeks after the time of leaf fall of the native species P. tremuloides and P. grandidentata, in Michigan and Wisconsin. They observed substantial rates of photosynthesis in the hybrids during this period, and suggested that this may be important in the accelerated growth of the hybrids. Pryor and Willing (1965) discussed the potential for developing clones adapted to specific latitudes through selection and hybridization.

#### Date Of Bud Break

Date of bud break is under strong genetic control (Ying and Bagley, 1976). Estimates of the broad-sense heritabilities of bud break in P. deltoides by Wilcox and Farmer (1967) were 0.97 and 0.99. Thielges and Beck (1976) observed comparable values, noting also that heritability increased markedly with the length of chilling period. Also using P. deltoides, Farmer (1970a) observed that familial variation accounted for 87 and 92 percent of the total variation in foliation date.

Date of bud break is likely less important than date of height growth cessation in determining the latitudinal trends in height growth observed in provenance trials. Negative correlations between latitude and date of bud break have been observed in provenance trials of P. deltoides (Ying and Bagley, 1976; Kelly et al., 1978) and P. tremuloides (Brissette and Barnes, 1984), with northern provenances

flushing before southern provenances. In most of these cases, however, wide within-provenance variation existed and the latitudinal trend was inconsistent. In fact, Eldridge et al. (1972) observed a positive correlation between latitude and date of bud break in a provenance trial of P. deltoides.

Bud break of Populus plants that have received their chilling requirements occurs largely in response to increases in springtime temperature, rather than increases in photoperiod (Thielges and Beck, 1976). This contrasts growth cessation, which is affected largely by photoperiod.

#### Variation In Assimilate Distribution

The distribution of assimilate among plant organs reflects important source-sink relationships within the plant. Relative sink strength affects the distribution of assimilate, and may thereby affect productivity (Farmer, 1978). In trees, the proportion of assimilate which is reinvested into photosynthetic apparatus (stem and leaves) versus non-photosynthetic apparatus (roots) will directly affect overall photosynthetic capacity.

The early growth of young plants generally proceeds at an exponential rate. The relative growth rate of both shoot and roots is constant during this period of exponential growth. An allometric function (Huxley, 1932) is frequently used to describe the relationship between the growth of shoot and roots, in the following manner:

$$\text{shoot weight} = a(\text{root weight})^K$$

In this function, K, the allometric constant, is the ratio of the relative growth rate of the shoot to that of roots in plants exhibiting exponential growth. If K is less than 1.0, the shoot/root ratio is decreasing with increasing plant weight, whereas if K is greater than 1.0, the shoot/root ratio is increasing with increasing plant weight (Hunt, 1978). A value of 1.0 implies that the relative growth rates of both shoot and roots are the same, and therefore, that the shoot/root ratio remains constant as plant weight increases.

It has been noted that shoot/root ratio generally decreases with total plant weight in woody species (Ledig and Perry, 1965). Treatments that affect plant size, therefore, may lead to changes in the shoot/root ratio which are independent of any real change in the relative growth rate of shoot versus that of roots, as indicated by the allometric constant. Ledig and Perry (1965) cite numerous examples which suggest that the allometric constant is indeed very stable and that "drastic treatments" are required to significantly alter the relative growth of shoot and roots. Nevertheless, these authors observed significant differences in allometric constants between certain progenies of loblolly pine (Pinus taeda L.).

In Populus, significant variation in the relative growth rate of shoot versus roots has been observed in some cases,

but not others. Cannell and Willett (1976) observed that the allometric constant for clones of P. trichocarpa decreased significantly with increasing source latitude. The shoot/root ratio was also negatively correlated with source latitude, due in part to the earlier height growth cessation of the more northern sources, and a subsequent increase in the relative growth rate of roots relative to that of shoots. Drew and Bazzaz (1978), on the other hand, found no significant differences in the allometric constants of three sources of P. deltoides selected along a latitudinal gradient spanning 14 degrees. They did note, however, that the intercepts of the allometric functions differed significantly and were positively correlated with source latitude. As the authors note, the more northern populations "were therefore allocating more dry matter to shoot growth relative to root growth than the more southerly populations, but the rate of relative growth as evidenced by allometric coefficients was not different for the three".

#### Variation In Leaf Morphology

Extensive geographic variation in leaf morphological characteristics has been observed within Populus. Marcet (1961) was able to distinguish two distinct leaf types of P. deltoides, and suggested that the two forms represented north and south ecotypes of the species. Extensive inter- and intra-clonal variation in leaf morphology within natural

stands of P. tremuloides and P. grandidentata has also been noted (Barnes, 1969).

Ying and Bagley (1976) observed genetic variation of a northwest to southeast clinal form in the leaf shape and morphology of P. deltoides, though its adaptive significance was not clear. In P. x euramericana (Dode) Guinier, clonal variation in leaf angle has been shown to affect light interception and to some extent growth performance (Gordon and Promnitz, 1976). Peck and Wallner (1982) demonstrated ecotypic variation in the heat tolerance of leaves of P. tremuloides from three sources of differing altitude. These workers observed a marked correlation between heat tolerance and the elevation of the source, which they suggested was the result of adaptation to the temperature associated with the source locale.

Many studies have examined the variation in leaf morphology and leaf area of species and hybrids of Populus, and their relation to observed variation in growth and physiology. Siwecki and Kozlowski (1973) examined the relationship between the rate of transpiration and the leaf characteristics of six clones of Populus. They observed significant differences among clones in both internal leaf anatomy and in stomatal size, frequency and control. Transpiration rates, which also varied markedly among clones, were closely related to the characteristics of the stomata, but not to internal leaf anatomy. Other work with these

clones suggests that variation in photosynthetic efficiency is related to variation in stomatal aperture (Luukkanen and Kozlowski, 1972).

Other studies have also revealed substantial variation in the stomatal characteristics within Populus species and hybrids that may be related to parentage and source origin (Pallardy and Kozlowski, 1979a; Ceulemans et al., 1984). Furthermore, variation in characteristics of adaptive significance (such as growth, water use efficiency, and gas exchange efficiency) may in part be related to observed differences in stomatal characteristics (Ceulemans et al., 1978, 1980; Pallardy and Kozlowski, 1979a, 1979b, 1981; Ceulemans and Impens, 1980; Blake et al., 1984).

#### Variation In Photosynthesis And Respiration

Rates of photosynthesis and respiration in Populus have been shown to vary with several factors. These include environmental variables such as temperature, irradiance, photoperiod, and moisture stress (Bate and Canvin, 1971; Furukawa, 1972; Tsel'niker et al., 1983; Reich, 1984a). Variation in rate of photosynthesis and respiration has also been observed among leaves of the same individual and has been related to leaf development, stem position, and age, and long-shoot versus short-shoot leaves (Larson and Gordon, 1969; Dickmann, 1971; Isebrands and Larson, 1973; Ceulemans and Impens, 1979; Nelson and Michael, 1982; Reich, 1984b). Bourdeau (1958) observed differences in photosynthesis and

respiration rates between male and female trees of P. tremuloides. It has been shown for P. tremuloides that the bark may also contribute significantly to photosynthate production (Schaedle and Foote, 1971; Foote and Schaedle, 1978), but in a pattern exhibiting an age-related decline (Brayman and Schaedle, 1982).

Ledig (1976) cited numerous references regarding genetic variation in the rates of photosynthesis and respiration of forest trees. Genetic variation has been observed within and among species and hybrids of Populus, in rates of photosynthesis, photorespiration, and dark respiration (Makedonska and Yordanov, 1969; Luukkanen and Kozlowski, 1972; Ceulemans and Impens, 1980).

Gordon and Promnitz (1976), working with P. x euramericana, also found substantial variation in rates of net photosynthesis and photorespiration as affected by leaf age and light intensity. They indicated that there was a direct relationship between these factors and plant growth. Positive correlations between photosynthetic rate and growth in Populus have been observed (e.g., Huber and Polster, 1955; Gatherum et al., 1967). Huber and Polster (1955), however, noted that clonal differences in the total leaf area caused more of the difference in the rates of photosynthesis per plant than did variation in the rate of photosynthesis per unit leaf area.

### Summary Of Yield Component Effects On Growth

Genetic variation of varying degrees exists in growth and yield within species of Populus. This variation may be associated with provenances, families, and clones. Similarly, variation has also been observed in several other yield components. The relative significance of these yield components in effecting variation in growth and yield is, however, difficult to ascertain.

Phenology has marked effects on height growth and assimilate distribution; date of growth cessation seems more important than date of bud break in this regard. Marked variation in leaf morphology and physiology has been observed, and frequently related to characteristics of adaptive significance, though not often directly to growth. But since they affect the potential for adaptability to adverse environments (and hence potential for survival), leaf characteristics must be considered as important components of growth and yield.

Variation in rates of photosynthesis and respiration have also been noted, and correlated with differences in growth and yield in some cases, but not in others. This could in part reflect shortcomings of the sampling procedure typically used in monitoring gas exchange rates; plants are usually sampled periodically and for short durations at a time.

## PLANT GROWTH ANALYSIS

Growth analysis is an analytical technique that is used to study the effects of genetic and environmental factors on plant growth. The technique focuses on relative changes in growth rate and growth processes, rather than on differences in final yields; plant growth is partitioned into component processes which help to explain the basis of yield differences.

The procedure of growth analysis was initially developed by Briggs et al. (1920a, 1920b), who combined the concepts of relative growth rate and net assimilation rate, first formulated by Gregory (1917), Blackman (1919), and Fisher (1920). The technique has frequently been applied in the study of growth variation in forest tree species (e.g., van den Driessche and Wareing, 1966; Newhouse and Madgwick, 1968; Ledig and Perry, 1969; Madgwick, 1971; Farmer, 1980).

### Component Indices Of Plant Growth

Growth analysis is based on three primary growth attributes or growth indices: total plant dry weight, leaf dry weight, and leaf area. By monitoring changes in these attributes over time, it is possible to derive estimates of relative growth rates, assimilation rates and photosynthate partitioning. These components of growth will be referred to as component indices.

Absolute growth rate (AGR) describes changes in plant weight over time:

$$\text{AGR} = d\text{Tw}/dt \quad [2.1]$$

where Tw = total plant dry weight  
t = time

However, absolute growth rate does not account for the effect of plant size on changes in weight; it is an absolute, not relative measure. Blackman (1919) described plant growth in terms of a compound interest function:

$$\text{Tw}_2 = \text{Tw}_1 * \exp(q * (t_2 - t_1)) \quad [2.2]$$

where Tw<sub>1</sub> = total plant dry weight at time t<sub>1</sub>  
Tw<sub>2</sub> = total plant dry weight at time t<sub>2</sub>

Blackman (1919) referred to q as the efficiency index of dry weight production for the stated period.

The parameter q is equivalent to the relative growth rate (on a total dry weight basis), or RGR. RGR is the change in plant dry weight per unit growing material per unit time. It is defined as follows:

$$\text{RGR} = (d\text{Tw}/dt)(1/\text{Tw}) \quad [2.3]$$

RGR is also referred to as the logarithmic growth rate, since the following is also true:

$$\text{RGR} = d(\ln(\text{Tw}))/dt \quad [2.4]$$

The same principle of relative growth rate that is applied to total plant dry weight to derive RGR, can be applied to leaf dry weight and leaf area to derive, respectively, relative leaf weight growth rate (RLwGR) and relative leaf area growth rate (RLaGR). These are defined as follows:

$$\text{RLwGR} = (dLw/dt)(1/Lw) \quad [2.5]$$

$$\text{RLaGR} = (dLa/dt)(1/La) \quad [2.6]$$

where Lw = leaf dry weight  
La = leaf area

Unit leaf rate, ULR (also referred to as net assimilation rate, NAR), is defined as the change in plant dry weight per unit of assimilatory material per unit time. It provides a measure of the efficiency of energy capture and conversion to photosynthate and dry matter. Where assimilatory capacity is measured as leaf area (La), unit leaf rate is defined as follows:

$$\text{ULR} = (dTw/dt)(1/La) \quad [2.7]$$

Relative growth rate (RGR) and unit leaf rate (ULR) define the change in total dry weight over time (dTw/dt), the former on a per unit total dry weight basis, the latter on a per unit leaf area basis.

Leaf area ratio, LAR, provides a measure of plant leaf production. It is the ratio of leaf area (La) to total dry weight (Tw) at any time:

$$\text{LAR} = (\text{La}/\text{Tw}) \quad [2.8]$$

LAR describes the amount of leaf area produced per unit total dry matter production.

Equations 2.3, 2.7, and 2.8 are related such that at any instant:

$$(\text{dT}/\text{dt})(1/\text{Tw}) = (\text{dT}/\text{dt})(1/\text{La}) * (\text{La}/\text{Tw}) \quad [2.9]$$

that is,

$$\text{RGR} = \text{ULR} * \text{LAR} \quad [2.10]$$

Leaf area ratio can be divided into two sub-components. The first of these, leaf weight ratio (LWR), describes the proportion of total dry matter production that has been invested into leaf weight:

$$\text{LWR} = \text{Lw}/\text{Tw} \quad [2.11]$$

The second sub-component of leaf area ratio is specific leaf area (SLA), the ratio of leaf area to leaf weight. It reflects the expansion of leaf matter into space:

$$\text{SLA} = \text{La}/\text{Lw} \quad [2.12]$$

Combining equations 2.11 and 2.12 yields

$$\text{LAR} = \text{LWR} * \text{SLA} \quad [2.13]$$

Combining equations 2.10 and 2.13 yields

$$\text{RGR} = \text{ULR} * \text{LWR} * \text{SLA} \quad [2.14]$$

The leaf area and leaf weight ratios describe the proportion of total dry matter that has been invested into leaf area and leaf dry matter, respectively, up to a specified point in time. Other measures of dry matter partitioning are found in the indices described by Potter and Jones (1977). The leaf area partition coefficient, LAP, describes at any instant, the proportion of dry matter production going into new leaf area. It is defined as follows:

$$\text{LAP} = (\text{dLa}/\text{dt})/(\text{dTw}/\text{dt}) \quad [2.15]$$

The leaf weight partition coefficient, LWP, similarly describes the proportion of dry matter production going into new leaf weight:

$$\text{LWP} = (\text{dLw}/\text{dt})/(\text{dTw}/\text{dt}) \quad [2.16]$$

Further discussions of these indices may be found in the reviews of Causton (1970), Evans (1972), Ledig (1974), Hunt (1978), and Wilson (1981).

### Procedures Of Growth Analysis

Growth analysis involves two distinct steps: 1) periodic sampling of plant material to derive estimates of growth indices over time; and 2) estimation of the component

indices. The sampling procedure is destructive, making it necessary to have a population of individual plants to draw from. One population of plants is required for each genetic and/or environmental treatment being studied; the population serves to reflect treatment effects on plant growth over time.

At specified times, a sample of plants is drawn from each population. The samples for any one time are collectively referred to as a harvest; the period between any two successive harvests is referred to as a growth period. Each harvest provides an estimate of treatment effects on plant growth, as reflected by the growth indices. Once all harvests have been completed, the component indices can be estimated.

Two general procedures have been developed to carry out growth analysis: the classical approach and the functional approach. These two approaches differ both in the sampling procedure used to collect the growth data, and the subsequent analysis used to derive estimates of the component indices.

#### Classical Growth Analysis

In the classical approach to growth analysis, sampling is designed to provide reliable estimates of average total dry weight, leaf dry weight, and leaf area at each harvest, for each population (treatment). Average values for the component indices, absolute growth rate (AGR), relative growth rate (RGR), unit leaf rate (ULR), and leaf area ratio

(LAR), are then estimated for each growth period. The following formulae are applied in classical growth analysis to derive estimates of component indices.

$$\begin{aligned} \text{AGR} &= 1/(t_2 - t_1) \int_{t_1}^{t_2} [(dT_w/dt)dt] \\ &= (T_{w2} - T_{w1}) / (t_2 - t_1) \end{aligned} \quad [2.17]$$

$$\begin{aligned} \text{RGR} &= 1/(t_2 - t_1) \int_{t_1}^{t_2} [(dT_w/dt)(1/T_w)dt] \\ &= [\ln(T_{w2}) - \ln(T_{w1})] / (t_2 - t_1) \end{aligned} \quad [2.18]$$

Equation 2.18 can be derived from Equation 2.2, noting that  $q$  is equivalent to RGR. For unit leaf rate,

$$\text{ULR} = 1/(t_2 - t_1) \int_{t_1}^{t_2} [(1/L_a)(dT_w/dt)dt] \quad [2.19]$$

This function cannot be integrated unless the relationship between  $T_w$  and  $L_a$  is known. If this relationship is assumed to be linear then,

$$\text{ULR} = [(T_{w2} - T_{w1}) / (L_{a2} - L_{a1})] * [(\ln(L_{a2}) - \ln(L_{a1})) / (t_2 - t_1)] \quad [2.20]$$

Other forms of this function, based on other assumptions about the relationship between  $T_w$  and  $L_a$ , are given by Radford (1967). For leaf area ratio,

$$\text{LAR} = 1/(t_2 - t_1) \int_{t_1}^{t_2} [(L_a/T_w)dt] \quad [2.21]$$

This function cannot be integrated unless the relationship

between  $La/Tw$  and  $t$  is known. If it is assumed to be linear, then,

$$LAR = [(La_1 / Tw_1) + (La_2 / Tw_2)] / 2 \quad [2.22]$$

Further discussion of these functions may be found in the work of Williams (1946), Whitehead and Myerscough (1962), Causton (1970), and Ondock and Kvet (1971).

### Functional Growth Analysis

The functional approach to growth analysis involves fitting mathematical functions to the primary growth data. A separate function is fit for each population (treatment) and growth index (total dry weight, leaf dry weight, and leaf area). Typically, this approach entails more frequent harvests, but smaller sample sizes, than the classical approach.

The form of the function is at the discretion of the investigator. A large body of work, however, has developed around the application of polynomial functions fitted to logarithmically transformed growth data (e.g., Hughes and Freeman, 1967; Elias and Causton, 1976; Nicholls and Calder, 1973; Hunt and Parsons, 1974, 1977; Hunt, 1978, 1979).

These functions are of the form

$$\ln(Y) = b_0 + b_1 t + b_2 t^2 + \dots \quad [2.23]$$

where  $Y = Tw, Lw, \text{ or } La$   
 $b_i = \text{regression coefficients}$   
 $t = \text{time}$

Functions of this form may be readily fit to data using linear regression analysis.

Once a regression equation has been fit for each growth index of a population, instantaneous estimates of the component indices may be derived for any point in time in the study using the equations previously described (Equations 2.1 to 2.16).

The functional approach to growth analysis has several advantages over the classical approach (Nicholls and Calder, 1973; Hunt, 1979):

1) estimates of growth indices are derived directly from the regression equations, without the need of assumptions regarding the relationship of growth indices over time;

2) information from all harvests is applied in determining component indices, not just information from adjacent harvests; and,

3) harvests can be smaller and at more frequent intervals, serving to more evenly distribute the sampling work over the entire study period.

### 3 METHOD

The current work involved two separate but related studies. The first of these was a nursery study that was carried out in the summer of 1983. The purpose of the nursery study was to examine variation in height growth and phenology within and between two provenances of balsam poplar.

The second study was carried out in a greenhouse in the summer of 1984. The purpose of the greenhouse study was to examine variation in growth, assimilation rate, leaf morphology, and assimilate distribution, and their interrelationships, within and among four provenances of balsam poplar. In addition, the effects of a reduced photosynthetic period were also examined.

#### SOURCE OF PLANT MATERIAL

Over the period of 1981 to 1983 a small nursery of balsam poplar was established at Lakehead University, Thunder Bay, Ontario, by Dr. R.E. Farmer. The nursery contains approximately 50 clones from each of four provenances: Northern Wisconsin (45 to 46° north latitude), Thunder Bay (48 to 49° N), Pickle Lake (51 to 52° N), and Severn River (53 to 54° N). The wide range in latitude given for each

provenance reflects the broad area over which clones within a provenance were selected. The four provenances roughly define a south to north latitudinal gradient.

### Nursery Layout

Each clone in the nursery was represented by several ramets, established in uniform rows within blocks. The manner in which ramets were assigned within blocks differed among the provenances. The Thunder Bay and Pickle Lake clones were established in the nursery in the summer of 1982. Fifty clones from each provenance were established in four rectangular blocks. A single ramet of each clone was assigned to each block. The randomization of ramets within blocks was in the manner of a split-plot design; one half of each block was restricted for ramets of the Thunder Bay clones, the other half for ramets of the Pickle Lake clones.

Approximately 50 clones from each of the N. Wisconsin and Severn River provenances were established in the nursery in the summer of 1983. Four to six ramets of each clone were assigned to one of two large blocks. They were not located in a random manner, nor with consideration for a particular experimental design.

## NURSERY STUDY

The purpose of the nursery study was to investigate the extent of genetic variation in height growth and phenology within, and differences between, two provenances of balsam poplar. The study entailed non-destructive sampling of all ramets of the Thunder Bay and Pickle Lake clones in the nursery over the 1983 growing season (the second year of growth for the plants). Sampling began in April of 1983 (prior to vegetative bud break) and continued until September of that year (the time of growth cessation). The use of these clones was possible because of the random manner in which the ramets had been established.

### Response Variables

A total of eight response variables were monitored for the nursery study. Initial plant height, date of bud break, periodic shoot growth, and total shoot elongation were measured directly from each ramet. Derived from these measurements were date of growth cessation, length of the shoot growth period, final plant height, and average daily shoot elongation. Periodic shoot growth and average daily shoot elongation consisted of several measurements for each ramet; all other variables consisted of a single measurement for each ramet. The following describes the response variables in detail.

Initial Plant Height. On April 10 and 11, 1983, prior to bud break, the height of each ramet was measured. Initial height was taken as the distance from the tip of the plant to the ground and was measured to the nearest 0.1 cm.

Date of Bud Break. Ramets were subsequently monitored at two to four day intervals for signs of bud break. Date of bud break was defined as the day on which 5 mm of preformed leaf protruded above the tip of the uppermost bud scale. The date of bud break was recorded for both the upper and lower most buds of each ramet and the average of the two was calculated. These dates were expressed as the number of days from May 1 to date of bud break.

Periodic Shoot Growth. Over the course of the summer, a total of eight shoot length measurements were made on each ramet. These measurements were taken on the following dates: June 15, 29; July 13, 27; August 11, 18, 30; and, September 7. Shoot elongation was taken as the distance from the tip of the plant to the point on the stem representing the initial (pre-bud break) height. Shoot elongation was measured to the nearest 0.1 cm.

Total Shoot Elongation. The last periodic shoot growth measurement, that taken on September 7, was used as a measure of the total shoot elongation for the 1983 growing season.

Date of Growth Cessation. The date of growth cessation was defined as the day on which a ramet reached 95 percent of its total shoot elongation for the 1983 growing season. This

value was estimated through linear interpolation between successive pairs of periodic shoot growth measurements. It was expressed as the number of days from May 1 to the day of estimated growth cessation.

Length of the Growth Period. The length of the growth period was measured as the number of days from the date of bud break to the date of growth cessation.

Final Plant Height. Final height was calculated as the sum of the initial plant height and the total shoot elongation for the 1983 growing season.

Average Daily Shoot Elongation. The average daily shoot elongation was calculated as the difference between successive pairs of periodic shoot growth measurements, divided by the length of the period (number of days) between measurements.

### Data Analysis

The statistical analysis of the data of the nursery study was performed using the SPSS statistical package (Nie et al., 1975; Hull and Nie, 1981).

The linear model which describes the experimental design used in the nursery study is as follows:

$$Y_{ijkl} = u + B_i + d(i) + P_j + BP_{ij} + w(ij) + C(j)_k + e(ijk)_l$$

where  $i = 1$  to  $4$                        $k = 1$  to  $50$   
 $j = 1, 2$                                  $l = 1$

$Y_{ijkl}$  = the response variable associated with the  $ijkl$ 'th treatment combination  
 $u$  = the overall mean  
 $B_i$  = the random effect of the  $i$ 'th block  
 $d(i)$  = the random error due to the restriction on randomization of provenances within blocks  
 $P_j$  = the fixed effect of the  $j$ 'th provenance  
 $BP_{ij}$  = the random effect of the interaction of the  $i$ 'th block with the  $j$ 'th provenance  
 $w(ij)$  = the random error due to the restriction on randomization of clones within provenances  
 $C(j)_k$  = the random effect of the  $k$ 'th clone within the  $j$ 'th provenance  
 $e(ijk)_l$  = the random experimental error

An analysis of variance was carried out on the independent response variables: initial plant height, date of bud break, total shoot elongation, and date of growth cessation. The mortality of several ramets resulted in an unbalanced experimental design. The sum of squares were calculated using the weighted squares of means, or Type III sum of squares, as recommended by Searle (1971) and Milliken and Johnson (1984) for unbalanced designs of mixed effects. The expected mean squares were derived using synthesis and components of variance were estimated using the method-of-moments technique (Milliken and Johnson, 1984).

The table of expected mean squares for the experimental design of the nursery study is presented in Table 3.1. The experimental design does not provide a direct test of the provenance effect. This effect was tested using a composite F-ratio (Milliken and Johnson, 1984). Estimates of the appropriate degrees of freedom for the test were derived using the Satterthwaite (1946) approximation.

The F-ratio to test the provenance effect,  $F_p$ , was calculated as follows:

$$F_p = MS(P) / Q, \text{ with } 1 \text{ and } v \text{ degrees of freedom,}$$

where

$$Q = q_1 - MS(BP) + q_2 - MS(C) + q_3 - MS(e), \text{ and}$$

$$q_1 = 40.62 / 41.41$$

$$q_2 = 3.249 / 3.480$$

$$q_3 = (1 - (q_1 + q_2))$$

$$v = Q^2 / [(q_1 - MS(BP))^2 / 3 + (q_2 - MS(C))^2 / 98 + (q_3 - MS(e))^2 / 243]$$

$$MS(x) = \text{the mean square of the specified effect } x$$

It is recognized that the provenance effect is confounded with the variance, if any, due to the restriction error,  $w$  (Anderson and McLean, 1974). The test of provenance effects may include variation due to this restriction error.

Table 3.1. The table of expected mean squares for the experimental design of the nursery study. The variance components for the restriction errors, w and d, form part of other expected mean squares, but the coefficients for these components could not be calculated; these coefficients are indicated as n, n' and n" for w, and m for d.

Source	df	Expected Mean Square
Block (B)	3	$\sigma^2_e + n''\sigma^2_w + 41.41\sigma^2_{BP} + m\sigma^2_d + 82.83\sigma^2_B$
d	0	$\sigma^2_e + n''\sigma^2_w + 41.41\sigma^2_{BP} + m\sigma^2_d$
Provenance (P)	1	$\sigma^2_e + 3.249\sigma^2_c + n'\sigma^2_w + 40.62\sigma^2_{BP} + Q(P)$
B x P	3	$\sigma^2_e + n\sigma^2_w + 41.41\sigma^2_{BP}$
w	0	$\sigma^2_e + n\sigma^2_w$
Clones / P	98	$\sigma^2_e + 3.480\sigma^2_c$
Error	243	$\sigma^2_e$

Product-moment correlation coefficients ( $r_p$ ), and genetic and environmental correlation coefficients ( $r_g$  and  $r_e$ , respectively), were calculated for each pair of response variables. The genetic and environmental correlation coefficients were calculated using covariance analysis as described by Falconer (1981). The general formula used to estimate correlation between two variables X and Y is

$$r = (\text{COV}_{XY}) / (\text{VAR}_X \cdot \text{VAR}_Y)^{1/2} \quad [3.1]$$

where  $\text{COV}_{XY}$  = the covariance of X and Y  
 $\text{VAR}_X$  &  $\text{VAR}_Y$  = the variance of X and Y

Estimates of  $r_g$  and  $r_e$  were derived by applying, respectively, estimates, of genetic and environmental variances and covariances in Equation 3.1. These variances and covariances were calculated from sum of squares and cross products derived from analysis of variance. Estimates of broad-sense heritabilities were calculated for each variable using the following formula:

$$h^2 = \sigma^2 c / (\sigma^2 e + \sigma^2 c) \quad [3.2]$$

## GREENHOUSE STUDY

The purpose of the greenhouse study was to examine variation in growth and specific yield components, within and among provenances of balsam poplar selected along a latitudinal gradient. The study involved all four provenances of balsam poplar: N. Wisconsin, Thunder Bay, Pickle Lake and Severn River. The effect of reducing the daily period of photosynthate production, i.e. the photosynthetic period, was studied in the context of 1) its effects on growth and the yield components studied; and, 2) variation in the degree of the response to this treatment.

For purposes of the latter objective, plants were grown under one of two photosynthetic periods: 1) a normal, approximately 16-hour photosynthetic period per day (as provided by natural day length); and, 2) a reduced, 8-hour, photosynthetic period per day. In both cases, however, plants were given a supplemented, 18-hour photoperiod to prevent height growth cessation.

Plant growth was monitored during the study through frequent, small harvests of plants. Harvested plants were destructively sampled so that several growth characteristics could be measured on each plant, and analyzed in the manner of functional growth analysis.

### Experimental Design Considerations

Two limiting factors required consideration in the design of the greenhouse study. The first of these was a limitation in the amount of available greenhouse space; the study was restricted to two greenhouse benches, both measuring 8 ft. (2.44 m) long by 4 ft. (1.22 m) wide. Secondly, the amount of available plant material was also limiting. Prior to the initiation of this test, the nursery of balsam poplar was used as a source of cuttings for a long-term provenance trial. This necessarily required the use of many cuttings from most clones of all four provenances. Consequently, the Pickle Lake and Severn River provenances had only seven to eight clones that had ramets of sufficient size to provide an adequate number of cuttings for this study.

### Selection Of Provenances and Clones

Clones from all four provenances were utilized for this study. Seven clones were selected from those of each of the N. Wisconsin, Thunder Bay, and Pickle Lake provenances. Six clones were selected from the Severn River provenance, bringing the total number of clones to 27. The selection of clones was random, though restricted by limitations discussed above. Table 3.2 lists the provenances and clones selected for this study.

Table 3.2. The provenances and clones within provenances selected for the greenhouse study. Clones were selected from those of the balsam poplar nursery at Lakehead University.

Northern Wisconsin	Thunder Bay	Pickle Lake	Severn River
223	5	136	345
233	36	121	322
227	44	142	326
247	35	116	327
238	30	102	320
278	19	152	335
279	45	117	

#### Photosynthetic Conditions

Two experimental photosynthetic conditions were evaluated in the greenhouse study. Under the first treatment, plants were grown under the normal photosynthetic period provided through natural day length (approximately 16 hours per day). This treatment served as the control, and will be referred to as the normal photosynthetic period. Under the second treatment, plants were subjected to a reduced photosynthetic period of only 8 hours per day.

Plants under the reduced photosynthetic period were exposed to natural day light conditions from 8:00 a.m. to 4:00 p.m., eight hours, each day. From 4:00 p.m. of one day until 8:00 a.m. of the next day, the plants were covered with opaque shade cloth, which effectively blocked all sunlight.

All plants, however, received the same photoperiod. Supplemental incandescent lighting was used to extend the

photoperiod from 6:00 a.m. to midnight (18 hours) under both treatments. The supplemental light was provided by 60-watt light bulbs, which produced about 12 foot-candles at bench level (radiant flux density of approximately 68 microwatts per  $\text{cm}^2$ ). The purpose of using such a low light intensity was to provide enough radiant energy to maintain the phytochrome reaction, and hence control photoperiodic response, while providing minimal or insufficient energy for photosynthate production. Nitsch (1957) used similar artificial lighting (60-watt light bulbs providing 8 foot-candles at bench level) to effectively extend the photoperiod and maintain shoot elongation of balsam poplar.

Under both photosynthetic treatments, the supplemental lights were on from 6:00 a.m. to 8:00 a.m. and then again from 4:00 p.m. to midnight. The supplemental lights for the reduced photosynthetic treatment were situated within the shade cloth enclosure. The photosynthetic treatments and the use of the extended photoperiod were initiated on May 19.

The purpose of extending the photoperiod was to ensure that plants under both treatments continued shoot elongation throughout the entire study. In the absence of the supplemental lighting, the plants under the reduced photosynthetic period would likely cease height growth, in response to the shorter, 8-hour photoperiod. In fact, growth differences among provenances of Populus growing in a common

environment have often been attributed to this photoperiodic response (e.g., Avanzo, 1969; Eldridge et al., 1972). The supplemental lighting used in the greenhouse study allowed for a reduction of the photosynthetic period, while maintaining the photoperiod necessary for continued shoot elongation. Hence, the effects of the reduced photosynthetic period could be examined independently of the photoperiodic response.

Nitsch (1957) used a modified version of this study. He examined the effect of varying photoperiods, combined with constant photosynthetic periods, on the stem development of several woody species including balsam poplar. More recently, Chatterton and Silvius (1979) examined the effects of photoperiod versus photosynthetic period duration on the growth and photosynthate partitioning in soybean (Glycine max [L.] Merr. cv. Amsoy 71).

#### Treatment Apparatus

A single greenhouse bench was used for each of the two treatments. The following apparatus was constructed on the bench which contained the reduced photosynthetic period treatment: a rectangular framework of 2 in. by 2 in. (5.1 cm by 5.1 cm) rough lumber was constructed to fit on top of the

bench. The frame measured 8 ft. (2.44 m) long by 4 ft. (1.22 m) wide by 4.5 ft. (1.37 m) high. It supported ventilation fans, lighting fixtures, and the necessary electrical wiring.

Black shade cloth was cut and stitched into panels that could be easily draped around the frame and snapped together to completely enclose the top and sides of the frame. A hole in each side panel accommodated ventilation fans. The wide housing of the ventilation fans prevented light from reaching plants in the enclosure through the ventilation holes. The shade cloth was left to hang loose about all sides of the bench to permit adequate air flow when the ventilation fans were on.

The black shade cloth readily heated when placed on the frame on sunny days. To minimize this effect, the cloth was covered with sheets of aluminum-coated polyethylene. The fans were left running at all times that the shade cloth was up. These fans, in combination with the polyethylene, were important in maintaining temperature and relative humidity underneath the cloth at levels similar to those associated with the normal photosynthetic period. A hygro-thermograph was placed in the centre of each bench to constantly monitor the temperature and relative humidity associated with each treatment, throughout the study period.

### Plant Propagation

The initial propagation of the cuttings was done in Spencer-Lemaire "45" flats. The relatively large cell size of these containers allowed for good rooting and growth of the cuttings before transplanting became necessary. These Spencer-Lemaire flats contained 27 cells, in a 3 by 9 arrangement.

Dormant cuttings were taken from selected clones in the nursery over a four day period beginning April 13. The cuttings were sealed in moistened plastic bags and stored in a walk-in cooler at a temperature of approximately 2° C. They were kept in the cooler until they were placed in the flats.

Each Spencer-Lemaire flat was designated as a separate harvest unit. That is, each flat contained one cutting of each clone. Prior to propagation of the cuttings, 44 Spencer-Lemaire flats were filled with the potting medium, a mixture of 60 percent peat moss and 40 percent vermiculite. The flats were placed on the two benches, 22 flats per bench, and each flat was randomly numbered from 1 to 44. Forty-four different random arrangements of the 27 clone numbers were generated. Each flat received a different random arrangement of the 27 clones. Propagation of the cuttings was carried out on May 6 and 7. The cuttings were 8 to 10 cm in length.

As the study progressed, it became necessary to transplant the plants because of increasing plant size and the potential for root binding and mutual shading of plants

in the Spencer-Lemaire flats. Two-litre milk cartons were used for the first transplant, which proved to be the only transplant required. As compared to regular greenhouse pots, the ratio of volume to surface area of the milk cartons is high. This, combined with the square, cross-sectional, shape of the cartons permitted good utilization of the available bench space.

Transplanting of cuttings from the Spencer-Lemaire flats into the milk cartons was done over a four day period beginning on June 24. Drainage holes were punched through the bottom of each milk carton prior to transplanting. A single carton was used for each cutting of a flat. Each Spencer-Lemaire flat, therefore, was replaced by a set of 27 milk cartons, which were maintained as a distinct flat or harvest unit. Benches and treatment apparatus were expanded slightly to accommodate the additional space required by the milk cartons.

#### Plant Harvesting and Assessment

The first harvest was conducted on May 31. The second harvest was conducted 11 days later, on June 11. Subsequently, harvests were carried out at seven-day intervals on the following dates: June 18, 25; July 2, 9, 16, 23, 30. A total of nine harvest were conducted; the length of the study period was 60 days. Throughout the study period plants maintained continuous shoot elongation.

For the first seven harvests, two flats were sampled from each treatment. For each of the eighth and ninth harvests, four flats were sampled per treatment. The larger sample size was used for the last two harvests for several reasons. It became apparent that the plants under the normal photosynthetic period were becoming too large for the available space and there was danger that mutual shading might have a significant effect on growth. Variation in plant size was also increasing and under that circumstance the larger samples would help provide better estimates of growth variables.

Each harvest began at approximately the same time of day, early morning. The flats were immediately placed in a dark, walk-in cooler at a temperature of approximately 2° C, to reduce physiological activity of the plants during the sampling procedure, which lasted several days.

For each plant that was sampled, the following growth variables were measured:

- leaf dry weight (Lw)
- stem dry weight (Sw)
- root dry weight (Rw)
- leaf area (La)
- number of leaves (Ln)
- number of primary roots (Rn)
- shoot length (SHl)

The area of fresh leaves was measured to the nearest 0.1 cm<sup>2</sup> with a Delta-T Area Meter. Dry weight measures were determined after material had been in drying ovens for 48 to 72 hours at 80° C. Dry weight was measured to the nearest 0.1

mg with a Mettler AE 100 balance. Shoot length was measured to the nearest 0.1 cm.

Additionally, the following variables were derived (functions describing the derivation of each variable are given in parenthesis):

- total plant dry weight (Tw):  $(Lw + Sw + Rw)$
- shoot dry weight (SHw):  $(Lw + Sw)$
- shoot/root ratio:  $(Lw + Sw)/Rw$

### Data Analysis

The statistical analysis of the data of the greenhouse study was performed using the SPSS statistical package (Nie et al., 1975; Hull and Nie, 1981).

### Analysis Of Variance

The greenhouse study included the following factors: provenances, clones within provenances, harvests, and photosynthetic treatments. The design of the experiment was unbalanced owing to differing numbers of flats per harvest, and differing numbers of clones per provenance. Consequently, the analysis of variance was based on only harvests eight and nine, for which four flats were sampled per treatment per harvest. Additionally, only six clones were used per provenance. As such, the design had no missing treatment combinations, and was only slightly unbalanced owing to the mortality of some ramets.

The linear model describing the experimental design used in the greenhouse study is as follows:

$$Y_{ijklmn} = u + T_i + d(i) + H_j + TH_{ij} + F(ij)_k + w(ijk) + P_l + TP_{il} + HP_{jl} + THP_{ijl} + C(1)_m + TC_{i(1)_m} + HC_{j(1)_m} + THC_{ij(1)_m} + e(ijklm)_n$$

where  $i = 1, 2$                        $l = 1$  to  $4$   
 $j = 1, 2$                        $m = 1$  to  $6$   
 $k = 1$  to  $4$                        $n = 1$

$Y_{ijklmn}$  = the response variable associated with the  $ijklmn$ 'th treatment combination  
 $u$  = the overall mean  
 $T_i$  = the fixed effect of the  $i$ 'th photosynthetic treatment  
 $d(i)$  = the random error due to the restriction on randomization of harvests within treatments  
 $H_j$  = the fixed effect of the  $j$ 'th harvest  
 $TH_{ij}$  = the fixed effect of the interaction of the  $i$ 'th photosynthetic treatment with the  $j$ 'th harvest  
 $F(ij)_k$  = the random effect of the  $k$ 'th flat within the  $ij$ 'th treatment combination  
 $w(ijk)$  = the random error due to the restriction on randomization of provenances and clones within flats  
 $P_l$  = the fixed effect of the  $l$ 'th provenance  
 $TP_{il}, HP_{jl}, THP_{ijl}$  = the fixed effect of the implied interactions  
 $C(1)_m$  = the random effect of the  $m$ 'th clone within the  $l$ 'th provenance  
 $TC_{i(1)_m}, HC_{j(1)_m}, THC_{ij(1)_m}$  = the random effect of the implied interactions  
 $e(ijklm)_n$  = the random experimental error

The analysis of variance was performed on each response variable. The sum of squares for the analysis were determined using the weighted squares of means, or the Type III analysis, as recommended by Searle (1971) and Milliken and Johnson (1984) for unbalanced designs of mixed effects.

Table 3.3 presents the expected mean squares for the experimental design of the greenhouse study. Due to the restriction errors in the design (Anderson and McLean, 1974), there was no direct test of either the treatment or harvest main effects. It is, however, the interaction of these effects with provenances and clones which were of major interest in this study.

The variation in the leaf, stem, and root dry weight, and in leaf area and shoot length, increased with the mean value of the response, the variance being roughly proportional to the mean. To minimize this effect, these variables were transformed to their natural logarithms. This type of transformation is commonly used to render variances independent of means (Snedecor and Cochran, 1980; Sokal and Rohlf, 1981).

Table 3.3. The table of expected mean squares for the experimental design of the greenhouse study.

Source	df	Expected Mean Square
Photosynthetic Treatment (T)	1	$\sigma^2 + 8\sigma^2_{TC} + 24\sigma^2_w + 24\sigma^2_F + 192\sigma^2_d + Q(T)$
d	0	$\sigma^2 + 8\sigma^2_{TC} + 24\sigma^2_w + 24\sigma^2_F + 192\sigma^2_d$
Harvest (H)	1	$\sigma^2 + 8\sigma^2_{HC} + 24\sigma^2_w + 24\sigma^2_F + Q(H)$
T x H	1	$\sigma^2 + 4\sigma^2_{THC} + 24\sigma^2_w + 24\sigma^2_F + Q(TH)$
Flat / T x H	12	$\sigma^2 + 24\sigma^2_w + 24\sigma^2_F$
w	0	$\sigma^2 + 24\sigma^2_w$
Provenance (P)	3	$\sigma^2 + 16\sigma^2_c + Q(P)$
T x P	3	$\sigma^2 + 8\sigma^2_{TC} + Q(TP)$
H x P	3	$\sigma^2 + 8\sigma^2_{HC} + Q(HP)$
T x H x P	3	$\sigma^2 + 4\sigma^2_{THC} + Q(THP)$
Clone / P (C)	20	$\sigma^2 + 16\sigma^2_c$
T x C	20	$\sigma^2 + 8\sigma^2_{TC}$
H x C	20	$\sigma^2 + 8\sigma^2_{HC}$
T x H x C	20	$\sigma^2 + 4\sigma^2_{THC}$
Error	257	$\sigma^2$

### Growth Analysis

Polynomial functions were derived, using linear regression analysis, to describe total dry weight, leaf dry weight, and leaf area in terms of time, time being the independent variable. The response variables were first transformed to their natural logarithms to render variances independent of means, and to transform the theoretical model, which is non-linear in its coefficients, into a model that is linear in its coefficients and amenable to linear regression analysis. The procedures of polynomial regression analysis are described by Sokal and Rohlf (1981) and Draper and Smith (1981).

For the greenhouse study, the general polynomial model was as follows:

$$\ln(Y) = b_0 + b_1 t + b_2 t^2 + \dots + b_n t^n$$

where Y = one of the response variables: total dry weight,  
leaf dry weight, or leaf area

t = time (in days)

$b_n t^n$  = the last regression coefficient found to be significant during the regression procedure

In the preliminary analysis, it was determined that a polynomial of a single degree was adequate in most cases. The quadratic term of the model was significant in only a few regressions; the cubic term was never significant. To facilitate the analysis, a polynomial of a single degree was used for all cases to provide a uniform family of curves, as

suggested by Hurd (1977). Hence, the following regression curves were fit to the growth data:

$$\ln(\text{total dry weight}) = b_0 + b_1 t \quad [3.3]$$

$$\ln(\text{leaf dry weight}) = b_0 + b_1 t \quad [3.4]$$

$$\ln(\text{leaf area}) = b_0 + b_1 t \quad [3.5]$$

where  $t$  = time  
 $b_0, b_1$  = regression coefficients unique to each function

Polynomial functions were derived for each provenance (all clones within a provenance combined) and for each clone individually, under both photosynthetic treatment regimes.

For each regression, there were several measurements or replicates at each value of time ( $t$ ). The residual sum of squares associated with each of the regressions could therefore be partitioned into two components: sum of squares due to pure error,  $SS_{PE}$ , and sum of squares due to lack of fit,  $SS_{LOF}$ . The significance of the lack of fit of each model was determined by comparing these two components in the manner described by Draper and Smith (1981). The comparison was based on the following  $F$ -ratio:

$$F = [SS_{LOF}/df_{LOF}] / [SS_{PE}/df_{PE}]$$

with  $df_{LOF}$  and  $df_{PE}$  degrees of freedom

where  $df_{LOF}$  and  $df_{PE}$  = the degrees of freedom for  $SS_{LOF}$  and  $SS_{PE}$  respectively

The coefficient of determination,  $R^2$ , describes the proportion of the total sum of squares,  $SS_{TOT}$ , accounted for by the regression sum of squares. In general, where a regression includes replicate measures, the maximum  $R^2$  that can be achieved is calculated as follows:

$$\text{maximum } R^2 = [SS_{TOT} - SS_{PE}] / SS_{TOT}$$

The ratio of  $R^2$  to maximum  $R^2$ , which indicates how well a model fits the data relative to the best possible fit, was calculated for each regression.

The comparison of any subset of  $n$  regression curves involved two null hypotheses. The first of these,  $H_{0a}$ , was that all curves of the given subset had a common slope, i.e., all  $n$   $b_1$  coefficients were equal. The second hypothesis,  $H_{0b}$ , was that all curves had the same intercept, i.e., all  $n$   $b_0$  were equal. The test of  $H_{0b}$  was considered only following acceptance of  $H_{0a}$ . Acceptance of both  $H_{0a}$  and  $H_{0b}$  would imply that the set of  $n$  functions were in fact not significantly different and described the same curve.

The tests of  $H_{0a}$  and  $H_{0b}$  were based on a comparison of the full linear model versus the appropriate reduced model. The full model, FM, consisted of separate estimates of  $b_0$  and  $b_1$  for each of the  $n$  functions being compared. The reduced model used to test  $H_{0a}$ ,  $RM(A)$ , consisted of separate estimates of  $b_0$  for each function, but a single pooled estimate of  $b_1$ . The reduced model used to test  $H_{0b}$ ,  $RM(B)$ ,

consisted of a single pooled estimate of both  $b_0$  and  $b_1$ . The tests were based on F-ratios constructed with the appropriate ratios of residual sum of squares, RSS, and corresponding residual degrees of freedom, df, associated with each model (Freese, 1964; Bolch and Huang, 1974; Weisberg, 1980). The test of common slopes ( $H_{0a}$ ) was based on the following F-ratio:

$$F_{H_{0a}} = \frac{(RSS_{RM(A)} - RSS_{FM})}{(df_{RM(A)} - df_{FM})} \cdot \frac{df_{FM}}{RSS_{FM}}$$

with  $(df_{RM(A)} - df_{FM})$  and  $df_{FM}$  degrees of freedom

The test of common intercepts ( $H_{0b}$ ) given that slopes were equal, was based on the following F-ratio:

$$F_{H_{0b}} = \frac{(RSS_{RM(B)} - RSS_{RM(A)})}{(df_{RM(B)} - df_{RM(A)})} \cdot \frac{df_{RM(A)}}{RSS_{RM(A)}}$$

with  $(df_{RM(B)} - df_{RM(A)})$  and  $df_{RM(A)}$  degrees of freedom

The regression curves were used to derive functions to predict total dry weight, leaf dry weight, and leaf area over time. These functions were of the following form:

$$\text{total dry weight} = \exp[b_0 + b_1 t + se^2/2] \quad [3.6]$$

$$\text{leaf dry weight} = \exp[b_0 + b_1 t + se^2/2] \quad [3.7]$$

$$\text{leaf area} = \exp[b_0 + b_1 t + se^2/2] \quad [3.8]$$

where  $se$  = the standard error of the estimate for the regression included to help correct for the bias created in taking the antilogarithms of predicted values based on functions fit to logarithmically transformed data (Baskerville, 1972; Beauchamp and Olson, 1973; Sprugel, 1983).

The relative rates of growth of total dry weight, leaf dry weight, and leaf area (RGR, RLwGR, and RLaGR, respectively) were estimated directly from the polynomial functions 3.3, 3.4, and 3.5, respectively. Since the functions were of a single degree, the relative rate of growth of the variables was constant, equal to the slope or  $b_1$  coefficient of the appropriate function (Hunt, 1978).

Functions describing growth component indices were derived using equations 3.6 to 3.8 and their derivatives. Unit leaf rate (ULR) and leaf area ratio (LAR) were estimated using the following functions:

$$\text{Unit Leaf Rate} = (dT_w/dt) (1/L_a) \quad [3.9]$$

$$\text{Leaf Area Ratio} = L_a/T_w \quad [3.10]$$

Additionally, the following growth component indices were derived: specific leaf area (SLA), leaf weight ratio (LWR), leaf area partition coefficient (LAP), and leaf weight partition coefficient (LWP). The following functions were used for this purpose:

$$\text{Specific Leaf Area} = L_a/L_w \quad [3.11]$$

$$\text{Leaf Weight Ratio} = L_w/T_w \quad [3.12]$$

$$\text{Leaf Area Partition Coefficient} = (dL_a/dt)/(dT_w/dt) \quad [3.13]$$

$$\text{Leaf Weight Partition Coefficient} = (dL_w/dt)/(dT_w/dt) \quad [3.14]$$

All functions, 3.3 to 3.14, were derived for each provenance (clones within provenances combined), and for each clone

individually, under both photosynthetic treatment regimes. The functions were then used to derive instantaneous estimates of the components. Linear and rank correlations between estimates of RGR and ULR, LAR, SLA, LWR, LAP, and LWP were estimated.

### Allometric Analysis

The allometric relationship between shoot and root dry weight may be described by the following function:

$$\text{shoot dry weight} = a(\text{root dry weight})^K \quad [3.15]$$

The coefficients  $a$  and  $K$  of this equation may be estimated by linear regression analysis applied to the equivalent model:

$$\ln(\text{shoot dry weight}) = \ln(a) + K(\ln(\text{root dry weight})) \quad [3.16]$$

The allometric constant,  $K$ , is equivalent to the slope of this straight line. Equation 3.16 was fit to the data of each provenance and clone, under both photosynthetic treatment regimes.

## 4 RESULTS

### 4.1 NURSERY STUDY

Of the 400 ramets initially established in the nursery in 1982, 51 were dead by the end of the 1983 growing season. Twenty of these ramets were from the Thunder Bay source, 31 were from the Pickle Lake source. Since much of this mortality occurred during the 1983 growing season, the number of ramets available for measurement was not the same for all response variables. All analysis was based on the 349 ramets that were available for all measurements.

Table 4.1.1 presents the summary statistics for six of the response variables of the nursery study. On average, the Pickle Lake clones broke bud one day earlier and ceased growth eight days sooner than the Thunder Bay clones. As a result, the average length of the growth period for the Thunder Bay clones was seven days longer than that of the Pickle Lake clones. The growth of the Pickle Lake clones was approximately 75 percent that of the Thunder Bay clones, in terms of all three height growth indices. The minimum and maximum values of the Thunder Bay clonal means were consistently greater than the corresponding values of the Pickle Lake clonal means.

Table 4.1.1. Means and range in clonal means of the response variables for the Thunder Bay and Pickle Lake provenances in the nursery study. Values in brackets specify the range in clonal means.

Response Variable	Provenance			
	Thunder Bay		Pickle Lake	
Date of Bud Break (days from May 1)	20.3	(14.3-29.0)	19.3	(12.0-26.0)
Date of Growth Cessation (days from May 1)	105.8	(93.0-114.3)	97.8	(76.8-111.3)
Length of Growth Period (days)	85.6	(74.0-98.8)	78.5	(61.0-96.7)
Initial Plant Height (cm)	34.7	(13.1-55.8)	26.1	(11.6-44.0)
Total Shoot Elongation (cm)	57.6	(34.7-85.6)	41.6	(13.4-61.6)
Final Plant Height (cm)	92.2	(55.7-130.6)	67.7	(29.9-95.2)

The mean periodic shoot growth measurements for each provenance are presented in Table 4.1.2. With the exception of the initial measurement, the Thunder Bay clones consistently exhibited greater shoot growth than the Pickle Lake clones. The magnitude of the difference between the provenances increased with time to the end of the study period.

Table 4.1.2. Periodic shoot growth measurements (cm) of the Thunder Bay and Pickle Lake provenances in the nursery study. The standard error is given in brackets.

Date	Provenance	
	Thunder Bay	Pickle Lake
June 15	4.5 (0.14)	4.9 (0.18)
June 29	12.1 (0.35)	11.8 (0.42)
July 13	23.5 (0.61)	22.2 (0.70)
July 27	37.5 (0.91)	33.3 (0.98)
Aug. 11	51.6 (1.33)	39.9 (1.27)
Aug. 18	55.7 (1.53)	41.0 (1.32)
Aug. 30	57.4 (1.63)	41.3 (1.34)
Sept. 7	57.6 (1.67)	41.6 (1.34)

The estimates of average daily shoot elongation for both provenances are presented in Table 4.1.3. With the exception of the first measurement period, the daily shoot growth rate was greater for the Thunder Bay clones than for the Pickle Lake clones over all measurement periods. The maximum daily rate of shoot elongation for both provenances occurred in the

measurement period of July 13 - July 27. At this time, the rate of shoot elongation for the Pickle Lake clones was only 79 percent that of the Thunder Bay clones. The reduction in shoot growth rates in the subsequent measurement periods occurred more rapidly for the Pickle Lake clones than for the Thunder Bay clones.

Table 4.1.3. Average daily shoot elongation (cm/day) between successive pairs of measurements for the Thunder Bay and Pickle Lake provenances in the nursery study.

Measurement Period	Provenance	
	Thunder Bay	Pickle Lake
bud break - June 15	0.180	0.188
June 15 - June 29	0.540	0.494
June 29 - July 13	0.816	0.745
July 13 - July 27	1.000	0.786
July 27 - Aug. 11	0.937	0.444
Aug. 11 - Aug. 18	0.593	0.151
Aug. 18 - Aug. 30	0.141	0.029
Aug. 30 - Sept. 7	0.024	0.038

The analysis of variance for date of bud break, date of growth cessation, initial plant height, and total shoot elongation is presented in Table 4.1.4. For all response variables, the variation among clones within provenances was significant ( $P < 0.01$ ). A significant effect due to provenances ( $P < 0.00$ ) was observed for date of growth cessation, but not for the other three response variables.

Table 4.1.4. Analysis of variance of the four independent response variables of the nursery study. A composite F-ratio was used to test the provenance effects. The degrees of freedom for the denominator of this F-ratio were as follows: date of bud break, 6.54; date of growth cessation, 23.99; initial plant height, 4.03; and total shoot elongation, 3.19. The corresponding degrees of freedom for the numerator was 1 for all four variables.

Source	df	Date of Bud Break			Date of Growth Cessation			Initial Plant Height			Total Shoot Elongation		
		Mean Square	F	PR>F	Mean Square	F	PR>F	Mean Square	F	PR>F	Mean Square	F	PR>F
Block (B)	3	136.6			431.3			192.2			7262		
d	0												
Provenance (P)	1	55.8	0.602	0.465	4699.0	46.76	0.000	6162.7	5.063	0.087	20260	3.392	0.157
B x P	3	63.6			32.5			1047.0			5904		
w	0												
Clones / P	98	42.6	4.114	0.000	95.4	4.27	0.000	282.1	3.532	0.000	420	1.838	0.000
Error	243	10.4			22.3			79.9			228		

Estimates of broad-sense heritability for the date of bud break and date of growth cessation were 0.47 and 0.48, respectively (Table 4.1.5). The estimates of heritability for initial plant height and total shoot elongation were 0.42 and 0.19, respectively.

Table 4.1.5. Estimates of broad-sense heritability for the four independent response variables of the nursery study.

Variable	Estimate of Variance		Broad-sense Heritability
	Clone	Error	
Date of Bud Break	9.27	10.36	0.472
Date of Growth Cessation	20.99	22.34	0.484
Initial Plant Height	58.12	79.88	0.421
Total Shoot Elongation	54.96	228.32	0.194

The product-moment correlation coefficient, and the genetic and environmental correlation coefficients for all pairs of the four independent response variables are presented in Table 4.1.6. The genetic correlations between date of growth cessation and both initial plant height and total shoot elongation were moderate and positive ( $r_g = .481$

and .418, respectively). Conversely, the genetic correlations between date of bud break and both initial plant height and total shoot elongation were low to moderate and negative ( $r_g = -.398$  and  $-.005$ , respectively). Environmental correlations were generally low.

Table 4.1.6. Correlation coefficients among the four independent response variables of the nursery study. Three correlation coefficients are presented for each variable pair: product-moment ( $r_p$ ), genetic ( $r_g$ ), and environmental ( $r_e$ ).

Response Variable		Date of Bud Break	Date of Growth Cessation	Initial Plant Height
Date of Growth Cessation	$r_p$	0.158		
	$r_g$	0.027		
	$r_e$	0.163		
Initial Plant Height	$r_p$	-0.104	0.297	
	$r_g$	-0.398	0.481	
	$r_e$	0.032	-0.115	
Total Shoot Elongation	$r_p$	-0.130	0.491	0.290
	$r_g$	-0.005	0.418	0.382
	$r_e$	-0.264	0.334	0.028

## 4.2 GREENHOUSE STUDY

### General Plant Development

Tables 4.2.1, 4.2.2, 4.2.3, and 4.2.4 present, respectively, the average leaf, stem, root, and total plant dry weights for each provenance at each harvest, under both photosynthetic periods. Dry weight, in terms of these four variables, increased exponentially with time over the study period. This was true of plants under both photosynthetic periods; however, growth was greater under the normal photosynthetic period than it was under the reduced photosynthetic period. By the final harvest, mean total dry weights based on provenances ranged from 6.57 to 7.72 g under the normal photosynthetic period, and from 2.20 to 3.01 g under the reduced photosynthetic period. There were no consistent trends in the rankings of provenances from one harvest to the next under either photosynthetic treatment, for these response variables.

Table 4.2.1. Average leaf dry weight (g) for the four provenances of balsam poplar over the nine harvests of the greenhouse study. Value in brackets is the standard error of the mean.

Photosyn- thetic Period	Harvest	Provenance			
		N. Wisconsin	Thunder Bay	Pickle Lake	Severn River
Normal	1	0.140 (.017)	0.141 (.018)	0.122 (.015)	0.122 (.022)
	2	0.191 (.014)	0.232 (.019)	0.172 (.024)	0.217 (.019)
	3	0.276 (.040)	0.309 (.025)	0.248 (.035)	0.379 (.051)
	4	0.329 (.038)	0.430 (.026)	0.306 (.035)	0.386 (.045)
	5	0.701 (.091)	0.814 (.068)	0.768 (.100)	0.605 (.099)
	6	0.933 (.163)	1.262 (.151)	1.062 (.135)	0.914 (.155)
	7	1.589 (.297)	1.686 (.251)	1.504 (.209)	1.468 (.227)
	8	2.024 (.247)	2.288 (.217)	2.190 (.257)	1.572 (.179)
	9	3.372 (.395)	4.013 (.392)	3.827 (.308)	3.599 (.465)
Reduced	1	0.088 (.010)	0.099 (.012)	0.090 (.010)	0.099 (.012)
	2	0.139 (.013)	0.131 (.012)	0.115 (.011)	0.147 (.014)
	3	0.165 (.021)	0.202 (.015)	0.200 (.018)	0.151 (.013)
	4	0.206 (.022)	0.296 (.020)	0.276 (.040)	0.195 (.027)
	5	0.348 (.049)	0.353 (.042)	0.369 (.041)	0.268 (.032)
	6	0.576 (.085)	0.614 (.061)	0.457 (.084)	0.467 (.114)
	7	0.693 (.098)	0.625 (.068)	0.787 (.093)	0.566 (.086)
	8	0.952 (.089)	1.106 (.097)	0.895 (.083)	0.898 (.091)
	9	1.481 (.155)	1.527 (.164)	1.395 (.111)	1.147 (.127)

Table 4.2.2. Average stem dry weight (g) for the four provenances of balsam poplar over the nine harvests of the greenhouse study. Value in brackets is the standard error of the mean.

Photosyn- thetic Period	Harvest	Provenance			
		N. Wisconsin	Thunder Bay	Pickle Lake	Severn River
Normal	1	0.042 (.005)	0.037 (.006)	0.034 (.005)	0.044 (.007)
	2	0.065 (.006)	0.070 (.008)	0.057 (.012)	0.077 (.008)
	3	0.099 (.019)	0.084 (.005)	0.083 (.012)	0.136 (.022)
	4	0.110 (.014)	0.132 (.014)	0.104 (.017)	0.155 (.025)
	5	0.315 (.048)	0.304 (.034)	0.375 (.058)	0.288 (.056)
	6	0.453 (.091)	0.552 (.074)	0.547 (.084)	0.507 (.100)
	7	0.898 (.192)	0.848 (.147)	0.932 (.157)	0.874 (.151)
	8	1.240 (.176)	1.270 (.142)	1.434 (.212)	0.982 (.139)
	9	2.272 (.322)	2.519 (.296)	2.748 (.279)	2.690 (.416)
Reduced	1	0.027 (.002)	0.024 (.004)	0.026 (.004)	0.031 (.006)
	2	0.042 (.006)	0.037 (.003)	0.034 (.003)	0.045 (.005)
	3	0.054 (.009)	0.050 (.003)	0.062 (.007)	0.045 (.005)
	4	0.070 (.010)	0.084 (.008)	0.099 (.020)	0.062 (.010)
	5	0.135 (.027)	0.111 (.015)	0.144 (.020)	0.104 (.012)
	6	0.304 (.048)	0.263 (.033)	0.228 (.053)	0.249 (.069)
	7	0.407 (.077)	0.278 (.035)	0.412 (.058)	0.291 (.056)
	8	0.587 (.069)	0.546 (.058)	0.504 (.056)	0.488 (.060)
	9	1.161 (.147)	0.924 (.128)	0.961 (.097)	0.752 (.119)

Table 4.2.3. Average root dry weight (g) for the four provenances of balsam poplar over the nine harvests of the greenhouse study. Value in brackets is the standard error of the mean.

Photosyn- thetic Period	Harvest	Provenance			
		N. Wisconsin	Thunder Bay	Pickle Lake	Severn River
Normal	1	0.015 (.002)	0.018 (.003)	0.016 (.003)	0.017 (.003)
	2	0.037 (.004)	0.032 (.006)	0.026 (.004)	0.026 (.004)
	3	0.054 (.009)	0.061 (.013)	0.044 (.008)	0.079 (.014)
	4	0.084 (.011)	0.089 (.008)	0.067 (.009)	0.093 (.017)
	5	0.167 (.031)	0.164 (.019)	0.178 (.030)	0.178 (.045)
	6	0.251 (.056)	0.330 (.043)	0.292 (.042)	0.358 (.079)
	7	0.486 (.091)	0.423 (.066)	0.433 (.064)	0.390 (.057)
	8	0.551 (.079)	0.534 (.052)	0.561 (.078)	0.430 (.053)
	9	0.923 (.135)	0.997 (.123)	1.143 (.132)	1.075 (.170)
Reduced	1	0.009 (.002)	0.008 (.002)	0.008 (.002)	0.009 (.001)
	2	0.021 (.003)	0.016 (.002)	0.012 (.002)	0.015 (.002)
	3	0.024 (.003)	0.030 (.005)	0.026 (.003)	0.017 (.002)
	4	0.042 (.006)	0.047 (.006)	0.048 (.011)	0.040 (.009)
	5	0.069 (.011)	0.074 (.010)	0.072 (.010)	0.058 (.010)
	6	0.110 (.018)	0.107 (.013)	0.093 (.025)	0.094 (.034)
	7	0.178 (.030)	0.139 (.019)	0.194 (.025)	0.136 (.026)
	8	0.251 (.028)	0.227 (.020)	0.219 (.027)	0.217 (.023)
	9	0.365 (.043)	0.356 (.048)	0.341 (.032)	0.304 (.036)

Table 4.2.4. Average total plant dry (g) for the four provenances of balsam poplar over the nine harvests of the greenhouse study.

Photosyn- thetic Period	Harvest	Provenance			
		Northern Wisconsin	Thunder Bay	Pickle Lake	Severn River
Normal	1	0.196	0.197	0.171	0.233
	2	0.293	0.339	0.255	0.319
	3	0.429	0.454	0.375	0.594
	4	0.522	0.651	0.476	0.634
	5	1.183	1.282	1.321	1.071
	6	1.636	2.144	1.900	1.779
	7	2.973	2.957	2.868	2.732
	8	3.815	4.093	4.185	2.984
	9	6.566	7.529	7.718	7.365
Reduced	1	0.132	0.132	0.130	0.138
	2	0.210	0.184	0.161	0.207
	3	0.243	0.282	0.288	0.213
	4	0.319	0.427	0.423	0.297
	5	0.553	0.537	0.585	0.430
	6	0.989	0.984	0.779	0.810
	7	1.279	1.043	1.393	0.993
	8	1.790	1.879	1.619	1.603
	9	3.007	2.807	2.697	2.202

Leaf area (Table 4.2.5) increased exponentially with time in a pattern similar to that of the dry weight variables. At the final harvest, mean leaf area of provenances ranged from 840 to 1024 cm<sup>2</sup> under the normal photosynthetic period, but only from 416 to 519 cm<sup>2</sup> under the reduced photosynthetic period. The extent to which leaf growth was reduced under the reduced photosynthetic period was more marked in terms of leaf weight than leaf area. This observation suggests that plants grown under the reduced photosynthetic period produced thinner leaves than those under the normal photosynthetic period (assuming that leaf density remained relatively constant).

Under the normal photosynthetic period, over the last five harvests, the Thunder Bay clones consistently had the greatest leaf growth. The Pickle Lake clones had greater leaf growth than the Severn River clones for the same harvest periods. With the exception of the last harvest, the N. Wisconsin clones generally ranked an overall second or third in terms of leaf growth. Under the reduced photosynthetic period, the Thunder Bay clones usually had the greatest leaf growth, while the Severn River clones had the poorest growth.

The average leaf number per plant increased throughout the study period (Table 4.2.6). Plants under the reduced photosynthetic period produced fewer leaves than those under the normal photosynthetic period, the difference being most marked in the latter harvests. The relative decrease in leaf

Table 4.2.5. Average leaf area (cm<sup>2</sup>) for the four provenances of balsam poplar over the nine harvests of the greenhouse study. Value in brackets is the standard error of the mean.

Photosyn- thetic Period	Harvest	Provenance			
		N. Wisconsin	Thunder Bay	Pickle Lake	Severn River
Normal	1	31.8 ( 3.3)	33.6 ( 3.9)	30.1 ( 2.9)	31.4 ( 6.1)
	2	49.9 ( 4.2)	58.7 ( 7.0)	47.6 ( 6.5)	58.6 ( 5.8)
	3	70.5 (10.2)	75.4 ( 4.1)	66.7 ( 8.1)	94.5 (11.0)
	4	79.0 ( 9.3)	100.6 ( 5.8)	75.8 ( 8.2)	96.1 ( 9.8)
	5	188.6 (22.0)	221.8 (19.0)	201.1 (25.0)	154.2 (19.2)
	6	265.0 (38.5)	336.0 (43.1)	293.4 (37.1)	240.1 (35.9)
	7	419.3 (73.3)	458.0 (66.3)	398.2 (51.5)	435.1 (60.4)
	8	543.4 (56.1)	620.2 (55.6)	602.4 (63.0)	484.5 (47.8)
	9	840.0 (82.6)	1023.5 (80.6)	967.3 (67.1)	929.3 (100.5)
Reduced	1	23.3 ( 2.7)	27.7 ( 2.9)	26.0 ( 3.0)	27.5 ( 3.4)
	2	39.4 ( 4.1)	38.9 ( 3.5)	36.8 ( 3.4)	45.4 ( 4.9)
	3	48.5 ( 6.6)	57.6 ( 3.6)	61.4 ( 5.9)	45.1 ( 4.6)
	4	60.4 ( 6.1)	87.7 ( 5.7)	82.5 (10.9)	58.8 ( 8.4)
	5	104.6 (16.1)	103.1 (12.3)	112.6 (12.4)	80.9 ( 9.8)
	6	183.7 (20.8)	192.7 (19.8)	148.6 (21.5)	163.7 (40.1)
	7	242.1 (32.1)	215.7 (21.9)	279.8 (28.7)	215.8 (32.0)
	8	317.1 (27.3)	374.5 (28.8)	306.4 (25.1)	333.7 (30.7)
	9	504.1 (47.9)	518.9 (52.1)	469.6 (32.1)	415.8 (41.8)

Table 4.2.6. Average leaf number for the four provenances of balsam poplar over the nine harvests of the greenhouse study. Value in brackets is the standard error of the mean.

Photosyn- thetic Period	Harvest	Provenance			
		N. Wisconsin	Thunder Bay	Pickle Lake	Severn River
Normal	1	6.21 (0.38)	6.57 (0.44)	7.79 (0.52)	7.75 (0.84)
	2	8.43 (0.65)	10.79 (1.60)	9.93 (0.78)	11.42 (0.51)
	3	9.00 (0.59)	9.64 (0.46)	11.00 (0.68)	12.42 (0.71)
	4	10.14 (0.49)	11.71 (0.46)	11.21 (0.52)	13.33 (1.03)
	5	12.77 (0.88)	13.50 (0.39)	12.71 (0.60)	12.25 (0.99)
	6	11.85 (0.82)	13.29 (0.71)	12.64 (0.98)	14.60 (1.01)
	7	13.43 (0.97)	15.00 (1.09)	15.29 (0.71)	16.00 (0.90)
	8	15.08 (0.72)	16.04 (0.62)	16.77 (0.76)	18.00 (0.89)
	9	16.67 (0.76)	19.32 (0.73)	21.43 (1.03)	23.00 (1.27)
Reduced	1	5.86 (0.38)	6.86 (0.35)	6.71 (0.56)	8.36 (0.36)
	2	7.71 (0.70)	8.43 (0.58)	9.71 (0.44)	10.58 (0.60)
	3	9.21 (1.03)	9.64 (0.53)	11.00 (0.42)	11.17 (0.58)
	4	8.92 (0.43)	13.00 (1.09)	11.39 (0.68)	10.64 (0.62)
	5	10.93 (0.91)	10.64 (0.73)	13.07 (0.78)	12.09 (1.19)
	6	11.79 (0.63)	13.14 (0.77)	13.17 (1.13)	13.44 (1.55)
	7	12.14 (0.73)	12.71 (0.66)	14.23 (0.59)	14.00 (1.14)
	8	13.21 (0.59)	13.67 (0.53)	13.84 (0.53)	15.23 (0.72)
	9	15.56 (0.72)	16.14 (0.51)	16.86 (0.55)	17.64 (0.77)

number in response to the reduced photosynthetic period was much less than that for leaf area or leaf weight, indicating that average leaf size for plants under the reduced photosynthetic period was less than that under the normal photosynthetic period. A positive correlation existed between the mean leaf number and the latitude of the provenance. This relationship, also most apparent in the latter harvests, was evident under both photosynthetic treatments.

Shoot length increased throughout the study period (Table 4.2.7), though this increase was more gradual than that observed for the dry weight and leaf area variables. Stem length was lower under the reduced photosynthetic period than it was under the normal photosynthetic period; however, the magnitude of this difference was less than that observed for the dry weight and leaf area variables. Plants under both photosynthetic treatments were still elongating at the time of the final harvest. At this time, mean stem length for provenances ranged from 52.1 to 58.8 cm under the normal photosynthetic period, and 33.8 to 47.4 cm under the reduced photosynthetic period.

Mean root number did not increase throughout the study period, though changes with time were evident (Table 4.2.8). The magnitude of the differences among provenances and treatments was most noticeable in the initial harvests, becoming less in the latter harvests. Root number under the

Table 4.2.7. Average shoot length (cm) for the four provenances of balsam poplar over the nine harvests of the greenhouse study. Value in brackets is the standard error of the mean.

Photosyn- thetic Period	Harvest	Provenance			
		N. Wisconsin	Thunder Bay	Pickle Lake	Severn River
Normal	1	4.64 (0.59)	3.76 (0.52)	4.51 (0.61)	4.39 (1.07)
	2	9.71 (0.87)	8.94 (1.02)	9.00 (1.21)	10.08 (0.79)
	3	12.04 (1.50)	10.48 (0.75)	11.58 (1.17)	13.79 (1.37)
	4	12.83 (1.27)	13.63 (0.98)	11.87 (1.77)	13.88 (1.52)
	5	24.01 (1.62)	22.89 (1.26)	25.49 (2.11)	18.88 (2.26)
	6	28.14 (1.97)	30.03 (2.30)	30.16 (2.58)	26.08 (3.32)
	7	34.69 (3.87)	33.65 (3.24)	37.52 (3.04)	37.14 (3.69)
	8	44.55 (2.94)	43.05 (2.29)	46.95 (3.24)	41.04 (3.46)
	9	52.08 (3.38)	54.61 (2.74)	58.46 (2.92)	58.84 (4.02)
Reduced	1	3.20 (0.51)	3.14 (0.49)	3.77 (0.85)	4.16 (0.96)
	2	6.31 (1.14)	6.74 (0.64)	7.36 (0.70)	7.08 (0.86)
	3	7.81 (1.29)	7.13 (0.65)	9.52 (1.01)	6.67 (0.77)
	4	10.34 (1.09)	9.32 (0.99)	11.48 (1.36)	6.66 (0.68)
	5	14.13 (1.88)	10.51 (1.13)	13.59 (1.46)	9.14 (1.23)
	6	24.52 (1.77)	18.64 (2.05)	18.78 (2.33)	18.91 (4.01)
	7	29.89 (2.20)	21.45 (1.88)	28.20 (2.44)	22.37 (2.86)
	8	34.66 (2.24)	33.69 (2.64)	31.69 (2.08)	29.52 (2.46)
	9	47.39 (2.89)	37.88 (2.63)	41.46 (2.10)	33.76 (3.29)

Table 4.2.8. Average root number for the four provenances of balsam poplar over the last seven harvests of the greenhouse study. Value in brackets is the standard error of the mean.

Photosyn- thetic Period	Harvest	Provenance			
		N. Wisconsin	Thunder Bay	Pickle Lake	Severn River
Normal	3	11.43 (1.80)	21.21 (5.57)	13.14 (1.93)	16.83 (2.60)
	4	15.93 (2.25)	17.93 (2.22)	11.29 (1.32)	11.75 (1.68)
	5	12.92 (1.97)	17.93 (2.65)	13.07 (1.84)	15.08 (1.64)
	6	15.00 (2.18)	21.14 (2.45)	14.36 (1.81)	15.60 (3.15)
	7	12.71 (1.29)	19.36 (2.42)	13.50 (1.34)	12.83 (2.00)
	8	13.50 (1.10)	15.00 (1.03)	13.73 (1.44)	12.57 (1.21)
	9	12.00 (0.89)	14.57 (1.50)	12.46 (0.93)	12.22 (1.48)
Reduced	3	9.07 (1.45)	14.29 (2.19)	10.23 (0.90)	8.00 (1.51)
	4	10.54 (1.80)	14.07 (2.02)	9.92 (1.30)	6.82 (1.14)
	5	9.93 (1.73)	14.57 (1.87)	10.36 (0.81)	9.91 (1.37)
	6	13.36 (1.87)	15.64 (2.71)	10.50 (1.31)	8.33 (2.02)
	7	12.29 (2.27)	13.14 (2.06)	12.69 (1.63)	10.09 (2.05)
	8	10.89 (0.92)	14.07 (1.49)	9.85 (0.80)	10.96 (0.95)
	9	10.33 (1.53)	11.64 (1.07)	9.04 (0.81)	8.09 (0.80)

reduced photosynthetic period was less than that under the normal photosynthetic period. The Thunder Bay clones consistently had the greatest root number, under either treatment. Under the reduced photosynthetic period, the Severn River clones generally had the lowest root number, while the N. Wisconsin and Pickle Lake clones were either second or third in ranking.

The product-moment correlation coefficients for the dry weight, leaf area, and stem length variables were all positive and high (Table 4.2.9). A multivariate analysis of variance was performed for these variables (Table 4.2.10). Additionally, an analysis of variance was performed separately for leaf, stem and root dry weight (Table 4.2.11) and for leaf area, leaf number, shoot length, and root number (Table 4.2.12). Only variation due to clones was consistently significant for all variables. The treatment by provenance and treatment by clone interactions were significant in the multivariate analysis ( $PR>F = 0.031$  and  $.000$ , respectively), but generally not significant when variables were analyzed individually. For leaf number, however, the treatment by clone and harvest by provenance interactions were significant ( $PR>F = 0.044$  and  $0.015$ , respectively), and the differences among provenances approached significance ( $PR>F = .055$ ).

Table 4.2.9. Product-moment correlation coefficients for the response variables of the greenhouse study. Each coefficient is based on data of harvests eight and nine, and six clones per provenance; a total of 365 pairs of values. All coefficients are significant at the 1% level.

	Response Variable					
	stem weight	root weight	leaf area	shoot length	leaf number	root number
leaf weight	.975	.954	.982	.866	.666	.349
stem weight		.957	.963	.887	.669	.302
root weight			.916	.803	.630	.335
leaf area				.909	.708	.351
shoot length					.698	.296
leaf number						.242

Table 4.2.10. Multivariate analysis of variance of leaf area, shoot length, and leaf, stem, and root dry weight for the four provenances of balsam poplar in the greenhouse study. Analysis was carried out on data of harvests eight and nine for six clones per provenance, and four flats per treatment-harvest combination.

Source	Hypoth. df	Error df	Hotelling's T statistic	Approx. F Value	PR>F
Treatment (T)					
d					
Harvest (H)					
T x H					
Flat / TxH					
w					
Provenance (P)	15	44	1.622	1.586	0.117
T x P	15	44	2.117	2.070	0.031
H x P	15	44	0.991	0.969	0.502
T x H x P	15	44	1.064	1.040	0.436
Clone / P (C)	100	1257	3.894	9.789	0.000
T x C	100	1257	0.743	1.868	0.000
H x C	100	1257	0.395	0.993	0.501
T x H x C	100	1257	0.501	1.260	0.048

Table 4.2.11. Analysis of variance of leaf, stem and root dry weight for the four provenances of balsam poplar in the greenhouse study. Analysis was carried out on data of harvests eight and nine for six clones per provenance, and four flats per treatment-harvest combination.

Source	df	Leaf Dry Weight			Stem Dry Weight			Root Dry Weight		
		Mean Square	F	PR>F	Mean Square	F	PR>F	Mean Square	F	PR>F
Treatment (T)	1	57.34			66.42			70.38		
d	0									
Harvest (H)	1	20.88			36.84			22.74		
T x H	1	1.38			0.72			1.65		
Flat / TxH	12	0.96			1.70			1.02		
w	0									
Provenance (P)	3	0.82	0.59	0.629	0.78	0.31	0.820	0.41	0.18	0.909
T x P	3	0.17	0.56	0.648	0.68	1.41	0.269	0.40	1.03	0.401
H x P	3	0.29	1.26	0.313	0.42	1.18	0.343	0.48	1.52	0.241
T x H x P	3	0.70	1.61	0.219	1.20	1.94	0.156	0.63	0.93	0.445
Clone / P (C)	20	1.40	4.81	0.000	2.55	5.94	0.000	2.30	6.33	0.000
T x C	20	0.30	1.03	0.431	0.48	1.13	0.322	0.38	1.06	0.397
H x C	20	0.23	0.80	0.713	0.35	0.83	0.681	0.32	0.87	0.628
T x H x C	20	0.44	1.50	0.080	0.62	1.44	0.105	0.68	1.88	0.014
Error	257	0.29			0.43			0.36		

Table 4.2.12. Analysis of variance of leaf area, leaf number, shoot length, and root number for the four provenances of balsam poplar in the greenhouse study. Analysis was carried out on data of harvests eight and nine for six clones per provenance, and four flats per treatment-harvest combination.

Source	df	Leaf Area			Leaf Number			Shoot Length			Root Number		
		Mean Square	F	PR>F	Mean Square	F	PR>F	Mean Square	F	PR>F	Mean Square	F	PR>F
Treatment (T)	1	28.27			776.5			9.52			720.0		
d	0												
Harvest (H)	1	17.71			786.5			5.45			191.9		
T x H	1	0.63			18.2			0.01			1.1		
Flat / TxH	12	0.86			19.4			0.42			51.6		
w	0												
Provenance (P)	3	0.56	0.46	0.715	184.1	3.00	0.055	0.43	0.47	0.704	109.2	0.92	0.450
T x P	3	0.13	0.58	0.636	34.5	2.00	0.147	0.30	1.98	0.149	19.5	0.55	0.653
H x P	3	0.14	0.78	0.519	21.0	4.45	0.015	0.12	1.46	0.256	20.9	1.11	0.369
T x H x P	3	0.58	1.88	0.166	15.8	1.46	0.256	0.42	3.06	0.052	27.3	1.54	0.234
Clone / P (C)	20	1.22	5.36	0.000	61.3	5.82	0.000	0.92	8.04	0.000	118.9	4.05	0.000
T x C	20	0.22	0.95	0.521	17.3	1.64	0.044	0.15	1.34	0.156	35.4	1.21	0.248
H x C	20	0.19	0.82	0.692	4.7	0.45	0.981	0.09	0.75	0.771	18.8	0.64	0.880
T x H x C	20	0.31	1.36	0.141	10.8	1.03	0.430	0.14	1.20	0.255	17.7	0.60	0.909
Error	257	0.23			10.5			0.11			29.4		

### Growth Analysis

For each provenance and photosynthetic treatment combination, the following linear model was derived:

$$\ln(Y) = b_0 + b_1 t \quad [4.1]$$

where Y = total dry weight, leaf dry weight, or leaf area.

The summary of the regression statistics are presented in Appendices I, II, and III (for total dry weight, leaf dry weight and leaf area respectively). All regressions were significant ( $PR>F < 0.05$ ), and in all cases, lack of fit was not significant ( $PR>F > 0.05$ ). Estimates of  $R^2$  adjusted for pure error variation ranged from 0.956 to 0.993.

Estimates of relative rates of growth for total dry weight, leaf dry weight and leaf area (RGR, RLWGR and RLaGR, respectively) are presented in Table 4.2.13. These values are based on the linear models summarized in Appendices I to III. For each provenance-treatment combination, the RGR and RLaGR were consistently greater than RLWGR. Under the normal photosynthetic period, the Pickle Lake source had the greatest relative rates of growth, followed by Thunder Bay, N. Wisconsin, and Severn River. The relative rates of growth were lower under the reduced photosynthetic period than under the normal photosynthetic period. The differences among provenances were also smaller under the former and there were changes in the rankings of the provenances. The Severn River clones, however, maintained the lowest relative rates of growth under both treatments.

Table 4.2.13. Relative rates of growth for the four provenances of balsam poplar in the greenhouse study. Values are given for the normal and reduced photosynthetic periods.

Provenance	Relative Growth Rate		Relative Leaf Weight Growth Rate		Relative Leaf Area Growth Rate	
	$(g \cdot g^{-1} \cdot day^{-1})$		$(g \cdot g^{-1} \cdot day^{-1})$		$(dm^2 \cdot dm^{-2} \cdot day^{-1})$	
	Normal	Reduced	Normal	Reduced	Normal	Reduced
N. Wisconsin	.05828	.05199	.05323	.04718	.05538	.05229
Thunder Bay	.05994	.05031	.05488	.04527	.05723	.04931
Pickle Lake	.06551	.05139	.05956	.04629	.06018	.04955
Severn River	.05391	.04723	.05164	.04180	.05491	.04769

The tests of the null hypotheses of common slope and intercept for growth functions of the provenances, comparing differences among provenances, is presented in Table 4.2.14. The test for slopes provides a test for differences in the relative rates of growth. The test for intercept, given that slopes are found equal, indicates whether growth differed by a constant factor independent of time. The test of common slope indicated that the slopes of the functions for total dry weight differed significantly among provenances under the normal photosynthetic period ( $PR > F = 0.030$ ). In no other case was a significant difference in slope among provenances indicated. In all other instances, however, intercepts of the functions differed significantly among provenances.

Table 4.2.14. Tests of common slope and intercept for growth functions of provenances in the greenhouse study, comparing differences among provenances. The degrees of freedom for the residual sum of squares of the reduced models A and B (RM(A) and RM(B)) are, respectively, 3 and 6 more than that specified for the full model (FM).

Response Variable	Photosynthetic Period	df (FM)	Residual Sum of Squares			Test of Common:			
						Slope		Intercept	
			FM	RM(A)	RM(B)	F	PR>F	F	PR>F
Total Dry Weight	Normal	564	219.1	222.6	225.2	2.992	.030	2.241	.083
	Reduced	561	182.0	182.7	185.6	0.689	.559	2.937	.033
Leaf Dry Weight	Normal	570	197.7	199.6	204.6	1.848	.137	4.782	.003
	Reduced	565	162.3	163.1	166.8	0.977	.403	4.278	.005
Leaf Area	Normal	570	166.8	167.8	171.3	1.082	.356	3.963	.008
	Reduced	565	151.3	151.9	154.4	0.735	.532	3.139	.025

Some of the unexplained variation found in the regressions of the provenances can be attributed to variation among clones within provenances. The linear model [4.1] was derived for each of the 27 clones individually, under both photosynthetic treatment regimes, for total dry weight, leaf dry weight and leaf area. The summary of the regression statistics are presented in Appendices IV to IX. All regressions were significant ( $P < 0.05$ ), and in all cases, lack of fit was not significant ( $P > 0.05$ ).

Table 4.2.15 presents the estimates of the relative rates of growth for clones. Both the RGR and RLaGR were generally greater than the RLwGR for any given clone, under either treatment. The relative growth rates were generally lower under the reduced photosynthetic period than under the normal photosynthetic period. RGR ranged from 0.0379 to 0.0705  $\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$  under the normal photosynthetic period and 0.0386 to 0.0611  $\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$  under the reduced photosynthetic period; RLwGR ranged from 0.0333 to 0.0662  $\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$  under the normal photosynthetic period and 0.0361 to 0.0543  $\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$  under the reduced photosynthetic period; RLaGR ranged from 0.0372 to 0.0682  $\text{dm}^2 \cdot \text{dm}^{-2} \cdot \text{day}^{-1}$  under the normal photosynthetic period and from 0.0402 to 0.0592  $\text{dm}^2 \cdot \text{dm}^{-2} \cdot \text{day}^{-1}$  under the reduced photosynthetic period.

Table 4.2.15. Estimates of relative rates of growth for the 27 clones of balsam poplar under the normal and reduced photosynthetic treatments of the greenhouse study.

Provenance	Clone	Relative Growth Rate		Relative Leaf Weight Growth Rate		Relative Leaf Area Growth Rate	
		$(g \cdot g^{-1} \cdot day^{-1})$		$(g \cdot g^{-1} \cdot day^{-1})$		$(dm^2 \cdot dm^{-2} \cdot day^{-1})$	
		Normal	Reduced	Normal	Reduced	Normal	Reduced
N. Wisconsin	223	0.0565	0.0571	0.0524	0.0499	0.0547	0.0529
	233	0.0515	0.0518	0.0481	0.0519	0.0521	0.0592
	227	0.0683	0.0540	0.0628	0.0469	0.0636	0.0517
	247	0.0657	0.0547	0.0609	0.0496	0.0632	0.0557
	238	0.0662	0.0611	0.0604	0.0543	0.0619	0.0565
	278	0.0405	0.0449	0.0362	0.0409	0.0404	0.0477
	279	0.0572	0.0424	0.0511	0.0361	0.0513	0.0416
Thunder Bay	5	0.0525	0.0419	0.0463	0.0371	0.0506	0.0431
	36	0.0657	0.0522	0.0608	0.0467	0.0646	0.0517
	44	0.0550	0.0505	0.0504	0.0451	0.0534	0.0486
	35	0.0702	0.0523	0.0662	0.0483	0.0661	0.0523
	30	0.0605	0.0538	0.0546	0.0478	0.0557	0.0514
	19	0.0543	0.0453	0.0490	0.0406	0.0533	0.0448
	45	0.0615	0.0568	0.0569	0.0519	0.0569	0.0540
Pickle Lake	136	0.0605	0.0546	0.0552	0.0476	0.0592	0.0540
	121	0.0685	0.0504	0.0620	0.0440	0.0624	0.0462
	142	0.0701	0.0518	0.0653	0.0458	0.0630	0.0477
	116	0.0680	0.0472	0.0606	0.0410	0.0614	0.0457
	102	0.0547	0.0512	0.0490	0.0461	0.0512	0.0486
	152	0.0705	0.0484	0.0637	0.0497	0.0631	0.0534
	117	0.0669	0.0546	0.0618	0.0502	0.0615	0.0515
Severn River	345	0.0671	0.0497	0.0620	0.0443	0.0623	0.0515
	322	0.0559	0.0526	0.0529	0.0475	0.0598	0.0536
	326	0.0531	0.0386	0.0615	0.0342	0.0682	0.0402
	327	0.0460	0.0427	0.0403	0.0362	0.0417	0.0423
	320	0.0636	0.0565	0.0601	0.0498	0.0600	0.0556
	335	0.0379	0.0413	0.0333	0.0366	0.0372	0.0408

Spearman rank correlations were calculated to compare clonal rankings based on estimates of RGR, RLwGR, and RLaGR, separately under each photosynthetic treatment (Table 4.2.16). The rank correlations were generally high, ranging from 0.778 to 0.932. Estimates of the product-moment correlation between relative growth rates were similarly high and positive, ranging from 0.868 to 0.969 (Table 4.2.16). Spearman rank correlations were also calculated to compare clonal rankings, based on the relative growth rates, under the two photosynthetic periods. The coefficients were 0.420, 0.312, and 0.303 for RGR, RLwGR, and RLaGR, respectively.

Table 4.2.16. Correlation among clones and clonal ranking based on the estimates of relative growth rates, for the 27 clones of balsam poplar in the greenhouse study. Both Spearman rank ( $r_s$ ) and product-moment ( $r_p$ ) correlation coefficients are presented, upper and lower values, respectively. All coefficients are significant at the 1% level.

Photosynthetic Period		Relative Growth Rates		
			RGR	RLwGR
Normal	RLwGR	$r_s$	0.920	---
		$r_p$	0.950	
	RLaGR	$r_s$	0.778	0.932
		$r_p$	0.873	0.969
Reduced	RLwGR	$r_s$	0.889	---
		$r_p$	0.940	
	RLaGR	$r_s$	0.840	0.917
		$r_p$	0.868	0.948

The tests of the growth functions of clones for common slope and intercept are presented in Table 4.2.17. Under the reduced photosynthetic period there were no significant differences among clones within provenances in the slopes of the growth functions. Under the normal photosynthetic period, differences among clones of the N. Wisconsin source in the slopes of the functions for all three variables were significant ( $PR>F < 0.05$ ). The slopes of the functions of the Severn River clones were significantly different, or nearly so:  $PR>F = 0.076, 0.016, \text{ and } 0.002$  for total dry weight, leaf dry weight and leaf area, respectively. The slopes of the functions for the Thunder Bay and Pickle Lake clones did not differ significantly ( $PR>F > 0.05$ ). In general, functions that did not differ significantly in slope, differed significantly in intercept. The only exceptions were the functions of the Severn River clones under the reduced photosynthetic period, which did not differ significantly in either slope or intercept.

Table 4.2.17. Tests of common slope and intercept for growth functions of clones in the greenhouse study, comparing differences among clones within provenances. The degrees of freedom for the residual sum of squares of the reduced models A and B (RM(A) and RM(B)) are, respectively, 6 and 12 more than that specified for the full model (FM), for N. Wisconsin, Thunder Bay, and Pickle Lake, and 5 and 10 more for Severn River.

Response Variable	Photosynthetic Period	Provenance	df (FM)	Residual Sum of Squares			Test of Common:			
				FM	RM(A)	RM(B)	Slope		Intercept	
							F	PR>F	F	PR>F
Total Dry Weight	Normal	N. Wisconsin	134	44.24	48.69	62.92	2.247	.042	6.815	.000
		Thunder Bay	139	34.94	37.00	42.00	1.371	.230	3.266	.005
		Pickle Lake	138	46.52	48.25	60.94	0.852	.532	6.314	.000
		Severn River	107	46.02	50.45	53.25	2.058	.076	1.244	.293
	Reduced	N. Wisconsin	135	41.48	43.63	52.91	1.164	.329	5.000	.000
		Thunder Bay	139	31.93	33.25	43.37	0.958	.456	7.355	.000
		Pickle Lake	132	33.34	33.73	39.53	0.257	.956	3.953	.001
		Severn River	109	40.42	42.45	46.22	1.093	.369	2.026	.080
Leaf Dry Weight	Normal	N. Wisconsin	135	40.03	44.37	55.75	2.440	.029	6.026	.000
		Thunder Bay	140	31.47	33.96	37.95	1.845	.095	2.854	.012
		Pickle Lake	138	40.51	42.13	52.48	0.918	.484	5.898	.000
		Severn River	111	44.60	50.47	51.53	2.925	.016	0.484	.788
	Reduced	N. Wisconsin	138	37.64	39.70	47.38	1.263	.279	4.643	.000
		Thunder Bay	139	28.33	29.61	37.82	1.047	.398	6.695	.000
		Pickle Lake	133	30.87	31.39	34.86	0.374	.895	2.560	.022
		Severn River	109	37.41	39.13	42.22	1.003	.420	1.800	.118
Leaf Area	Normal	N. Wisconsin	135	35.58	39.09	49.47	2.222	.045	6.242	.000
		Thunder Bay	140	26.04	27.81	31.77	1.591	.154	3.461	.003
		Pickle Lake	138	34.65	35.54	43.90	0.591	.737	5.644	.000
		Severn River	111	34.46	40.66	41.71	3.994	.002	0.599	.701
	Reduced	N. Wisconsin	138	35.10	36.88	45.26	1.166	.328	5.452	.000
		Thunder Bay	139	25.53	26.37	34.52	0.768	.596	7.469	.000
		Pickle Lake	133	26.15	26.71	29.95	0.483	.820	2.807	.013
		Severn River	109	36.04	37.99	41.55	1.180	.324	2.132	.067

A test was carried out to determine if the growth functions of clones differed significantly under the two photosynthetic treatment regimes. The test was performed separately for clones of each provenance and for each growth variable (total dry weight, leaf dry weight and leaf area). The results of the test are given in Table 4.2.18. The slopes of the growth functions for the Pickle Lake clones were significantly different ( $PR > F < 0.05$ ) under the two photosynthetic treatments, for all three growth variables. Differences in slopes were significant, or nearly so, for the Thunder Bay clones in terms of total dry weight ( $PR > F = 0.066$ ) and leaf dry weight ( $PR > F = 0.037$ ), and for the Severn River clones in terms of leaf dry weight ( $PR > F = 0.040$ ) and leaf area ( $PR > F = 0.054$ ). In all other cases, the intercepts of functions were significantly different ( $PR > F < 0.01$ ) under the two photosynthetic treatments.

Table 4.2.18. Tests of common slope and intercept for the growth functions fit to clones within provenances, comparing differences due to photosynthetic treatments. The degrees of freedom for the residual sum of squares of the reduced models A and B (RM(A) and RM(B)) are respectively, 7 and 14 more than that specified for the full model (FM) for N. Wisconsin, Thunder Bay, and Pickle Lake, and 6 and 12 more for Severn River.

Response Variable	Provenance	df (FM)	Residual Sum of Squares			Test of Common:			
			FM	RM(A)	RM(B)	Slope		Intercept	
						F	PR>F	F	PR>F
Total Dry Weight	N. Wisconsin	269	85.72	88.14	116.8	1.081	.376	12.82	.000
	Thunder Bay	278	66.87	70.10	113.6	1.923	.066	25.27	.000
	Pickle Lake	270	79.87	87.04	120.3	3.464	.001	15.12	.000
	Severn River	216	86.45	88.67	127.1	0.928	.476	16.04	.000
Leaf Dry Weight	N. Wisconsin	273	77.67	80.51	108.7	1.425	.195	14.03	.000
	Thunder Bay	279	59.80	63.05	101.3	2.166	.037	24.79	.000
	Pickle Lake	271	71.39	77.53	106.9	3.333	.002	15.04	.000
	Severn River	220	82.01	87.03	116.2	2.246	.040	12.62	.000
Leaf Area	N. Wisconsin	273	70.68	72.46	87.1	0.984	.443	8.06	.000
	Thunder Bay	279	51.56	53.82	74.2	1.747	.098	15.45	.000
	Pickle Lake	271	60.79	64.81	78.7	2.555	.015	8.51	.000
	Severn River	220	70.50	74.54	90.8	2.102	.054	8.21	.000

Tables 4.2.19 and 4.2.20 present point estimates of growth indices under the normal and reduced photosynthetic treatments, respectively, for specified times. The estimates are based on provenances, and are given for the study period at ten-day intervals. The corresponding estimates for clones are presented in Appendices X and XI.

Under the normal photosynthetic period, unit leaf rate (ULR) increased throughout the study period for all provenances except Severn River, which showed a slight decline in unit leaf rate with time. Estimates of unit leaf rate were comparable for the N. Wisconsin and Thunder Bay clones, whereas those for the Pickle Lake clones were substantially greater. Under the reduced photosynthetic period, the change in unit leaf rate with time was less than that under the normal photosynthetic period. This constancy was most noticeable for the N. Wisconsin, Thunder Bay, and Severn River clones, for which estimates of initial and final unit leaf rate varied by no more than seven percent under the reduced photosynthetic period.

For each provenance, the estimates of unit leaf rate on any day were lower under the reduced photosynthetic period than under the normal photosynthetic period. The estimates of unit leaf rate at day 56 under the reduced photosynthetic period were 75, 66, 62, and 64 percent of those under the normal photosynthetic period, for the N. Wisconsin, Thunder

Table 4.2.19. Point estimates of component indices for the four provenances of balsam poplar under the normal photosynthetic period, at specified days. Estimates are given for ten-day intervals, from day 26 to day 86, the days of the first and last harvests, respectively.

Provenance	Day	Unit Leaf Rate	Leaf Area Ratio	Specific Leaf Area	Leaf Weight Ratio	Leaf Area Partition Coefficient	Leaf Weight Partition Coefficient
		$\frac{\text{g} \cdot \text{dm}^{-2}}{\text{day}}$	$\text{dm}^2 \cdot \text{g}^{-1}$	$\text{dm}^2 \cdot \text{g}^{-1}$	$\text{g} \cdot \text{g}^{-1}$	$\frac{\text{dm}^2 \cdot \text{day}^{-1}}{\text{g} \cdot \text{day}^{-1}}$	$\frac{\text{g} \cdot \text{day}^{-1}}{\text{g} \cdot \text{day}^{-1}}$
N. Wisconsin	26	0.0353	1.652	2.382	0.694	1.570	0.633
	36	0.0363	1.605	2.434	0.659	1.525	0.602
	46	0.0374	1.559	2.487	0.627	1.482	0.573
	56	0.0385	1.515	2.541	0.596	1.439	0.544
	66	0.0396	1.471	2.596	0.567	1.398	0.518
	76	0.0408	1.429	2.653	0.539	1.358	0.492
	86	0.0420	1.388	2.710	0.512	1.319	0.468
Thunder Bay	26	0.0351	1.708	2.348	0.727	1.630	0.666
	36	0.0361	1.662	2.404	0.691	1.587	0.633
	46	0.0371	1.617	2.461	0.657	1.544	0.602
	56	0.0381	1.574	2.519	0.625	1.503	0.572
	66	0.0391	1.532	2.579	0.594	1.463	0.544
	76	0.0402	1.491	2.641	0.565	1.424	0.517
	86	0.0413	1.451	2.703	0.537	1.386	0.492
Pickle Lake	26	0.0361	1.816	2.558	0.710	1.669	0.646
	36	0.0380	1.722	2.574	0.669	1.582	0.608
	46	0.0401	1.633	2.590	0.630	1.500	0.573
	56	0.0423	1.548	2.606	0.594	1.422	0.540
	66	0.0446	1.468	2.622	0.560	1.348	0.509
	76	0.0471	1.391	2.638	0.527	1.278	0.480
	86	0.0497	1.319	2.655	0.497	1.212	0.452
Severn River	26	0.0376	1.432	2.385	0.601	1.459	0.575
	36	0.0373	1.447	2.464	0.587	1.473	0.562
	46	0.0369	1.461	2.546	0.574	1.488	0.550
	56	0.0365	1.476	2.630	0.561	1.503	0.537
	66	0.0362	1.491	2.718	0.548	1.518	0.525
	76	0.0358	1.506	2.808	0.536	1.534	0.514
	86	0.0355	1.521	2.901	0.524	1.549	0.502

Table 4.2.20. Point estimates of component indices for the four provenances of balsam poplar under the reduced photosynthetic period, at specified days. Estimates are given for ten-day intervals, from day 26 to day 86, the days of the first and last harvests, respectively.

Provenance	Day	Unit Leaf Rate	Leaf Area Ratio	Specific Leaf Area	Leaf Weight Ratio	Leaf Area Partition Coefficient	Leaf Weight Partition Coefficient
		$\frac{g \cdot dm^{-2}}{day}$	$dm^2 \cdot g^{-1}$	$dm^2 \cdot g^{-1}$	$g \cdot g^{-1}$	$\frac{dm^2 \cdot day^{-1}}{g \cdot day^{-1}}$	$\frac{g \cdot day^{-1}}{g \cdot day^{-1}}$
N. Wisconsin	26	0.0290	1.794	2.602	0.689	1.804	0.626
	36	0.0289	1.799	2.738	0.657	1.809	0.596
	46	0.0288	1.804	2.882	0.626	1.815	0.568
	56	0.0287	1.810	3.033	0.597	1.820	0.542
	66	0.0286	1.815	3.192	0.569	1.826	0.516
	76	0.0286	1.821	3.359	0.542	1.831	0.492
	86	0.0285	1.826	3.535	0.517	1.837	0.469
Thunder Bay	26	0.0244	2.059	2.715	0.758	2.018	0.682
	36	0.0247	2.039	2.827	0.721	1.998	0.649
	46	0.0249	2.018	2.944	0.686	1.978	0.617
	56	0.0252	1.998	3.065	0.652	1.959	0.587
	66	0.0254	1.978	3.191	0.620	1.939	0.558
	76	0.0257	1.959	3.323	0.589	1.920	0.530
	86	0.0259	1.939	3.460	0.561	1.901	0.504
Pickle Lake	26	0.0248	2.076	2.868	0.724	2.001	0.652
	36	0.0252	2.038	2.963	0.688	1.965	0.620
	46	0.0257	2.001	3.061	0.654	1.929	0.589
	56	0.0262	1.964	3.162	0.621	1.894	0.560
	66	0.0266	1.929	3.267	0.590	1.859	0.532
	76	0.0271	1.893	3.375	0.561	1.826	0.505
	86	0.0276	1.859	3.487	0.533	1.792	0.480
Severn River	26	0.0236	1.998	2.703	0.739	2.018	0.654
	36	0.0235	2.007	2.867	0.700	2.027	0.620
	46	0.0234	2.017	3.041	0.663	2.036	0.587
	56	0.0233	2.026	3.226	0.628	2.046	0.556
	66	0.0232	2.035	3.422	0.595	2.055	0.526
	76	0.0231	2.045	3.629	0.563	2.064	0.499
	86	0.0230	2.054	3.849	0.534	2.074	0.472

Bay, Pickle Lake, and Severn River clones, respectively.

Since RGR was constant for each provenance-treatment combination, unit leaf rate and leaf area ratio (LAR) were inversely related, since  $ULR=RGR/LAR$ . Thus, the time trends observed for leaf area ratio were the opposite of those observed for unit leaf rate, for each provenance-treatment combination. Leaf area ratio was consistently greater under the reduced photosynthetic period than under the normal photosynthetic period. At day 56, estimates of leaf area ratio under the normal photosynthetic period were 84, 79, 79, and 73 percent of those under the reduced photosynthetic period, for the N. Wisconsin, Thunder Bay, Pickle Lake, and Severn River sources, respectively.

Leaf weight ratio (LWR) decreased with time through the study period. For each provenance-treatment combination, estimates of leaf weight ratio were generally greater under reduced photosynthetic period than under the normal photosynthetic period. The magnitude of the differences, however, were not as great as those for leaf area ratio. At day 56, estimates of leaf weight ratio under the normal photosynthetic period were 99, 96, 96, and 89 percent of those under the reduced photosynthetic period, for the N. Wisconsin, Thunder Bay, Pickle Lake, and Severn River sources, respectively. The rate at which leaf weight ratio decreased with time was generally comparable among

provenances and treatments.

Unlike leaf weight ratio, specific leaf area (SLA), increased with time. The rate of increase was much greater under the reduced photosynthetic period than under the normal photosynthetic period. For each provenance-treatment combination, estimates of specific leaf area were consistently greater under the reduced photosynthetic period than under the normal photosynthetic period. Differences in specific leaf area under the two photosynthetic treatments were of similar magnitude for all provenances: at day 56, estimates of specific leaf area under the normal photosynthetic period ranged from to 82 to 84 percent of those under the reduced photosynthetic period.

Since RLaGR was constant, estimates of leaf area partition coefficient (LAP) were negatively correlated with unit leaf rate (since  $ULR = RLaGR/LAP$ ), and positively correlated with leaf area ratio (since  $LAR = RGR/RLaGR \times LAP$ ), for each provenance-treatment combination. Thus, the time trends in leaf area partition coefficient paralleled those of leaf area ratio. The estimates of leaf area partition coefficient were generally very close to those of leaf area ratio. This reflects the similar magnitude of RGR and RLaGR (if  $RGR = RLaGR$ , then  $LAR = LAP$ ). For those provenance-treatment combinations for which RGR was greater than RLaGR, all estimates of leaf area ratio were greater than those of

leaf area partition coefficient; the reverse was also true. Since both RGR and RLwGR were constant, estimates of leaf weight ratio and leaf weight partition coefficient, LWP, were positively correlated (since  $LWR = RGR/RLwGR \times LWP$ ).

Estimates of growth component indices were calculated for each clone and photosynthetic treatment (Appendices X and XI). The linear correlation between these estimates of RGR and the other growth component indices were calculated for days 26, 41, 56, 71, 86 (Table 4.2.21). Unit leaf rate consistently had high positive correlations with RGR, most noticeably in the latter half of the study period. Several correlations between RGR and both leaf area ratio and leaf area partition coefficient were significant, though none were greater than 0.50. Of these, most were negative and in the latter half of the study period. The correlations between RGR and both leaf weight ratio and leaf weight partition coefficient were not significant.

Table 4.2.21. Product-moment correlation between estimates of relative growth rate (RGR) and other growth component indices for the balsam poplar clones in the greenhouse study. Estimates of component indices were made for clones on days 26, 41, 56, 71, and 86; each coefficient is based on 27 pairs of values.

Growth Component Index	Photosyn- thetic Period	Date of Estimation				
		26	41	56	71	86
Unit Leaf Rate	Normal	.34	.65**	.88**	.92**	.88**
	Reduced	.53**	.72**	.86**	.90**	.87**
Leaf Area Ratio	Normal	.43*	.32	.06	-.33	-.46*
	Reduced	.21	.08	-.12	-.34	-.44*
Specific Leaf Area	Normal	.58**	.46*	.15	-.23	-.43*
	Reduced	.26	.16	-.02	-.22	-.32
Leaf Weight Ratio	Normal	.12	.06	-.06	-.26	-.33
	Reduced	.05	-.03	-.15	-.26	-.29
Leaf Area Parti- tion Coefficient	Normal	.35	.09	-.29	-.42*	-.43*
	Reduced	.04	-.19	-.39*	-.45*	-.45*
Leaf Weight Part- ition Coefficient	Normal	.25	.19	.02	-.12	-.17
	Reduced	.17	.08	-.03	-.11	-.14

\* significant at the 5% level

\*\* significant at the 1% level

### Allometric Analysis

Under both photosynthetic treatments, shoot/root ratio decreased with time and increasing plant size. Table 4.2.22 presents the mean shoot/root ratio of each provenance for the nine harvests under the two photosynthetic treatments. No consistent differences among provenances were evident under either treatment. There was a marked difference, however, due to the photosynthetic treatments. On the first harvest, the shoot/root ratio of provenances under the reduced photosynthetic period was greater than that under the normal photosynthetic period. By the final harvest, however, there was only a slight difference in shoot/ratio due to treatments.

The summary statistics for the regression of  $\ln(\text{shoot dry weight})$  on  $\ln(\text{root dry weight})$ , i.e.,

$\ln(\text{shoot dry weight}) = \ln(a) + K(\ln(\text{root dry weight}))$ , are presented in Table 4.2.23. The slope,  $K$ , of this function is the allometric constant.

The null hypothesis of common slopes among provenances within a treatment was tested and rejected ( $PR > F = 0.004$  and  $0.000$ , for the normal photosynthetic and reduced photosynthetic period, respectively). The allometric constant for the provenances under the reduced photosynthetic period, and to a lesser extent under the normal photosynthetic period, had a distinct inverse correlation with the latitude of the source. The same relationship

Table 4.2.22. Average shoot/root ratio at each harvest for the four provenances of balsam poplar in the greenhouse study.

Photosyn- thetic Period	Harvest	Provenance			
		Northern Wisconsin	Thunder Bay	Pickle Lake	Severn River
Normal	1	12.38	10.99	12.68	13.11
	2	7.42	12.05	9.69	12.72
	3	7.74	8.57	9.81	7.92
	4	5.60	6.82	6.56	6.61
	5	6.99	7.35	7.18	6.92
	6	6.03	5.82	5.84	5.48
	7	5.06	6.34	5.69	5.97
	8	6.28	6.65	6.60	6.31
	9	6.80	6.85	6.28	6.24
Reduced	1	19.71	17.61	24.89	21.13
	2	9.60	12.80	16.19	17.18
	3	10.26	10.38	10.59	13.13
	4	7.11	9.51	9.25	8.53
	5	7.59	7.27	7.75	9.80
	6	8.85	8.75	9.85	9.11
	7	6.55	6.89	6.31	7.12
	8	6.33	7.33	6.98	6.69
	9	7.60	7.22	7.27	6.77

Table 4.2.23. Summary of the regression statistics for the regression of  $\ln(\text{shoot dry weight})$  on  $\ln(\text{root dry weight})$  for provenances in the greenhouse study. The allometric function is of the following form:  $\ln(\text{SHw}) = \ln(a) + K(\ln(\text{Rw}))$ .

Photosyn- thetic Period	Provenance	coefficients		95% Confidence of Limits K		r
		$\ln(a)$	K	upper	lower	
Normal	N. Wisconsin	1.663	0.880	0.847	0.912	.976
	Thunder Bay	1.720	0.857	0.824	0.890	.973
	Pickle Lake	1.678	0.856	0.829	0.882	.982
	Severn River	1.533	0.793	0.754	0.832	.966
Reduced	N. Wisconsin	1.583	0.814	0.775	0.852	.961
	Thunder Bay	1.569	0.785	0.753	0.818	.968
	Pickle Lake	1.450	0.732	0.702	0.762	.971
	Severn River	1.309	0.705	0.666	0.744	.956

existed for the  $\ln(a)$  coefficients of provenances, under the reduced photosynthetic period. The allometric constant was less than 1.0 in all cases, indicating that the shoot/root ratio decreased with increasing plant age and size; the relative growth rate of roots was greater than that of shoots.

The regression of  $\ln(\text{shoot dry weight})$  versus  $\ln(\text{root dry weight})$  was performed for each clone-photosynthetic treatment combination. The null hypothesis of a common slope for all clones was tested and rejected ( $P > F = 0.001$  and  $0.000$  for the normal and reduced photosynthetic periods, respectively). Significant differences among clones were also found when the test for common slope was based on clones within provenances (Table 4.2.24). Under the normal

Table 4.2.24. Tests of common slope and intercept for the allometric functions fit to clones within provenances in the greenhouse study, comparing differences among clones. The degrees of freedom for the residual sum of squares of the reduced models A and B (RM(A) and RM(B)) are respectively, 6 and 12 more than that given for the full model (FM) for N. Wisconsin, Thunder Bay, and Pickle Lake, and 5 and 10 more for Severn River.

Photosyn- thetic Period	Proven- ance	df (FM)	Residual Sum of Squares			Test of Common:			
						Slope		Intercept	
			FM	RM(A)	RM(B)	F	PR>F	F	PR>F
Normal	N. Wisconsin	134	10.56	10.90	11.90	0.712	.641	2.141	.052
	Thunder Bay	139	9.32	11.09	13.07	4.408	.000	4.302	.001
	Pickle Lake	138	9.27	9.93	10.83	1.652	.137	2.162	.050
	Severn River	107	7.73	8.34	11.19	1.689	.143	7.646	.000
Reduced	N. Wisconsin	135	13.09	14.45	15.22	2.330	.036	1.266	.277
	Thunder Bay	139	9.22	10.24	11.58	2.547	.023	3.180	.006
	Pickle Lake	132	8.48	9.50	10.47	2.662	.018	2.343	.035
	Severn River	109	9.22	9.55	12.34	0.790	.559	6.654	.000

photosynthetic period, the allometric constants of the Thunder Bay clones were significantly different ( $P < 0.000$ ), whereas those of the other provenances were not. Under the reduced photosynthetic period, the allometric constants of the N. Wisconsin, Thunder Bay, and Pickle Lake clones, were significantly different ( $P < 0.05$ ); those of the Severn River clones were not.

A test was carried out to determine if the allometric functions for the clones within provenances differed significantly under the two photosynthetic treatment regimes (Table 4.2.25). The null hypothesis of a common slope was rejected for all provenances ( $P < 0.05$ ); the allometric constants were significantly less under the reduced photosynthetic period than under the normal photosynthetic period. This suggests that under the reduced photosynthetic period, plants tended toward greater root weight relative to shoot weight at a faster rate than those under the normal photosynthetic period. Additionally, the negative correlation between source latitude and the allometric constant (Table 4.2.23) indicates that the rate at which plants tended toward greater root weight relative to shoot weight was positively correlated with source latitude, the correlation being more distinct under the reduced photosynthetic period.

**Table 4.2.25.** Tests of common slope and intercept for allometric functions fit to clones within provenances in the greenhouse study, comparing differences due to the photosynthetic treatments. The degrees of freedom for the residual sum of squares of the reduced models A and B (RM(A) and RM(B)) are respectively, 7 and 14 more than that given for the full model (FM) for N. Wisconsin, Thunder Bay, and Pickle Lake, and 6 and 12 more for Severn River.

Provenance	df (FM)	Residual Sum of Squares			Test of Common:			
		-----			Slope		Intercept	
		FM	RM(A)	RM(B)	F	PR>F	F	PR>F
N. Wisconsin	269	23.66	24.92	25.74	2.05	.049	1.30	.248
Thunder Bay	278	18.54	19.92	20.73	2.96	.005	1.65	.120
Pickle Lake	270	17.74	20.23	20.77	5.40	.000	1.07	.386
Severn River	216	16.94	18.20	18.66	2.67	.016	0.93	.471

## 6 DISCUSSION

### NURSERY STUDY

The nursery study demonstrated significant variation among the clones of P. balsamifera tested, in terms of shoot growth, date of bud break, and date of growth cessation. These observations are in general agreement with other studies of Populus (e.g, Wilcox and Farmer, 1967; Farmer, 1970b; Mohn and Randall, 1973).

Date of height growth cessation differed significantly between provenances, occurring eight days later for the Thunder Bay source than for the Pickle Lake source. Negative correlations between the date of height growth cessation and source latitude have similarly been observed in provenance studies of P. deltoides, P. trichocarpa, P. balsamifera, and P. tremuloides (Pauley and Perry, 1954; Cannell and Willett, 1976; Brissette and Barnes, 1984). This relationship may in part be explained by source differences in day length. During the growing season in the northern hemisphere, photoperiod is positively correlated with latitude. Sources adapted to a more northern latitude, when moved south, cease growth sooner than local sources in response to the relative decrease in photoperiod (Vaartaja, 1959).

Negative correlations have also been observed between

height growth and source latitude in provenance studies of P. deltoides (Avanzo, 1969; Eldridge et al., 1972; Ying and Bagley, 1976). Eldridge et al. (1972) attributed this trend to the later height growth cessation of the southern sources. In the nursery study, the height growth of the Thunder Bay source was markedly greater than that of the Pickle Lake source (though the difference was not statistically significant). This source difference in height growth coincided with differences in times of growth cessation. A relationship between growth cessation and height growth is further suggested in the moderate and positive correlations between date of growth cessation and total shoot elongation ( $r_p = .49$ ,  $r_g = .42$ ); Cannell and Willett (1976) observed a similar relationship for P. trichocarpa ( $r_p = 0.55$ ). In addition to growing for a longer period, the Thunder Bay source generally grew at a faster rate than the Pickle Lake source. This difference in growth rate likely contributed to differences in final height.

Clonal variation in date of bud break was significant in the nursery study, in agreement with the work of Ying and Bagley (1976) and Kelly et al. (1978) with P. deltoides. Date of bud break apparently had little influence on height growth, however, as suggested by the low correlations between these two variables ( $r_p = -.130$ ,  $r_g = -.005$ ). Date of bud break did not differ significantly between provenances; bud break of the Pickle Lake source occurred one day earlier than

that of the Thunder Bay source. Ying and Bagley (1976) and Kelly et al. (1978) observed significant source differences in date of bud break in provenance trials of P. deltoides. In general, northern sources broke bud before southern sources, though within-source variation was high. Similar observations were made for P. tremuloides by Brissette and Barnes (1984). They concluded that the early-flushing sources were adapted to break bud at lower accumulated degree-days than the later-flushing sources. In natural populations of P. deltoides, the time of growth initiation at high latitudes coincided with lower temperatures and longer photoperiods than the time of initiation at lower latitudes (Kaszakurewicz and Fogg, 1967). If similar trends as these exist in P. balsamifera, a broader range in source latitude, than that used in the nursery study, may be required to detect them.

#### GREENHOUSE STUDY

The greenhouse study provided further indications of variation in P. balsamifera. Clonal variation in all morphological characteristics studied was significant, in agreement with other studies of Populus (e.g., Farmer, 1970b; Randall and Cooper, 1973; Cain and Ormrod, 1984). Differences among provenances approached significance only for leaf number.

Rank and linear correlations for clones based on the estimates of RGR, RLwGR, and RLaGR were relatively high.

This observation suggests that the different forms of production efficiency reflected in these component indices are related, and probably reflect a broader, underlying efficiency index of general plant growth, which varies among clones. Several studies of Populus have revealed genetic variation in the efficiency or rate of certain physiological processes. These include photosynthetic efficiency (Gatherum et al., 1967; Siwecki and Kozlowski, 1973), rate of dark respiration (Luukkanen and Kozlowski, 1972; Fasehun, 1978), rate of gas exchange (Ceulemans et al., 1978; Pallardy and Kozlowski, 1981), and water use efficiency (Ceulemans and Impens, 1980; Blake et al., 1984). Gatherum et al. (1967) and Fasehun (1978) both referred to the selection of "metabolically superior genotypes" as a means of improving growth and yield. The results of the greenhouse study suggest that within P. balsamifera, potential exists for selecting clones that exhibit superior efficiencies of dry matter and leaf area production. Furthermore, selection for any one of the relative growth rate indices (RGR, RLwGR, and RLaGR) should result in concomitant improvement in the other two.

Linear correlations between RGR and other growth component indices suggested that RGR was affected to a greater degree by unit leaf rate than by leaf development. Similarly, van den Driessche (1968) found that unit leaf rate had a greater effect on RGR than did leaf area ratio, in

several conifer species. Farmer (1980) observed moderate to high correlations between RGR and both unit leaf rate and leaf area partition coefficient for several hardwood species. Newhouse and Madgwick (1968) attributed differences in total growth of P. balsamifera to differences in leaf area growth rate, rather than unit leaf rate; differences in RGR were not examined.

Selection for high RGR among the clones of P. balsamifera examined in the greenhouse study would result in indirect selection for high unit leaf rate. In part, variation in unit leaf rate reflects variation in photosynthetic efficiency, which has previously been observed in Populus (Gatherum et al. 1967; Siwecki and Kozlowski, 1973). Since, however, unit leaf rate actually represents the result of photosynthetic gain over respiratory loss (Leopold and Kriedemann, 1975), variation in unit leaf rate may also reflect variation in respiration rates, which has also been observed in Populus (Luukkanen and Kozlowski, 1972; Fasehun, 1978). Selection for high RGR and unit leaf rate will result in the selection of those individuals which have a high photosynthesis-respiration differential to allocate into dry matter production.

For all sources under both the normal and reduced photosynthetic periods, the allometric constant was less than 1.0, indicating that the relative growth rate of roots was greater than that of shoots: shoot/root ratio decreased with

increasing plant size over the study period. The allometric constant was negatively correlated with source latitude; the rate of decrease in shoot/root ratio was greater for the northern sources than it was for the southern sources. Drew and Bazzaz (1978) found no significant differences in the allometric constants of three sources of P. deltoides, though the intercepts of the allometric functions differed significantly. A negative correlation between the allometric constant and source latitude was observed for P. trichocarpa by Cannell and Willett (1976), who attributed the differences in final shoot/root ratio to the earlier height growth cessation of the northern sources. In the greenhouse study, height growth continued throughout the study period. The differences in the allometric constant observed in this case likely reflect inherent source differences in the relative growth rates of shoots versus that of roots.

#### Photosynthetic Period Effects

The reduced photosynthetic period did not merely slow plant growth in proportion to the reduction in the photosynthetic period. Had this been the case, the growth functions for plants under the two photosynthetic periods would have differed accordingly in their intercepts, but not in their slopes (i.e., relative growth rates). As observed, however, plants under the reduced photosynthetic period had lower relative growth rates than those under the normal photosynthetic period. This result suggests that the reduced

photosynthetic period reduced the efficiency of daily dry matter and leaf area production.

The decrease in plant growth efficiency under the reduced photosynthetic period was also implied in the differences in final plant dry weights. Plants under the reduced photosynthetic period received half the daily photosynthetic period of those under the normal photosynthetic period. The former, however, generally produced less than half the dry weight of the latter, by the end of the study.

The lower relative growth rate of plants under the reduced photosynthetic period may in part reflect differing treatment effects on photosynthesis and respiration. The fifty percent reduction in the photosynthetic period likely resulted in a concomitant reduction in the daily rate of photosynthesis. It may, however, have had less of an effect on the daily rate of respiration. If such were the case, the plants under the reduced photosynthetic period would have a smaller photosynthesis-respiration differential to divert into dry matter production, and hence lower relative growth rates. Such a response was suggested by the lower unit leaf rate observed for plants under the reduced photosynthetic period.

To a certain extent, the reduction in unit leaf rate under the reduced photosynthetic period was partly offset by changes in leaf development. Plants under the reduced

photosynthetic period produced more leaf area per unit total and leaf dry matter production than plants under the normal photosynthetic period, largely due to an increase in specific leaf area. Chatterton and Silvius (1979) observed similar changes in the leaf morphology of soybean in response to a reduced photosynthetic period. Consequently, the decrease in RGR in response to the reduced photosynthetic period of the greenhouse study was not as great as the decrease in unit leaf rate.

The allometric constants of the plants under the reduced photosynthetic period were less than those of plants under the normal photosynthetic period, indicating that the shoot/root ratio of the former was decreasing at a faster rate than that of the latter. Chatterton and Silvius (1979) found that soybean plants grown under a 7-hour photosynthetic period had greater shoot/root ratios than those under a 14-hour photosynthetic period. However, the shoot/root ratio of a seedling typically decreases with increasing plant size (Ledig et al., 1970). Thus, a treatment that reduces plant size, may also result in greater shoot/root ratios, relative to controls, without actually affecting the relative growth rate of shoots versus that of roots. In the greenhouse study, as in that of Chatterton and Silvius (1979), the shoot/root ratio of the plants under the reduced photosynthetic period was greater than that of those under the normal photosynthetic period. As the allometric

constants show, however, the relative growth rate of shoots versus that of roots was lower for the plants under the reduced photosynthetic period than for those under the normal photosynthetic period.

Several observations suggest that differences exist among the provenances and clones tested in their tolerance to the reduction in photosynthetic period. Firstly, there were marked changes in clonal rankings based on estimates of RGR, RLwGR, and RLaGR, for plants under the normal versus reduced photosynthetic period, suggesting a clone by photosynthetic period interaction. This conclusion is supported by the multivariate analysis of variance of the growth response variables, which indicated a significant clone by photosynthetic period interaction.

Secondly, provenances differed in their relative response to the reduced photosynthetic period. In general, the relative difference in estimates of component indices for plants under the normal versus reduced photosynthetic period increased with source latitude. For example, the ratio of estimates of RGR for plants under the reduced versus the normal photosynthetic period ranged from 78 percent for the Pickle Lake clones to 89 percent for Northern Wisconsin clones. Analogous ratios for estimates of unit leaf rate ranged from 64 percent for the Severn River clones to 75 percent for the Northern Wisconsin clones. Additionally, the relative reduction in final total dry weight due to the

reduced photosynthetic period increased with increasing source latitude.

Lastly, the negative correlation between the allometric constant and source latitude was much more distinct under the reduced photosynthetic period than under the normal photosynthetic period. The magnitude of the decrease in the allometric constant, in response to the reduced photosynthetic period, increased with increasing source latitude. These general trends suggest that the southern sources were less affected by the reduction in photosynthetic period than the northern sources.

During the growing season of the northern hemisphere, the length of the photosynthetic period, like the photoperiod, is positively correlated with latitude. The importance of photoperiod in controlling the seasonal extent of shoot growth has been well demonstrated for Populus. The length of the photosynthetic period may also, however, be important in controlling plant growth and development. As demonstrated in the greenhouse study, the length of the photosynthetic period affected 1) plant growth efficiency, 2) the daily photosynthesis-respiration differential, 3) leaf morphology, and 4) the distribution of assimilate, of P. balsamifera. Additionally, variation exists among the sources and clones tested in their relative response to the length of the photosynthetic period. These results may warrant consideration in provenance studies of P.

balsamifera. Though a dramatic reduction in photosynthetic period was used in the greenhouse study, it may be that smaller reductions produce proportionally similar results. If this is the case, it seems tenable that in provenance studies of individuals relocated over wide latitudes, a response to relative changes in the photosynthetic period could affect source and clone differences in plant growth and development.

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## **APPENDICES**

APPENDIX I

SUMMARY OF REGRESSION ANALYSIS FOR GROWTH FUNCTIONS DESCRIBING TOTAL DRY WEIGHT (Tw) OVER TIME (t),  $\ln(Tw) = b_0 + b_1 t$ , FOR PROVENANCES UNDER BOTH PHOTOSYNTHETIC PERIODS

Photosyn- thetic Period	Provenance	b <sub>0</sub>	b <sub>1</sub>	Regress.		Residual		Pure Error		F-ratio <sup>+</sup>		R-squared <sup>++</sup>		Standard Error
				SS	df	SS	df	SS	Lack of Fit	Regres- sion	Actual	Adjust		
Normal	N. Wisconsin	-3.447	0.0583	192.31	146	62.92	139	60.71	0.723	446.27	0.753	0.989	0.656	
	Thunder Bay	-3.382	0.0599	210.01	151	42.00	144	40.47	0.781	754.98	0.833	0.993	0.527	
	Pickle Lake	-3.855	0.0655	251.14	150	60.94	143	56.37	1.657	618.15	0.805	0.982	0.637	
	Severn River	-3.164	0.0539	121.22	117	53.25	110	47.70	1.827	266.34	0.695	0.956	0.675	
Reduced	N. Wisconsin	-3.658	0.0520	148.95	147	52.91	140	50.54	0.936	413.81	0.738	0.984	0.600	
	Thunder Bay	-3.525	0.0503	148.83	151	43.37	144	41.70	0.825	518.19	0.774	0.989	0.536	
	Pickle Lake	-3.625	0.0514	149.61	144	39.53	137	37.26	1.192	544.99	0.791	0.985	0.524	
	Severn River	-3.525	0.0472	105.61	119	46.22	112	43.86	0.861	271.88	0.696	0.978	0.623	

<sup>+</sup> For all functions, the F-ratio testing lack of fit was not significant ( $PR > F > 0.05$ ), the F-ratio testing the regression was significant ( $PR > F < 0.05$ ).

<sup>++</sup> The Adjusted R<sup>2</sup> is the Actual R<sup>2</sup> adjusted for pure error variation.

APPENDIX II

SUMMARY OF REGRESSION ANALYSIS FOR GROWTH FUNCTIONS DESCRIBING LEAF DRY WEIGHT ( $L_w$ ) OVER TIME ( $t$ ),  $\ln(L_w) = b_0 + b_1 t$ , FOR PROVENANCES UNDER BOTH PHOTOSYNTHETIC PERIODS

Photosyn- thetic Period	Provenance	$b_0$	$b_1$	Regress.		Pure Error			F-ratio <sup>†</sup>		R-squared <sup>††</sup>		Standard Error
				SS	df	SS	df	SS	Lack of Fit	Regres- sion	Actual	Adjust	
Normal	N. Wisconsin	-3.656	0.0532	164.07	147	55.75	140	53.52	0.836	432.60	0.746	0.987	0.616
	Thunder Bay	-3.555	0.0549	177.99	152	37.95	145	36.64	0.736	712.98	0.824	0.993	0.500
	Pickle Lake	-4.014	0.0596	207.55	150	52.48	143	48.64	1.615	593.18	0.798	0.982	0.592
	Severn River	-3.601	0.0516	124.54	121	51.53	114	46.84	1.629	292.45	0.707	0.964	0.653
Reduced	N. Wisconsin	-3.883	0.0472	129.96	150	47.38	143	46.15	0.547	411.44	0.733	0.991	0.562
	Thunder Bay	-3.652	0.0453	120.52	151	37.82	144	36.11	0.971	481.24	0.761	0.986	0.500
	Pickle Lake	-3.798	0.0463	124.19	145	34.86	138	33.28	0.939	516.52	0.781	0.987	0.490
	Severn River	-3.669	0.0418	82.74	119	42.22	112	39.89	0.934	233.22	0.662	0.973	0.596

<sup>†</sup> For all functions, the F-ratio testing lack of fit was not significant ( $PR > F > 0.05$ ), the F-ratio testing the regression was significant ( $PR > F < 0.05$ ).

<sup>††</sup> The Adjusted  $R^2$  is the Actual  $R^2$  adjusted for pure error variation.

APPENDIX III

SUMMARY OF REGRESSION ANALYSIS FOR GROWTH FUNCTIONS DESCRIBING LEAF AREA (La) OVER TIME (t),  $\ln(La) = b_0 + b_1 t$ , FOR PROVENANCES UNDER BOTH PHOTOSYNTHETIC PERIODS

Photosyn- thetic Period	Provenance	b <sub>0</sub>	b <sub>1</sub>	Regress.		Residual		Pure Error		F-ratio <sup>+</sup>		R-squared <sup>++</sup>		Standard Error
				SS	df	SS	df	SS	Lack of Fit	Regres- sion	Actual	Adjust		
Normal	N. Wisconsin	-2.823	0.0554	177.56	147	49.47	140	46.93	1.084	527.59	0.782	0.986	0.580	
	Thunder Bay	-2.742	0.0572	193.57	152	31.77	145	30.22	1.060	926.24	0.859	0.992	0.457	
	Pickle Lake	-3.062	0.0602	211.90	150	43.90	143	40.21	1.874	724.08	0.828	0.983	0.541	
	Severn River	-2.776	0.0549	140.79	121	41.71	114	38.36	1.421	408.46	0.771	0.977	0.587	
Reduced	N. Wisconsin	-3.053	0.0523	159.65	150	45.26	143	43.71	0.725	529.13	0.779	0.990	0.549	
	Thunder Bay	-2.747	0.0493	142.99	151	34.52	144	32.76	1.105	625.45	0.806	0.988	0.478	
	Pickle Lake	-2.812	0.0496	142.27	145	29.95	138	28.64	0.902	688.76	0.826	0.991	0.454	
	Severn River	-2.825	0.0477	107.68	119	41.55	112	38.20	1.400	308.42	0.722	0.970	0.591	

<sup>+</sup> For all functions, the F-ratio testing lack of fit was not significant ( $PR > F > 0.05$ ), the F-ratio testing the regression was significant ( $PR > F < 0.05$ ).

<sup>++</sup> The Adjusted R<sup>2</sup> is the Actual R<sup>2</sup> adjusted for pure error variation.

APPENDIX IV

SUMMARY OF REGRESSION ANALYSIS FOR GROWTH FUNCTIONS DESCRIBING TOTAL DRY WEIGHT (Tw)  
OVER TIME (t),  $\ln(Tw) = b_0 + b_1 t$ , FOR CLONES UNDER THE NORMAL PHOTOSYNTHETIC PERIOD

Provenance	Clone	b <sub>0</sub>	b <sub>1</sub>	Regress.		Residual		Pure Error		F-ratio <sup>+</sup>		R-squared <sup>++</sup>		Standard Error
				SS	df	SS	df	SS	Lack of Fit	Regression	Actual	Adjust		
N. Wisconsin	223	-3.535	0.0565	26.96	20	4.83	13	3.09	1.049	111.64	0.848	0.939	0.491	
	233	-3.132	0.0515	21.59	19	5.16	12	3.64	0.715	79.56	0.807	0.934	0.521	
	227	-3.723	0.0683	39.40	20	5.52	13	4.43	0.455	142.87	0.877	0.973	0.525	
	247	-4.197	0.0657	32.28	16	7.09	9	2.75	2.036	72.79	0.820	0.881	0.666	
	238	-3.509	0.0662	37.04	20	4.16	13	3.58	0.302	178.20	0.899	0.985	0.456	
	278	-2.749	0.0405	11.60	19	11.51	12	9.78	0.304	19.14	0.502	0.870	0.778	
	279	-3.200	0.0572	27.59	20	5.97	13	3.17	1.638	92.34	0.822	0.908	0.547	
Thunder Bay	5	-2.928	0.0525	23.26	20	4.60	13	4.22	0.165	101.16	0.835	0.984	0.480	
	36	-3.535	0.0657	36.42	20	5.37	13	4.83	0.207	135.59	0.871	0.985	0.518	
	44	-3.146	0.0550	25.56	20	3.73	13	3.22	0.295	137.20	0.873	0.980	0.432	
	35	-3.811	0.0702	38.40	19	1.56	12	0.70	2.105	466.65	0.961	0.978	0.287	
	30	-3.312	0.0605	30.88	20	5.80	13	4.25	0.674	106.58	0.842	0.952	0.538	
	19	-3.364	0.0543	24.88	20	6.82	13	3.57	1.689	72.98	0.785	0.885	0.584	
Pickle Lake	45	-3.589	0.0615	31.91	20	7.06	13	3.13	2.337	90.38	0.819	0.890	0.594	
	136	-4.035	0.0605	30.94	20	14.42	13	9.69	0.907	42.90	0.682	0.867	0.849	
	121	-3.831	0.0685	38.16	19	5.38	12	2.94	1.418	134.79	0.876	0.940	0.532	
	142	-4.181	0.0701	41.43	20	6.73	13	3.64	1.576	123.02	0.860	0.931	0.580	
	116	-3.560	0.0680	39.01	20	6.21	13	3.49	1.446	125.66	0.863	0.935	0.557	
	102	-3.450	0.0547	25.24	20	3.73	13	2.79	0.626	135.44	0.871	0.964	0.432	
	152	-4.015	0.0705	41.99	20	5.75	13	4.89	0.330	145.93	0.879	0.980	0.536	
Severn River	117	-3.933	0.0669	36.48	19	4.30	12	2.67	1.039	161.33	0.895	0.957	0.476	
	345	-3.995	0.0671	35.24	18	9.13	11	5.56	1.009	69.50	0.794	0.908	0.712	
	322	-3.460	0.0559	18.73	17	6.28	10	2.58	2.043	50.72	0.749	0.835	0.608	
	326	-2.811	0.0531	15.74	18	7.41	12	5.66	0.616	38.24	0.680	0.900	0.642	
	327	-2.693	0.0460	17.87	19	8.84	12	5.04	1.293	38.41	0.669	0.825	0.682	
	320	-3.701	0.0636	22.88	16	8.35	9	6.14	0.463	43.83	0.733	0.912	0.722	
	335	-2.317	0.0379	11.29	19	6.02	12	3.46	1.264	35.63	0.652	0.815	0.563	

\* For all functions, the F-ratio testing lack of fit was not significant ( $PR > F > 0.05$ ), the F-ratio testing the regression was significant ( $PR > F < 0.05$ ).

\*\* The Adjusted R<sup>2</sup> is the Actual R<sup>2</sup> adjusted for pure error variation.

APPENDIX V

SUMMARY OF REGRESSION ANALYSIS FOR GROWTH FUNCTIONS DESCRIBING LEAF DRY WEIGHT ( $L_w$ ) OVER TIME ( $t$ ),  $\ln(L_w) = b_0 + b_1 t$ , FOR CLONES UNDER THE NORMAL PHOTOSYNTHETIC PERIOD

Provenance	Clone	$b_0$	$b_1$	Regress.		Residual		Pure Error			F-ratio <sup>+</sup>		R-squared <sup>++</sup>		Standard Error
				SS	df	SS	df	SS	Lack of Fit	Regression	Actual	Adjust			
N. Wisconsin	223	-3.824	0.0524	23.16	20	4.19	13	2.67	1.050	110.62	0.847	0.939	0.458		
	233	-3.388	0.0481	18.82	19	4.20	12	3.10	0.612	85.06	0.817	0.945	0.470		
	227	-3.915	0.0628	33.30	20	5.06	13	3.99	0.501	131.48	0.868	0.969	0.503		
	247	-4.411	0.0609	27.68	16	6.30	9	2.40	2.090	70.34	0.815	0.877	0.627		
	238	-3.704	0.0604	30.78	20	3.87	13	3.35	0.287	159.02	0.888	0.983	0.440		
	278	-2.934	0.0362	11.08	20	10.72	13	9.31	0.282	20.66	0.508	0.887	0.732		
	279	-3.410	0.0511	22.04	20	5.69	13	2.95	1.726	77.51	0.795	0.889	0.533		
Thunder Bay	5	-3.059	0.0463	18.13	20	4.29	13	4.02	0.126	84.51	0.809	0.985	0.463		
	36	-3.770	0.0608	31.23	20	4.42	13	3.96	0.213	141.36	0.876	0.986	0.470		
	44	-3.345	0.0504	21.46	20	3.62	13	3.21	0.238	118.48	0.856	0.981	0.426		
	35	-4.039	0.0662	36.96	20	1.51	13	1.01	0.920	488.64	0.961	0.987	0.275		
	30	-3.422	0.0546	25.14	20	5.45	13	3.94	0.713	92.30	0.822	0.943	0.522		
	19	-3.475	0.0490	20.23	20	5.91	13	3.11	1.670	68.45	0.774	0.878	0.544		
	45	-3.772	0.0569	27.33	20	6.27	13	2.84	2.246	87.17	0.813	0.888	0.560		
Pickle Lake	136	-4.212	0.0552	25.74	20	12.57	13	8.56	0.870	40.93	0.672	0.865	0.793		
	121	-3.982	0.0620	31.31	19	4.60	12	2.61	1.307	129.39	0.872	0.940	0.492		
	142	-4.414	0.0653	35.96	20	6.09	13	3.18	1.697	118.04	0.855	0.925	0.552		
	116	-3.689	0.0606	30.95	20	5.11	13	2.92	1.386	121.23	0.858	0.934	0.505		
	102	-3.584	0.0490	20.28	20	3.44	13	2.47	0.725	117.90	0.855	0.955	0.415		
	152	-4.155	0.0637	34.25	20	5.09	13	4.22	0.380	134.58	0.871	0.975	0.504		
	117	-4.088	0.0618	31.11	19	3.61	12	2.22	1.079	163.62	0.896	0.957	0.436		
Severn River	345	-4.210	0.0620	30.05	18	7.96	11	4.81	1.026	67.96	0.791	0.905	0.665		
	322	-3.789	0.0529	20.14	18	5.35	11	2.40	1.931	67.70	0.790	0.872	0.545		
	326	-4.064	0.0615	31.95	20	11.04	13	6.12	1.493	57.87	0.743	0.867	0.743		
	327	-2.839	0.0403	13.67	19	7.51	12	4.24	1.320	34.59	0.645	0.807	0.629		
	320	-4.120	0.0601	24.53	17	8.05	10	6.09	0.460	51.83	0.753	0.926	0.688		
	335	-2.589	0.0333	8.72	19	4.69	12	2.78	1.175	35.32	0.650	0.821	0.497		

\* For all functions, the F-ratio testing lack of fit was not significant ( $PR > F > 0.05$ ), the F-ratio testing the regression was significant ( $PR > F < 0.05$ ).

\*\* The Adjusted  $R^2$  is the Actual  $R^2$  adjusted for pure error variation.

APPENDIX VI

SUMMARY OF REGRESSION ANALYSIS FOR GROWTH FUNCTIONS DESCRIBING LEAF AREA ( $L_a$ )  
OVER TIME ( $t$ ),  $\ln(L_a) = b_0 + b_1 t$ , FOR CLONES UNDER THE NORMAL PHOTOSYNTHETIC PERIOD

Provenance	Clone	$b_0$	$b_1$	Regress.		Residual		Pure Error		F-ratio <sup>+</sup>		R-squared <sup>++</sup>		Standard Error
				SS	df	SS	df	SS	Lack of Fit	Regression	Actual	Adjust		
N. Wisconsin	223	-2.903	0.0547	25.24	20	4.18	13	2.66	1.067	120.60	0.858	0.943	0.457	
	233	-2.638	0.0521	22.10	19	4.31	12	3.00	0.747	97.44	0.837	0.944	0.476	
	227	-3.003	0.0636	34.19	20	3.35	13	2.72	0.436	203.93	0.911	0.982	0.409	
	247	-3.529	0.0632	29.86	16	5.34	9	2.14	1.916	89.49	0.848	0.903	0.578	
	238	-2.868	0.0619	32.34	20	3.57	13	2.95	0.391	181.25	0.901	0.981	0.422	
	278	-2.304	0.0404	13.79	20	10.38	13	8.62	0.378	26.57	0.571	0.887	0.720	
	279	-2.520	0.0513	22.25	20	4.44	13	2.66	1.246	100.11	0.833	0.926	0.471	
Thunder Bay	5	-2.436	0.0506	21.63	20	4.17	13	3.83	0.166	103.77	0.838	0.984	0.457	
	36	-3.007	0.0646	35.23	20	3.34	13	2.67	0.462	211.25	0.914	0.981	0.408	
	44	-2.537	0.0534	24.06	20	3.04	13	2.77	0.184	158.33	0.888	0.989	0.390	
	35	-3.039	0.0661	36.93	20	1.89	13	1.52	0.453	391.46	0.951	0.990	0.307	
	30	-2.612	0.0557	26.22	20	5.09	13	3.81	0.625	102.94	0.837	0.953	0.505	
	19	-2.713	0.0533	23.95	20	3.59	13	2.11	1.306	133.62	0.870	0.942	0.423	
Pickle Lake	45	-2.850	0.0569	27.33	20	4.93	13	2.69	1.544	110.95	0.847	0.924	0.496	
	136	-3.403	0.0592	29.58	20	11.67	13	7.45	1.051	50.68	0.717	0.875	0.764	
	121	-3.024	0.0624	31.69	19	4.22	12	2.85	0.830	142.54	0.882	0.958	0.472	
	142	-3.281	0.0630	33.52	20	4.63	13	2.66	1.376	144.85	0.879	0.944	0.481	
	116	-2.785	0.0614	31.79	20	4.20	13	2.29	1.553	151.50	0.883	0.943	0.458	
	102	-2.735	0.0512	22.16	20	3.07	13	2.08	0.879	144.55	0.878	0.957	0.392	
	152	-3.144	0.0631	33.65	20	4.19	13	3.36	0.463	160.44	0.889	0.976	0.458	
Severn River	117	-3.088	0.0615	30.79	19	2.67	12	1.82	0.801	219.33	0.920	0.973	0.375	
	345	-3.146	0.0623	30.39	18	4.66	11	3.28	0.659	117.33	0.867	0.957	0.509	
	322	-3.154	0.0598	25.72	18	3.49	11	1.82	1.445	132.47	0.880	0.939	0.441	
	326	-3.521	0.0682	39.22	20	10.16	13	4.86	2.027	77.20	0.794	0.881	0.713	
	327	-1.846	0.0417	14.64	19	4.57	12	2.93	0.956	60.88	0.762	0.899	0.490	
	320	-3.189	0.0600	24.45	17	8.74	10	6.54	0.479	47.57	0.737	0.918	0.717	
	335	-1.779	0.0372	10.85	19	2.83	12	2.00	0.712	72.76	0.793	0.929	0.386	

\* For all functions, the F-ratio testing lack of fit was not significant ( $PR > F > 0.05$ ), the F-ratio testing the regression was significant ( $PR > F < 0.05$ ).

\*\* The Adjusted  $R^2$  is the Actual  $R^2$  adjusted for pure error variation.

APPENDIX VII

SUMMARY OF REGRESSION ANALYSIS FOR GROWTH FUNCTIONS DESCRIBING TOTAL DRY WEIGHT ( $T_w$ ) OVER TIME ( $t$ ),  $\ln(T_w) = b_0 + b_1 t$ , FOR CLONES UNDER THE REDUCED PHOTOSYNTHETIC PERIOD

Provenance	Clone	$b_0$	$b_1$	Regress.		Residual		Pure Error		F-ratio <sup>+</sup>		R-squared <sup>++</sup>		Standard Error
				SS	df	SS	df	SS	Lack of Fit	Regression	Actual	Adjust		
N. Wisconsin	223	-3.942	0.0571	27.534	20	7.31	13	5.38	0.66	75.38	0.790	0.935	0.604	
	233	-3.835	0.0518	19.010	19	14.76	12	8.25	1.35	24.48	0.563	0.745	0.881	
	227	-3.597	0.0540	24.575	20	4.19	13	2.52	1.23	117.33	0.854	0.936	0.458	
	247	-4.146	0.0547	20.657	18	4.88	11	3.62	0.55	76.17	0.809	0.943	0.521	
	238	-3.772	0.0611	31.527	20	4.03	13	2.61	1.01	156.52	0.887	0.957	0.449	
	278	-3.470	0.0449	14.570	18	3.07	11	1.84	1.05	85.52	0.826	0.922	0.413	
	279	-3.037	0.0424	15.160	20	3.25	13	2.02	1.14	93.20	0.823	0.925	0.403	
Thunder Bay	5	-3.065	0.0419	14.835	20	5.30	13	3.61	0.87	56.01	0.737	0.898	0.515	
	36	-3.353	0.0522	22.195	19	1.90	12	1.74	0.16	221.45	0.921	0.993	0.317	
	44	-3.574	0.0505	21.497	20	4.18	13	3.30	0.49	102.84	0.837	0.961	0.457	
	35	-3.637	0.0523	23.080	20	3.81	13	3.21	0.35	121.14	0.858	0.974	0.436	
	30	-3.455	0.0538	24.467	20	3.68	13	2.49	0.88	133.14	0.869	0.954	0.429	
	19	-3.752	0.0453	17.352	20	9.68	13	6.84	0.77	35.87	0.642	0.859	0.696	
	45	-3.862	0.0568	27.186	20	3.39	13	1.45	2.48	160.58	0.889	0.934	0.411	
Pickle Lake	136	-4.024	0.0546	25.169	20	5.53	13	4.15	0.62	90.99	0.820	0.948	0.526	
	121	-3.363	0.0504	20.408	17	6.18	10	1.97	3.04	56.17	0.768	0.829	0.603	
	142	-3.640	0.0518	21.758	19	6.56	12	3.75	1.29	63.01	0.768	0.886	0.588	
	116	-3.268	0.0472	18.830	20	2.24	13	2.02	0.20	168.36	0.894	0.988	0.334	
	102	-3.913	0.0512	21.854	19	4.39	12	3.70	0.32	94.60	0.833	0.969	0.481	
	152	-3.122	0.0484	16.026	17	4.96	10	3.48	0.61	54.87	0.763	0.915	0.540	
	117	-3.898	0.0546	25.186	20	3.48	13	2.40	0.84	144.64	0.879	0.959	0.417	
Severn River	345	-3.478	0.0497	20.850	20	5.20	13	3.59	0.83	80.18	0.800	0.928	0.510	
	322	-3.869	0.0526	22.188	18	6.47	11	2.60	2.34	61.74	0.774	0.852	0.599	
	326	-2.745	0.0386	12.563	19	4.78	12	4.30	0.19	49.94	0.724	0.963	0.502	
	327	-3.476	0.0427	10.324	16	12.74	9	7.58	0.87	12.97	0.448	0.667	0.892	
	320	-4.189	0.0565	26.449	17	7.92	11	6.82	0.30	56.74	0.769	0.960	0.683	
	335	-3.320	0.0413	14.367	19	3.31	12	2.47	0.58	82.42	0.813	0.945	0.418	

\* For all functions, the F-ratio testing lack of fit was not significant ( $PR > F > 0.05$ ), the F-ratio testing the regression was significant ( $PR > F < 0.05$ ).

\*\* The Adjusted  $R^2$  is the Actual  $R^2$  adjusted for pure error variation.

APPENDIX VIII

SUMMARY OF REGRESSION ANALYSIS FOR GROWTH FUNCTIONS DESCRIBING LEAF DRY WEIGHT ( $L_w$ ) OVER TIME ( $t$ ),  $\ln(L_w) = b_0 + b_1 t$ , FOR CLONES UNDER THE REDUCED PHOTOSYNTHETIC PERIOD

Provenance	Clone	$b_0$	$b_1$	Regress.		Residual		Pure Error		F-ratio <sup>+</sup>		R-squared <sup>++</sup>		Standard Error
				SS	df	SS	df	SS	Lack of Fit	Regression	Actual	Adjust		
N. Wisconsin	223	-4.058	0.0499	20.98	20	6.50	13	4.80	0.659	64.57	0.764	0.925	0.570	
	233	-4.357	0.0519	22.73	20	13.99	13	8.24	1.296	32.49	0.619	0.798	0.836	
	227	-3.675	0.0469	18.59	20	3.36	13	2.14	1.061	110.70	0.847	0.938	0.410	
	247	-4.300	0.0496	20.47	19	4.38	12	3.23	0.611	88.78	0.824	0.947	0.480	
	238	-3.909	0.0543	24.88	20	3.60	13	2.39	0.937	138.34	0.874	0.954	0.424	
	278	-3.701	0.0409	13.10	19	3.14	12	1.71	1.442	79.20	0.807	0.901	0.407	
	279	-3.171	0.0361	11.03	20	2.67	13	1.64	1.153	82.74	0.805	0.915	0.365	
Thunder Bay	5	-3.206	0.0371	11.59	20	4.73	13	3.38	0.742	49.03	0.710	0.896	0.486	
	36	-3.506	0.0467	17.76	19	1.51	12	1.41	0.119	222.97	0.921	0.994	0.282	
	44	-3.688	0.0451	17.15	20	3.68	13	2.93	0.474	93.30	0.823	0.958	0.429	
	35	-3.825	0.0483	19.73	20	3.60	13	2.99	0.379	109.57	0.846	0.970	0.424	
	30	-3.526	0.0478	19.28	20	3.23	13	2.20	0.869	119.55	0.857	0.949	0.402	
	19	-3.838	0.0406	13.89	20	8.75	13	6.00	0.849	31.75	0.614	0.835	0.661	
Pickle Lake	45	-3.994	0.0519	22.75	20	2.84	13	1.19	2.578	160.06	0.889	0.932	0.377	
	136	-4.056	0.0476	19.16	20	4.75	13	3.50	0.661	80.68	0.801	0.939	0.487	
	121	-3.466	0.0440	15.51	17	5.13	10	1.66	2.973	51.42	0.752	0.817	0.549	
	142	-3.769	0.0458	16.98	19	5.95	12	3.20	1.476	54.25	0.741	0.861	0.560	
	116	-3.395	0.0410	14.18	20	1.80	13	1.58	0.258	157.57	0.887	0.985	0.300	
	102	-4.026	0.0461	17.76	19	3.92	12	3.27	0.340	86.15	0.819	0.965	0.454	
	152	-3.804	0.0497	20.07	18	6.19	11	4.78	0.466	58.36	0.764	0.934	0.586	
Severn River	117	-4.056	0.0502	21.26	20	3.14	13	2.05	0.991	135.49	0.871	0.951	0.396	
	345	-3.649	0.0443	16.53	20	4.17	13	2.73	0.977	79.22	0.798	0.920	0.457	
	322	-4.020	0.0475	18.12	18	7.05	11	2.81	2.366	46.26	0.720	0.810	0.626	
	326	-2.968	0.0342	9.88	19	3.80	12	3.48	0.160	49.37	0.722	0.968	0.447	
	327	-3.522	0.0362	7.43	16	12.79	9	7.68	0.857	9.29	0.367	0.592	0.894	
	320	-4.276	0.0498	20.54	17	6.77	11	5.86	0.285	51.56	0.752	0.958	0.631	
	335	-3.493	0.0366	11.32	19	2.82	12	2.04	0.653	76.32	0.801	0.936	0.385	

\* For all functions, the F-ratio testing lack of fit was not significant ( $PR > F > 0.05$ ), the F-ratio testing the regression was significant ( $PR > F < 0.05$ ).

\*\* The Adjusted  $R^2$  is the Actual  $R^2$  adjusted for pure error variation.

APPENDIX IX

SUMMARY OF REGRESSION ANALYSIS FOR GROWTH FUNCTIONS DESCRIBING LEAF AREA ( $L_a$ )  
OVER TIME ( $t$ ),  $\ln(L_a) = b_0 + b_1 t$ , FOR CLONES UNDER THE REDUCED PHOTOSYNTHETIC PERIOD

Provenance	Clone	$b_0$	$b_1$	Regress.		Residual		Pure Error		F-ratio <sup>†</sup>		R-squared <sup>**</sup>		Standard Error
				SS	df	SS	df	SS	Lack of Fit	Regression	Actual	Adjust		
N. Wisconsin	223	-3.017	0.0529	23.60	20	5.13	13	3.67	0.736	92.08	0.822	0.942	0.506	
	233	-3.705	0.0592	29.56	20	14.26	13	8.44	1.281	41.47	0.675	0.836	0.844	
	227	-2.799	0.0517	22.57	20	2.66	13	1.60	1.218	170.02	0.895	0.955	0.364	
	247	-3.476	0.0557	25.80	19	3.86	12	2.51	0.916	127.04	0.870	0.950	0.451	
	238	-2.912	0.0565	26.91	20	3.63	13	2.20	1.209	148.28	0.881	0.950	0.426	
	278	-3.055	0.0477	17.83	19	3.28	12	1.73	1.533	103.38	0.845	0.920	0.415	
	279	-2.384	0.0416	14.61	20	2.30	13	1.35	1.318	127.02	0.864	0.939	0.339	
	Thunder Bay	5	-2.525	0.0431	15.69	20	5.39	13	4.21	0.523	58.17	0.744	0.930	0.519
36		-2.809	0.0517	21.74	19	1.27	12	1.19	0.114	325.06	0.945	0.996	0.259	
44		-2.742	0.0486	19.97	20	2.65	13	2.17	0.414	150.73	0.883	0.976	0.364	
35		-2.810	0.0523	23.05	20	2.62	13	2.16	0.394	176.22	0.898	0.981	0.362	
30		-2.646	0.0514	22.28	20	2.38	13	1.56	0.979	186.89	0.903	0.964	0.345	
19		-2.909	0.0448	16.91	20	9.05	13	6.41	0.763	37.38	0.651	0.865	0.673	
45		-3.015	0.0540	24.65	20	2.16	13	1.05	1.958	227.81	0.919	0.957	0.329	
Pickle Lake	136	-3.241	0.0540	24.60	20	3.66	13	2.93	0.460	134.56	0.871	0.971	0.428	
	121	-2.405	0.0462	17.12	17	3.99	10	1.30	2.944	73.02	0.811	0.864	0.484	
	142	-2.718	0.0477	18.39	19	5.27	12	2.75	1.568	66.36	0.777	0.880	0.526	
	116	-2.495	0.0457	17.66	20	1.23	13	1.06	0.295	287.64	0.935	0.991	0.248	
	102	-2.990	0.0486	19.70	19	3.77	12	3.00	0.436	99.32	0.839	0.963	0.445	
	152	-2.873	0.0534	23.21	18	6.14	11	4.76	0.456	68.06	0.791	0.944	0.584	
	117	-2.947	0.0515	22.39	20	2.10	13	1.28	1.206	212.88	0.914	0.964	0.324	
Severn River	345	-2.856	0.0515	22.38	20	3.91	13	2.21	1.424	114.46	0.851	0.930	0.442	
	322	-3.261	0.0536	23.05	18	8.40	11	3.18	2.585	49.40	0.733	0.815	0.683	
	326	-2.108	0.0402	13.63	19	3.89	12	3.27	0.324	66.60	0.778	0.957	0.452	
	327	-2.640	0.0423	10.11	16	11.18	9	7.14	0.728	14.46	0.475	0.714	0.836	
	320	-3.454	0.0556	25.61	17	6.09	11	4.90	0.444	71.49	0.808	0.956	0.599	
	335	-2.544	0.0408	14.05	19	2.57	12	1.74	0.816	103.85	0.845	0.944	0.368	

<sup>†</sup> For all functions, the F-ratio testing lack of fit was not significant ( $PR > F > 0.05$ ), the F-ratio testing the regression was significant ( $PR > F < 0.05$ ).

<sup>\*\*</sup> The Adjusted  $R^2$  is the Actual  $R^2$  adjusted for pure error variation.

## APPENDIX X

POINT ESTIMATES OF GROWTH COMPONENT INDICES FOR  
CLONES UNDER THE NORMAL PHOTOSYNTHETIC PERIOD OF  
THE GREENHOUSE STUDY, AT SPECIFIED DAYS

UNIT LEAF RATE ( $\text{g} \cdot \text{dm}^{-2} \cdot \text{day}^{-1}$ )

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	0.0320	0.0329	0.0338	0.0348	0.0357
	233	0.0316	0.0314	0.0311	0.0308	0.0305
	227	0.0396	0.0425	0.0456	0.0489	0.0525
	247	0.0380	0.0394	0.0409	0.0425	0.0441
	238	0.0397	0.0423	0.0452	0.0482	0.0515
	278	0.0271	0.0272	0.0272	0.0272	0.0273
	279	0.0350	0.0382	0.0417	0.0455	0.0497
Thunder Bay	5	0.0340	0.0350	0.0360	0.0371	0.0381
	36	0.0419	0.0426	0.0433	0.0440	0.0447
	44	0.0318	0.0325	0.0334	0.0342	0.0350
	35	0.0359	0.0382	0.0406	0.0432	0.0459
	30	0.0346	0.0371	0.0399	0.0428	0.0460
	19	0.0315	0.0320	0.0325	0.0330	0.0335
	45	0.0349	0.0374	0.0400	0.0429	0.0459
Pickle Lake	136	0.0357	0.0364	0.0371	0.0379	0.0387
	121	0.0369	0.0404	0.0442	0.0485	0.0531
	142	0.0360	0.0401	0.0445	0.0495	0.0550
	116	0.0391	0.0432	0.0477	0.0527	0.0582
	102	0.0297	0.0313	0.0330	0.0347	0.0365
	152	0.0372	0.0416	0.0464	0.0519	0.0580
	117	0.0346	0.0375	0.0407	0.0442	0.0479
Severn River	345	0.0368	0.0395	0.0425	0.0457	0.0491
	322	0.0406	0.0383	0.0361	0.0340	0.0321
	326	0.0697	0.0556	0.0444	0.0354	0.0283
	327	0.0247	0.0264	0.0282	0.0301	0.0321
	320	0.0419	0.0442	0.0466	0.0492	0.0519
	335	0.0246	0.0248	0.0251	0.0254	0.0257

(continued...)

## APPENDIX X (continued)

LEAF AREA RATIO ( $\text{dm}^2 \cdot \text{g}^{-1}$ )

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	1.765	1.717	1.670	1.625	1.581
	233	1.627	1.642	1.657	1.672	1.687
	227	1.723	1.607	1.498	1.397	1.302
	247	1.730	1.667	1.605	1.546	1.489
	238	1.670	1.564	1.466	1.373	1.286
	278	1.492	1.490	1.488	1.486	1.484
	279	1.632	1.495	1.370	1.255	1.150
	Thunder Bay	5	1.542	1.499	1.457	1.417
36		1.567	1.542	1.518	1.493	1.470
44		1.732	1.690	1.650	1.610	1.571
35		1.958	1.841	1.731	1.628	1.531
30		1.749	1.628	1.516	1.412	1.315
19		1.721	1.695	1.670	1.644	1.619
45		1.763	1.646	1.537	1.435	1.339
Pickle Lake	136	1.697	1.663	1.630	1.597	1.565
	121	1.857	1.695	1.548	1.413	1.290
	142	1.943	1.749	1.574	1.416	1.275
	116	1.737	1.573	1.425	1.290	1.168
	102	1.840	1.747	1.659	1.576	1.497
	152	1.896	1.697	1.519	1.359	1.217
	117	1.936	1.784	1.644	1.515	1.397
Severn River	345	1.823	1.697	1.579	1.470	1.368
	322	1.378	1.461	1.549	1.643	1.742
	326	0.763	0.956	1.197	1.500	1.879
	327	1.861	1.743	1.633	1.529	1.432
	320	1.515	1.437	1.362	1.292	1.225
	335	1.545	1.528	1.511	1.494	1.478

(continued...)

## APPENDIX X (continued)

SPECIFIC LEAF AREA ( $\text{dm}^2 \cdot \text{g}^{-1}$ )

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	2.666	2.760	2.856	2.957	3.060
	233	2.357	2.504	2.660	2.826	3.002
	227	2.438	2.469	2.500	2.532	2.564
	247	2.494	2.584	2.677	2.773	2.872
	238	2.382	2.437	2.493	2.550	2.608
	278	2.076	2.211	2.354	2.507	2.670
	279	2.375	2.383	2.392	2.400	2.409
	Thunder Bay	5	2.078	2.216	2.363	2.520
36		2.303	2.437	2.580	2.731	2.891
44		2.390	2.498	2.612	2.731	2.856
35		2.742	2.740	2.739	2.738	2.737
30		2.296	2.337	2.378	2.419	2.462
19		2.263	2.414	2.576	2.748	2.932
45		2.432	2.432	2.432	2.432	2.432
Pickle Lake		136	2.437	2.587	2.746	2.915
	121	2.607	2.621	2.636	2.650	2.665
	142	2.824	2.731	2.640	2.552	2.468
	116	2.465	2.495	2.526	2.558	2.589
	102	2.454	2.538	2.624	2.713	2.806
	152	2.647	2.625	2.603	2.581	2.559
	117	2.630	2.617	2.605	2.593	2.581
	Severn River	345	2.667	2.681	2.695	2.709
322		2.143	2.376	2.635	2.922	3.240
326		2.001	2.211	2.442	2.698	2.980
327		2.591	2.646	2.703	2.761	2.820
320		2.582	2.578	2.574	2.570	2.566
335		2.367	2.508	2.657	2.815	2.982

(continued...)

## APPENDIX X (continued)

LEAF WEIGHT RATIO ( $g \cdot g^{-1}$ )

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	0.662	0.622	0.585	0.550	0.517
	233	0.690	0.656	0.623	0.592	0.562
	227	0.707	0.651	0.599	0.552	0.508
	247	0.694	0.645	0.600	0.558	0.519
	238	0.701	0.642	0.588	0.538	0.493
	278	0.718	0.674	0.632	0.593	0.556
	279	0.687	0.627	0.573	0.523	0.477
Thunder Bay	5	0.742	0.676	0.617	0.562	0.513
	36	0.681	0.633	0.588	0.547	0.508
	44	0.725	0.677	0.631	0.589	0.550
	35	0.714	0.672	0.632	0.595	0.559
	30	0.761	0.697	0.638	0.584	0.534
	19	0.761	0.702	0.648	0.598	0.552
	45	0.725	0.677	0.632	0.590	0.551
Pickle Lake	136	0.696	0.643	0.593	0.548	0.506
	121	0.712	0.647	0.587	0.533	0.484
	142	0.688	0.640	0.596	0.555	0.517
	116	0.705	0.630	0.564	0.504	0.451
	102	0.750	0.689	0.632	0.581	0.533
	152	0.716	0.646	0.584	0.527	0.475
	117	0.736	0.682	0.631	0.584	0.541
Severn River	345	0.683	0.633	0.586	0.543	0.502
	322	0.643	0.615	0.588	0.562	0.538
	326	0.381	0.432	0.490	0.556	0.631
	327	0.718	0.659	0.604	0.554	0.508
	320	0.587	0.557	0.529	0.503	0.477
	335	0.653	0.609	0.569	0.531	0.496

(continued...)

## APPENDIX X (continued)

LEAF AREA PARTITION COEFFICIENT  $(\text{dm}^2 \cdot \text{day}^{-1}) / (\text{g} \cdot \text{day}^{-1})$

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	1.707	1.661	1.616	1.572	1.530
	233	1.646	1.661	1.676	1.691	1.707
	227	1.606	1.497	1.396	1.301	1.213
	247	1.665	1.603	1.544	1.488	1.433
	238	1.560	1.462	1.369	1.283	1.202
	278	1.489	1.487	1.485	1.483	1.481
	279	1.465	1.343	1.230	1.127	1.033
Thunder Bay	5	1.487	1.445	1.405	1.366	1.328
	36	1.542	1.517	1.493	1.469	1.446
	44	1.681	1.640	1.601	1.562	1.524
	35	1.843	1.733	1.630	1.533	1.441
	30	1.611	1.500	1.397	1.301	1.212
	19	1.689	1.663	1.638	1.613	1.589
	45	1.632	1.523	1.422	1.328	1.240
Pickle Lake	136	1.659	1.626	1.593	1.561	1.530
	121	1.692	1.545	1.410	1.287	1.175
	142	1.748	1.573	1.416	1.274	1.147
	116	1.568	1.420	1.286	1.165	1.055
	102	1.724	1.637	1.555	1.477	1.403
	152	1.697	1.519	1.360	1.217	1.089
	117	1.778	1.639	1.510	1.392	1.283
Severn River	345	1.693	1.576	1.466	1.365	1.270
	322	1.474	1.563	1.657	1.757	1.864
	326	0.978	1.226	1.536	1.924	2.411
	327	1.684	1.578	1.478	1.384	1.297
	320	1.431	1.357	1.286	1.220	1.156
	335	1.515	1.498	1.482	1.465	1.449

(continued...)

## APPENDIX X (continued)

LEAF WEIGHT PARTITION COEFFICIENT ( $g \cdot day^{-1}$ )/( $g \cdot day^{-1}$ )

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	0.614	0.577	0.542	0.509	0.479
	233	0.644	0.612	0.581	0.552	0.524
	227	0.650	0.598	0.551	0.507	0.467
	247	0.643	0.597	0.556	0.517	0.480
	238	0.639	0.585	0.536	0.491	0.450
	278	0.643	0.603	0.565	0.530	0.497
	279	0.614	0.561	0.512	0.467	0.427
Thunder Bay	5	0.655	0.597	0.544	0.496	0.453
	36	0.630	0.586	0.545	0.506	0.471
	44	0.664	0.620	0.579	0.540	0.504
	35	0.673	0.633	0.595	0.560	0.527
	30	0.687	0.629	0.575	0.527	0.482
	19	0.686	0.633	0.584	0.539	0.498
	45	0.671	0.626	0.585	0.546	0.510
Pickle Lake	136	0.635	0.586	0.541	0.500	0.461
	121	0.645	0.586	0.532	0.483	0.438
	142	0.641	0.597	0.555	0.517	0.481
	116	0.628	0.562	0.502	0.449	0.402
	102	0.672	0.617	0.567	0.521	0.478
	152	0.647	0.584	0.527	0.476	0.429
	117	0.680	0.629	0.583	0.540	0.500
Severn River	345	0.631	0.584	0.541	0.501	0.464
	322	0.609	0.582	0.557	0.532	0.509
	326	0.441	0.501	0.568	0.644	0.730
	327	0.628	0.576	0.528	0.485	0.444
	320	0.555	0.527	0.501	0.475	0.451
	335	0.574	0.536	0.500	0.467	0.436

## APPENDIX XI

POINT ESTIMATES OF GROWTH COMPONENT INDICES FOR  
 CLONES UNDER THE REDUCED PHOTOSYNTHETIC PERIOD OF  
 THE GREENHOUSE STUDY, AT SPECIFIED DAYS

UNIT LEAF RATE ( $\text{g} \cdot \text{dm}^{-2} \cdot \text{day}^{-1}$ )

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	0.0267	0.0285	0.0303	0.0323	0.0344
	233	0.0388	0.0348	0.0311	0.0279	0.0250
	227	0.0267	0.0277	0.0286	0.0296	0.0306
	247	0.0282	0.0278	0.0274	0.0270	0.0266
	238	0.0295	0.0316	0.0339	0.0363	0.0389
	278	0.0275	0.0263	0.0253	0.0242	0.0232
	279	0.0230	0.0233	0.0236	0.0239	0.0241
Thunder Bay	5	0.0236	0.0232	0.0228	0.0224	0.0220
	36	0.0256	0.0258	0.0260	0.0262	0.0264
	44	0.0239	0.0246	0.0253	0.0260	0.0267
	35	0.0236	0.0236	0.0236	0.0236	0.0236
	30	0.0264	0.0274	0.0284	0.0295	0.0306
	19	0.0201	0.0203	0.0205	0.0207	0.0208
	45	0.0269	0.0280	0.0292	0.0304	0.0317
Pickle Lake	136	0.0266	0.0268	0.0271	0.0273	0.0276
	121	0.0230	0.0246	0.0262	0.0279	0.0297
	142	0.0238	0.0253	0.0270	0.0287	0.0306
	116	0.0233	0.0238	0.0243	0.0249	0.0254
	102	0.0221	0.0230	0.0239	0.0249	0.0258
	152	0.0324	0.0300	0.0279	0.0259	0.0240
	117	0.0237	0.0248	0.0260	0.0273	0.0286
Severn River	345	0.0263	0.0256	0.0250	0.0243	0.0237
	322	0.0264	0.0260	0.0256	0.0252	0.0249
	326	0.0201	0.0196	0.0191	0.0187	0.0182
	327	0.0196	0.0198	0.0199	0.0200	0.0202
	320	0.0292	0.0296	0.0300	0.0305	0.0309
	335	0.0196	0.0198	0.0199	0.0200	0.0202

(continued...)

## APPENDIX XI (continued)

LEAF AREA RATIO ( $\text{dm}^2 \cdot \text{g}^{-1}$ )

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	2.138	2.006	1.883	1.767	1.659
	233	1.335	1.491	1.665	1.859	2.075
	227	2.017	1.951	1.886	1.824	1.764
	247	1.938	1.968	1.997	2.028	2.058
	238	2.074	1.934	1.804	1.682	1.569
	278	1.632	1.703	1.776	1.853	1.933
	279	1.839	1.818	1.797	1.777	1.756
Thunder Bay	5	1.774	1.806	1.839	1.872	1.905
	36	2.041	2.025	2.009	1.993	1.977
	44	2.109	2.053	1.997	1.943	1.891
	35	2.218	2.217	2.216	2.214	2.213
	30	2.040	1.966	1.895	1.826	1.760
	19	2.253	2.233	2.213	2.194	2.175
	45	2.108	2.024	1.943	1.866	1.791
Pickle Lake	136	2.055	2.037	2.018	2.000	1.981
	121	2.189	2.054	1.928	1.810	1.698
	142	2.179	2.047	1.922	1.805	1.696
	116	2.031	1.986	1.942	1.899	1.858
	102	2.314	2.226	2.141	2.059	1.981
	152	1.496	1.612	1.738	1.873	2.018
	117	2.306	2.200	2.100	2.004	1.912
Severn River	345	1.887	1.938	1.991	2.045	2.100
	322	1.990	2.021	2.052	2.084	2.116
	326	1.925	1.972	2.020	2.069	2.119
	327	2.175	2.160	2.146	2.132	2.118
	320	1.930	1.904	1.879	1.853	1.829
	335	2.103	2.088	2.073	2.059	2.044

(continued...)

## APPENDIX XI (continued)

SPECIFIC LEAF AREA ( $\text{dm}^2 \cdot \text{g}^{-1}$ )

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	2.960	3.097	3.241	3.391	3.548
	233	2.335	2.604	2.905	3.241	3.615
	227	2.672	2.871	3.085	3.315	3.562
	247	2.635	2.887	3.163	3.465	3.796
	238	2.871	2.966	3.064	3.165	3.270
	278	2.285	2.531	2.803	3.105	3.439
	279	2.509	2.723	2.956	3.209	3.483
Thunder Bay	5	2.351	2.575	2.820	3.088	3.382
	36	2.773	2.988	3.220	3.469	3.738
	44	2.753	2.904	3.064	3.233	3.411
	35	2.981	3.161	3.352	3.554	3.769
	30	2.593	2.737	2.888	3.048	3.216
	19	2.846	3.030	3.227	3.436	3.659
	45	2.767	2.856	2.949	3.044	3.142
Pickle Lake	136	2.595	2.854	3.139	3.453	3.798
	121	2.962	3.063	3.167	3.274	3.386
	142	2.951	3.034	3.120	3.208	3.299
	116	2.744	2.947	3.165	3.399	3.651
	102	2.993	3.106	3.222	3.344	3.469
	152	2.792	2.953	3.124	3.304	3.495
	117	3.056	3.117	3.178	3.241	3.306
Severn River	345	2.649	2.953	3.291	3.668	4.088
	322	2.597	2.845	3.117	3.415	3.741
	326	2.768	3.027	3.311	3.622	3.962
	327	2.690	2.945	3.224	3.530	3.864
	320	2.592	2.827	3.084	3.365	3.671
	335	2.860	3.044	3.241	3.450	3.673

(continued...)

## APPENDIX XI (continued)

LEAF WEIGHT RATIO ( $g \cdot g^{-1}$ )

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	0.722	0.648	0.581	0.521	0.467
	233	0.572	0.572	0.573	0.573	0.574
	227	0.755	0.679	0.611	0.550	0.495
	247	0.735	0.682	0.632	0.585	0.542
	238	0.722	0.652	0.589	0.532	0.480
	278	0.714	0.673	0.634	0.597	0.562
	279	0.733	0.668	0.608	0.554	0.504
Thunder Bay	5	0.755	0.701	0.652	0.606	0.563
	36	0.736	0.678	0.624	0.574	0.529
	44	0.766	0.707	0.652	0.601	0.554
	35	0.744	0.701	0.661	0.623	0.587
	30	0.787	0.718	0.656	0.599	0.547
	19	0.792	0.737	0.686	0.638	0.594
	45	0.762	0.709	0.659	0.613	0.570
Pickle Lake	136	0.792	0.714	0.643	0.579	0.522
	121	0.739	0.671	0.609	0.553	0.502
	142	0.739	0.675	0.616	0.563	0.514
	116	0.740	0.674	0.614	0.559	0.509
	102	0.773	0.717	0.664	0.616	0.571
	152	0.536	0.546	0.556	0.567	0.577
	117	0.755	0.706	0.661	0.618	0.578
Severn River	345	0.712	0.656	0.605	0.557	0.514
	322	0.766	0.710	0.658	0.610	0.566
	326	0.696	0.651	0.610	0.571	0.535
	327	0.809	0.734	0.666	0.604	0.548
	320	0.745	0.673	0.609	0.551	0.498
	335	0.735	0.686	0.640	0.597	0.557

(continued...)

## APPENDIX XI (continued)

LEAF AREA PARTITION COEFFICIENT  $(\text{dm}^2 \cdot \text{day}^{-1}) / (\text{g} \cdot \text{day}^{-1})$

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	1.979	1.858	1.743	1.636	1.536
	233	1.525	1.702	1.901	2.122	2.370
	227	1.934	1.870	1.808	1.748	1.691
	247	1.974	2.004	2.034	2.065	2.096
	238	1.916	1.787	1.667	1.554	1.450
	278	1.735	1.810	1.888	1.969	2.055
	279	1.806	1.785	1.765	1.744	1.724
Thunder Bay	5	1.824	1.857	1.891	1.925	1.959
	36	2.020	2.004	1.988	1.973	1.957
	44	2.033	1.979	1.925	1.873	1.823
	35	2.217	2.215	2.214	2.213	2.211
	30	1.947	1.876	1.808	1.743	1.679
	19	2.224	2.204	2.185	2.165	2.146
	45	2.007	1.927	1.850	1.776	1.705
Pickle Lake	136	2.032	2.014	1.995	1.977	1.959
	121	2.005	1.882	1.766	1.658	1.556
	142	2.003	1.882	1.767	1.660	1.559
	116	1.967	1.924	1.881	1.840	1.799
	102	2.197	2.113	2.033	1.955	1.881
	152	1.650	1.778	1.916	2.065	2.226
	117	2.174	2.075	1.980	1.889	1.803
Severn River	345	1.955	2.008	2.062	2.118	2.175
	322	2.029	2.060	2.092	2.124	2.157
	326	2.005	2.053	2.103	2.154	2.207
	327	2.152	2.138	2.124	2.110	2.096
	320	1.899	1.874	1.849	1.824	1.799
	335	2.079	2.064	2.050	2.035	2.021

(continued...)

## APPENDIX XI (continued)

LEAF WEIGHT PARTITION COEFFICIENT (g-day<sup>-1</sup>)/(g-day<sup>-1</sup>)

Provenance	Clone	Day				
		26	41	51	72	86
N. Wisconsin	223	0.631	0.566	0.507	0.455	0.408
	233	0.573	0.573	0.574	0.574	0.575
	227	0.657	0.591	0.532	0.479	0.431
	247	0.667	0.618	0.573	0.531	0.492
	238	0.642	0.579	0.523	0.472	0.426
	278	0.651	0.613	0.577	0.544	0.512
	279	0.625	0.569	0.518	0.472	0.430
Thunder Bay	5	0.667	0.620	0.576	0.536	0.498
	36	0.658	0.606	0.558	0.514	0.473
	44	0.684	0.631	0.582	0.537	0.495
	35	0.688	0.648	0.611	0.576	0.543
	30	0.698	0.638	0.582	0.532	0.486
	19	0.708	0.659	0.614	0.571	0.532
	45	0.697	0.648	0.603	0.561	0.521
Pickle Lake	136	0.691	0.623	0.561	0.505	0.455
	121	0.644	0.585	0.531	0.482	0.437
	142	0.652	0.596	0.544	0.497	0.454
	116	0.642	0.585	0.532	0.485	0.441
	102	0.697	0.646	0.599	0.555	0.515
	152	0.550	0.560	0.571	0.581	0.592
	117	0.693	0.649	0.607	0.568	0.532
Severn River	345	0.634	0.584	0.539	0.496	0.457
	322	0.693	0.642	0.595	0.552	0.511
	326	0.617	0.577	0.541	0.506	0.474
	327	0.686	0.622	0.565	0.512	0.465
	320	0.656	0.594	0.537	0.485	0.439
	335	0.653	0.609	0.568	0.530	0.494