Indices for the rapid early selection of Populus clones

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INTRODUCTION

The Problem

Since 1920 very large increases in productivity have been achieved with agricultural crops such as corn and soybeans but no comparable increases have been attained with woody plants. Thus, in the last ten years, an increasing amount of attention has been focused on the need for more intensive silvicultural practices to increase fiber production per unit area of land.

For the past five years cooperative research under the project title "Maximum Fiber Yield" has been conducted between the Department of Forestry at Iowa State University and the North Central Forest Experiment Station. The main purpose of this research has been to obtain information leading to the development of woody plant agrisystems. A woody plant agrisystem is a system in which woody plants are cultured intensively to produce high per acre yields of industrial raw material.

One focus of the project is simulation modelling of the growth and yield of Populus clones. Yield models are being developed through field and laboratory experimentation; the selection indices that are presented in this study constitute one of the inputs to overall yield models (Figure 1).

The idea of selection indices is not new in forestry but has been used more extensively in crop improvement and animal
breeding programs, especially since the early 1940's. The ideal selection index is one which combines physiological, morphological, pathological and phenological information. However all the information necessary to create such an index is not available at this time for the genus *Populus*.

In this study both existing and new data were utilized to calculate the various indices and to determine their reliability. The existing data was obtained from past growth studies conducted by Mr. Paul Wray in both the greenhouses and growth chambers. The new data was collected from a controlled-environment study carried out in growth chambers from November 1973 to June 1974 by the author.

In this latter study the vegetative growth and dry-weight accumulation of eight selected *Populus* clones was monitored in growth chambers over a range of environments formed by combining various levels of photoperiod and air temperature. These two factors were used because past studies have shown that the growth of *Populus* species and hybrids are markedly affected by these conditions (Bogdanov, 1968).

Although the artificial environments created in the growth chambers are only simplifications of the complex natural environments found in the field useful data can be obtained. It is in fact impossible and not necessary to reproduce field conditions in these growth chambers.
Figure 1. Flow chart showing the major inputs with associated data sources that are needed by the simulation modelling process.
PHYSIOLOGICAL FACTORS

PHOTOSYNTHESIS
RESPIRATION
ASSIMILATION
ENZYME ACTIVITY
SHADE TOLERANCE

PLANT DENSITIES
AND MIXTURES

LIGHT INTERCEPTION
MODEL

SIMULATION
MODELLING
OF GROWTH
AND YIELD

GROWTH RELATIONSHIP BETWEEN FIELD
AND CONTROLLED ENVIRONMENT

SELECTION INDICES

DATA INPUTS
1 = FIELD
2 = GREENHOUSE
3 = GROWTH CHAMBER
Why intensive culture?

In the last few years demand for forest products, especially pulp and paper, has surpassed supply. The traditional supply has been natural stands which do not efficiently utilize light, water and nutrients. Since industry is interested in rapid prolific vegetative growth a good solution to the demand problem would be to intensively culture trees in stands under five to ten year rotation periods located some feasible economical distance from a mill.

What do we grow?

The genus *Populus* was chosen to be studied because its members exhibit fast growth, the various species of the genus propagate vegetatively with ease and for their ability to form many hybrids.

Why selection indices?

Since the silviculturist is faced with a wide variety of genetic material, traditional field growth trials are impractical. All the available clones could not possibly be grown in monocultures at various densities or in clonal mixtures with all the possible combinations. This would be prohibitively expensive and time consuming. Therefore, the silviculturist must undertake to choose from the thousands of clones available to him those clones which consistently demonstrate superior growth over a wide range of environments.
Hence, a rapid selection procedure is needed which would indicate in a short period of time those phenotypes that exhibit rapid juvenile growth, and that could be field-tested with a minimum probability of failure.

**Where are the clones to be grown?**

The subpopulation of 'promising' clones from which selection is to made should be grown under controlled-environmental conditions. This state enables the experimenter to select phenotypes during the winter months and to have greater control over some of the environmental factors affecting plant growth. This approach also permits the separation of effects which would otherwise be confounded with one another outdoors and results in less variability.

**Literature Review**

The major factors affecting plant growth are light intensity and quality, photoperiod, soil moisture, air and soil temperature, and nutrients. Factors affecting tree growth usually interact and similar growth patterns can be produced by different combinations of several factors. One or more factors, however, usually can be regarded as more important than others in the overall success or failure of plants in a particular environment (Spurr and Barnes, 1973).

The effects of photoperiod and temperature on the growth of *Populus* clones are considered in this study. The importance of these factors in regulating the growth of
woody plants has often been discussed. Only those papers particularly relevant to this study are reviewed here.

**Photoperiod**

Photoperiod influences both vegetative and reproductive phases of plant growth. Some of the processes known to be influenced by photoperiod are shoot and diameter growth, breaking of dormancy, leaf abscission, frost resistance, seed germination and flowering (Kramer and Kozlowski, 1960).

In many species the rate of growth is directly proportional to the length of daily exposure to light (Garner and Allard, 1920) but the growth response varies markedly with species (Downs and Borthwick, 1956). Long photoperiods tend to promote elongation growth and short photoperiods inhibit growth and may induce dormancy (Downs and Borthwick, 1956; Kramer, 1936, 1957; Nitsch, 1957; Pauley and Perry, 1954; Roberts and Stuckmeyer, 1938; Veen, 1951; Wassink and Wiersema, 1955).

Hellmers and Pharis (1968) reported that continuous light resulted in the maximum dry-weight but not the tallest trees. Plants used light energy for height growth and dry matter production most efficiently when grown under a 20 hour photoperiod.

Usually, long photoperiods cause *Populus* species to grow continuously (Kramer, 1936; Nitsch, 1957).

Wareing (1950) reported that the growth of Scotch pine decreased when the photoperiod exceeded 20 hours.
Downs and Piringer (1958) stated that continuous light caused greater total growth and stem dry-weight than a 16 hour photoperiod for ponderosa pine.

Jester and Kramer (1939) reported that height growth was affected by photoperiod as well as temperature for maple, oak and black locust.

Florence and Malajczuk (1970) stated that Pinus radiata seedlings grown at long photoperiods (16 hours) were twice the height of those grown at short photoperiods (8 hours) and total dry weight production was 63% greater.

**Temperature**

Temperature affects growth through its influence on practically all factors which affect growth directly (Kramer and Kozlowski, 1960; Went, 1953).

The rates of important physiological processes such as photosynthesis, respiration and transpiration are all affected by temperature (Kramer and Kozlowski, 1960). Growth occurs over a wide temperature range but optimum growth occurs over only a small portion of this range (Hellmers, 1962). This optimum temperature range for growth varies with species (Brix, 1971; Olson et al., 1959; Went, 1944). Day temperature (Brix, 1971), night temperature (Hellmers, 1962), day-night temperature differential (Kramer, 1957), and the total daily temperature (Hellmers, 1963; Hellmers and Ashby, 1958) all have been found to affect plant growth.
The effects of long photoperiods on growth are modified by temperature (Wareing, 1956).

Ballantine and Forde (1970) stated that plants under high temperatures grew more rapidly than those at lower temperature, had higher final dry-weights and showed a higher rate of leaf expansion on the main stem.

Florence and Malajczuk (1970) observed that Pinus radiata seedlings grew faster in height at high (30|25°C) than low temperature (18|13°C) but dry-weight production was greatest at the medium temperature (24|19°C).

Went (1953) observed decreased growth with increased night temperature.

Growth in height and stem diameter decreased when day and night temperatures exceeded certain maximums (Domingo, 1971) and temperature had an inhibitory effect on growth when it dropped below certain minimums (Downs and Borthwick, 1956).

Selection indices

Selection indices have been proposed and used by many authors as criteria for selection in animal and plant breeding programs when several quantitative characters are considered at a time (Elston, 1963; Hazel, 1943; Hazel and Lush, 1942; Kempthorne and Nordskog, 1959; Panse, 1946; Smith, 1936; Tallis, 1962).

Some authors have discussed methods for calculating a
general selection index based on pooled information from two or more experiments (Hanson and Johnson, 1957). The index proposed was one similar to index \( I_1 \) which will be discussed in a subsequent section. Two data sets were combined to minimize sampling errors and improve the estimation of the genotype by environment interaction. The two populations which were combined were grown under identical environments. In this manner a selection index determined from one data source could be used successfully as a general index. The expected genetic advance was used as a means of index reliability.

Okuna et al., (1971) evaluated the performance of 29 rice varieties grown in several environments using seven different methods. One of the methods used by the authors involved principal components but since the entire article was in Japanese with a short English summary it was not clear whether the seven methods were compared or not. The conclusions were sketchy.

A selection index often considered appropriate is a function of the form

\[
I = w_1x_1 + w_2x_2 + \ldots + w_px_p
\]

where \( w_i = i\)-th known or unknown economic weight

\( x_i = i\)-th measured trait

(Hazel, 1943; Smith, 1936).
However such a linear function may not be appropriate, or, if the economic weights are unknown, the experimenter may not want to go through the involved estimation procedure necessary. The researcher may not even want to consider any weights.

An alternative is to consider a nonlinear function of the form

\[ I = (w_1x_1)(w_2x_2)...(w_px_p) = w'x_1x_2...x_p \]

Suppose, for simplicity, \( p = 2 \) so that only two traits are being considered. Then Figure 2 illustrates selection on the basis of a linear index, \( x_1 + wx_2 \) and Figure 3 illustrates selection on the basis of a nonlinear index, \( wx_1x_2 \). In both cases the shaded area represents the specified fraction, \( \lambda \), of the individuals to be selected from the known population. This fraction is obtained by assigning ranks within the group of clonal values for each index and selecting the clones with highest rank from each group. This way the selection ability of each index can be compared with that of another.

In addition to linear or nonlinear indices of the forms mentioned above, the literature suggests a variety of approaches to the problem of discriminating among individuals on the basis of several traits. These are discussed below, together with my own further development of some of them.
Figure 2. Selection based on the linear index $x_1 + wx_2$.

Figure 3. Selection based on the nonlinear index $wx_1x_2$. 
Consider the index (in matrix notation) of the form

\[ H = a'X \]

where \( a \) = vector of known economic weights
\( X \) = vector (mx1) of unknown genotypic values of the individual clone for the m attributes of interest on which selection is to be based.

Since index \( H \) cannot be easily estimated let selection be based on a linear function which correlates best with the index \( H \) of the form

\[ I_1 = b'Y \]  \hspace{1cm} (1)\]

where \( Y \) = vector (mx1) of phenotypic values of the individual clone for the m attributes of interest on which selection is to be based
\( b \) = vector of coefficients to be determined from the system \( Pb = Ga \) (Appendix A; Hazel, 1943; Smith, 1936).

where \( P \) = matrix of phenotypic variances and covariances
\( G \) = matrix of genotypic variances and covariances
\( a \) = vector of previously defined constants.

This implies \( b = P^{-1} Ga \) and

\[ I_1 = (P^{-1} Ga)'Y \]  \hspace{1cm} (2)
Assumptions

Provided that the following conditions hold the selection index, \( I_1 \), will be a correct predictor of superior growth potential:

1. The phenotypic value, \( P_i \), for the \( i \)-th trait of an individual clone will be made up of the sum of two parts, the genotypic value, \( G_i \), defined as the average of the phenotypic values possible over a range of environments and the environmental contribution, \( E_i \), i.e., \( P_i = G_i + E_i \). The \( \text{Cov}(G_iE_i) = 0 \) but genotypic by environment interactions, \( (GE)_i \), can be present provided genotypes and environments are associated with each other at random and then \( (GE)_i \) is incorporated with \( E_i \).

2. The genetic value, \( G_i \), is composed entirely of additive gene effects.

3. The quantities \( Y_i \) and \( H \) are such that the regression of \( H \) on any linear function of the \( Y_i \) is linear (Kempthorne and Nordskog, 1959).

4. The matrices of variances and covariances \( P \) and \( G \) are known.

Weight-free index

Elston (1963) suggested the following nonlinear index for selection with respect to \( p \) traits at a time

\[
I_2 = \frac{P}{\Pi_{i=1}^p} (x_i - k_i)
\]
where $x_i = i$-th trait measured on a particular individual clone

$k_i = \text{greatest lower bound of the } x_i \text{ for all the individuals under consideration for selection.}$

However this index is not independent of the scales used to measure the $x_i$'s so one defines

$$x'_i = \log_{10}(x_i - k_i)$$

and the index becomes

$$I_2 = \frac{\sum_{i=1}^{P} x'_i}{P}$$

If the index is to be based on weighted measurements $w_1x_1, w_2x_2, \ldots, w_px_p$ and the $w_i$'s are unknown than an index which is invariant under the choice of the $w_i$'s should be used. The index becomes

$$I'_2 = \frac{\sum_{i=1}^{P} (x'_i - k'_i)}{P}$$

where

$$x'_i = \log_{10}(x_i - k'_i)$$

$$k'_i = \text{lower bound of } x'_i.$$  

The index $I_2$ was evaluated for each clone within each environment and since environments were assumed independent of each other a simple average value for each clone over all environments was calculated.

Adaptation index Finlay and Wilkinson (1963) proposed a method of analyzing the adaptation of a randomly
chosen group of 277 varieties of barley from a world collection, grown in replicated trials for several seasons at three sites in South Australia. For each variety a linear regression of individual grain yield on mean grain yield over all varieties for each environment (site and season) was computed. A slope of 1.00 meant that the variety was well adapted to all environments. This regression coefficient was then a measure of variety adaptation. The authors transformed their data logarithmically to induce independence between means and their variances.

The adaptation study of the whole population of varieties was assisted by the use of a scatter diagram plotting variety regression coefficients (slopes) against variety means. However no attempts were made by the authors to select a fraction, \( \lambda \), of the varieties showing superior growth potential with respect to yield over all environments. I propose to go a step further than Finlay and Wilkinson and create the following index

\[
I_3 = (\hat{\mu}_i - k_1)[(b_i - 1.0)^2 - k_2]
\]

where

\( \hat{\mu}_i \) = mean of i-th variety over all environments for a particular variate of interest on which selection is to be based

\( b_i \) = regression coefficient (slope) of \( \hat{Y}_{ij} \) on \( \hat{\mu}_j \)

where

\( Y_{ij} \) = mean of i-th variety at the j-th environment
\[ \mu_j = \text{mean of } j\text{-th environment over all varieties} \]

\[ k_1 = \text{greatest lower bound of } \hat{\mu}_i. \]

\[ k_2 = \text{greatest lower bound of } (b_i - 1.0)^2. \]

The index \( I_3 \) was evaluated for each clone for each of several variates of interest.

An alternative approach was to consider a canonical variable (Morrison, 1967), which is a linear combination of all the variates of interest in the selection process, as a variate on which selection is to be based. New environment and variety by environment means were found and the coefficients \( b_i^{(\ell)} \) were obtained by linear regression techniques.

Then the index

\[ I^{(\ell)}_3 = (\hat{\mu}_i^{(\ell)} - k_1)[(b_i^{(\ell)} - 1.0)^2 - k_2] \]  

was calculated for each clone where the superscript \( \ell \) stands for the \( \ell \)-th canonical variable used to evaluate the above previously defined parameters.

**Curvature index** Wu (1973) proposed that if the response of a variety to various environments is quadratic, that is

\[ y_i = a + bx_i + cx_i^2, \quad i = 1, m \]

where \( m = \text{number of environments} \)

\[ y_i = \text{observed response of a clone at the } i\text{-th environment} \]
$x_i$ = independent i-th environmental measure
then a measure of plant stability is the reciprocal of the
radius of curvature of Equation 7. If the curvature was
nearly zero this implied the curve was nearly linear and
clonal response to various environments was stable.

Now

$$\rho = \left| \frac{[1 + (y')^2]^{3/2}}{y''} \right|$$

and

$$y' = b + 2cx = r$$

and

$$y'' = 2c$$

Hence

$$\rho^{-1} = \left| \frac{[1 + (b+2cx)^2]^{3/2}}{2c} \right|^{-1}$$

where $x$ is day temperature and is evaluated at $x$ and $b$ and $c$
are the coefficients of Equation 7. Next consider the index

$$I_4 = (\bar{y}_i - k_1)(k_2 - |\rho^{-1} - (\bar{\rho})^{-1}|)$$

where $\bar{y}_i$ = i-th clonal mean over all environments for a
particular trait

$\rho^{-1}$ = curvature of the i-th clone

$(\bar{\rho})^{-1}$ = average curvature over all clones

$k_1$ = greatest lower bound of $\bar{y}_i$

$k_2$ = greatest lower bound of $|\rho^{-1} - (\bar{\rho})^{-1}|$

However this index deals with only one trait at a time
so consider the index

$$I_4^{(\ell)} = (\bar{y}_i^{(\ell)} - k_1)[k_2 - |\rho_{\ell}^{-1} - (\bar{\rho})_{\ell}^{-1}|]$$

(8)
where $y_i^{(l)}$ = i-th clonal mean of the l-th canonical variable associated with the clone source of variation in the MANOVA

$\rho_{l}^{-1}$ = curvature of the i-th clone based on l-th canonical variable

$(\bar{\rho})_{l}^{-1}$ = average curvature over all clones based on l-th canonical variable

$k_1$ = greatest lower bound of $y_i^{(l)}$

$k_2$ = greatest lower bound of $|\rho_{l}^{-1} - (\bar{\rho})_{l}^{-1}|$

With this index clones whose curvature is near the average curvature will be preferred to those with curvature far from the average.

**Hamiltonian index** Wu (1973) also considered the function $H = f(y,r)$ where $y = g(x)$ and $r = h(x)$. Here $y$ and $r$ are total growth and growth rate respectively of the clones or varieties over various environments. The function, $H$, is the Hamiltonian for the system represented by the equations

\[
y' = b + 2cx = r \tag{9}
\]

\[
y'' = 2c
\]

(Brauer and Nohel, 1969) if the above system can be written in the form

\[
\frac{dy}{dx} = y' = \frac{\partial H}{\partial r}
\]

\[
\frac{dr}{dx} = y'' = - \frac{\partial H}{\partial y}
\]

But $H$ is defined as the total energy of the system (Equation 9) and assuming the principle of conservation of energy the
function $H$ is a constant for different values of $x$. Therefore

$$\frac{dH}{dx} = 0$$

and using one of the chain rules of calculus

$$\frac{dH}{dx} = \frac{\partial H}{\partial y} \frac{dy}{dx} + \frac{\partial H}{\partial r} \frac{dr}{dx}$$

which leads to the system (Equation 10). Substituting values for $y'$ and $y''$ the system (Equation 10) becomes

$$\frac{\partial H}{\partial r} = r$$

$$\frac{\partial H}{\partial y} = -2c$$

The solutions to this system of equations are $H = r^2/2 + c_1$ and $H = -2cy + c_2$ where $c_1$ and $c_2$ are constants. Since a linear combination of these two solutions is also a solution to the system

$$H = \frac{r^2}{2} - 2cy$$

is also a solution and substituting for $y$ and $r$ produces

$$H = \frac{1}{2} b^2 - 2ac$$

where $a$, $b$ and $c$ are the coefficients of Equation 7. Similar to the curvature index consider

$$I_5^{(\ell)} = (\overline{y}_i^{(\ell)} - k_1)(k_2 - |H_\ell - \overline{H}_\ell|)$$

(11)

where $\overline{y}_i^{(\ell)}$ and $k_1$ are defined as the index $I_4^{(\ell)}$ and

$H_\ell = Hamiltonian$ of $i$-th clone based on $\ell$-th canonical variable
\( \bar{H}_\ell = \) average Hamiltonian over all clones based on \( \ell \)-th canonical variable

\( k_2 = \) greatest lower bound of \( |H_\ell - \bar{H}_\ell| \)

Again clones with a Hamiltonian, \( H \) close to \( \bar{H} \) will be preferred.

**Distance index** The first step in this procedure is to calculate all the possible pairwise squared generalized distances between the clones of interest using a pooled variance-covariance matrix whose rank equals the number of variates used as discriminators. Then

\[
D^2(i|j) = (\bar{x}_i - \bar{x}_j)' \text{Cov}^{-1}(\bar{x}_i - \bar{x}_j)
\]

where \( \bar{x}_i - \bar{x}_j = \) a vector \((s \times 1)\) of clonal mean differences

\( \text{Cov} = \) pooled variance-covariance matrix \((s \times s)\)

\( s = \) number of variates used as discriminators.

Next these distances are used to cluster the clones into subgroups which are hopefully more homogeneous by the unweighted pair group method and the results are displayed as a dendrogram (McCannmon and Wenninger, 1970).

The dendrograph is looked at subjectively to determine which clones demonstrate superior growth.

**Canonical index** A canonical analysis is performed on the combined data over all environments for the variates (dependent variables) on which selection is to be based. Canonical variables of the form

\[
Y^{(\ell)} = R\ell X
\]
where $s = 1, \ldots, s$

$s = \text{number of variates considered in the analysis}$

$X = \text{a vector of correlated dependent variables on which selection is to be based}$

$R_{\ell}^j = \text{\ell-th normalized characteristic vector of } E^{-1} H$

where $R_{\ell}^j E R_{\ell} = 1 \ (a \ scalar)$

$E = \text{pooled error matrix}$

$H = \text{partial sums of squares and cross products matrix due to clone by environment source of variation in the Multivariate Analysis of Variance (MANOVA) table.}$

$\text{Means of the canonical variables are obtained by replacing the vector } X \text{ by } \bar{X} \text{ such that}$

$$\bar{Y}_{ij}^{(\ell)} = R_{\ell}^j \bar{X}_{ij}$$

where $i = 1, \ldots, p$

$j = 1, \ldots, m$

$p = \text{number of clones}$

$m = \text{number of environments}$

$\bar{X}_{ij} = \text{a vector of means (s x 1) for the i-th clone at the j-th environment.}$

Then $\bar{Y}^{(2)}$ is plotted against $\bar{Y}^{(3)}$ and the resultant plot viewed subjectively. One looks for those clones in each environment which consistently are furthest away from the origin. These are the superior clones.
Difficulties

As stated earlier the H-S index is a correct predictor of superior growth potential only if all the mentioned assumptions hold. Immediately one observes that the variance-covariance matrices, P and G are not known and that only estimates of these are available. Often there are insufficient data to estimate G. So the index is subject to sampling and estimation errors. Also the assumption that \( P_i = G_i + E_i \) is usually unrealistic and \( \text{Cov}(G_i E_j) \neq 0 \). This would change the estimation procedure for obtaining the vector of coefficients, \( b \). There also exists the problem of assigning the proper weight to each trait in the index.

It should be noted that even if some of the weights in the original index, \( H \), are zero all of the coefficients estimated for \( I_1 \) will be nonzero.

The weight-free index contrary to its name is really an index which assigns equal weights to all variates or traits. This may not be desirable since one may want to select a small fraction of individuals on the basis of several traits that are to be unequally emphasized. This index also selects individuals with larger measurements on each trait, so one must arrange to measure each trait on a scale that will meet this criterion. Thus if there is a trait for which a smaller measurement is desired, one would change the direction of the scale on which the trait is measured.

The distributions of the measurements on each of the
traits should be as similar as possible for the weight-free index to be reliable. Frequently when histograms are drawn up for the various traits contained in the index the distributions of the measurements on some of the traits are of an entirely different type, e.g., bimodal instead of unimodal, from those of the others. Those measurements should then be transformed to lessen these differences.

The adaptation index seems the most promising although index $I_3$ selects individuals on the basis of only one trait at a time. Either one must look at each group of clonal values for index $I_3$ for each trait of interest in the selection process separately, remembering that these traits are highly correlated with each other or use index $I_3^{(2)}$. With this index, however, it is difficult to know which canonical variable to use.

The curvature index, like the adaptation index, selects individuals based on only one trait at a time. It also requires an independent variable with at least three levels to fit the assumed quadratic. The radius of curvature of this function varies with different values of the independent variable (some environmental measure). For comparison index $I_4$ is evaluated at the mean of the independent variable, but this may not be appropriate.

The Hamiltonian index comes from a principle of motion in physics which states that the total energy of a system is equal to the sum of the potential and kinetic energy. Apply-
ing this idea to biology involves substituting growth and growth rate for potential and kinetic energy. The index $I_5$ represents the biological total energy of the system. The principle of conservation of energy is assumed so that along any solution of a Hamiltonian system the total energy is constant. This may not be true when one considers growth and growth rate of a plant as position and speed of a particle.

The problem with the distance index is that this is a subjective instead of objective procedure. Certain clones will be segregated from the main group of clones but it will not be clear from the dendrograph whether these segregated clones are superior or inferior. Additional prior information is needed to interpret the results correctly.

The canonical index again is a subjective procedure but seems to hold great promise especially if $y(2)$ and $y(3)$ are plotted against each other instead of $y(1)$ and $y(2)$. This procedure appears to work best when the number of clones is greater than the number of environments.

**Reliability of indices**

To make any reliability statements such as confidence intervals about the various indices their probability density functions (p.d.f.'s) or distributions must be known exactly or approximated by some known tabulated distributions. An alternative is to assume some limiting distributions.
For the H-S index, $I_1$, one could easily find the expected value of $I_1$, $E(I_1)$, and the variance of $I_1$, $V(I_1)$, if the $P$ and $G$ matrices were known. Then, if one assumed that the phenotypic values, $Y$, were distributed normally with some finite mean and variance the distribution of index $I_1$ could be found. But matrices $P$ and $G$ must be estimated because they are usually not known. This makes it extremely difficult to find the variance of $I_1$.

On the other hand the p.d.f. for the weight-free index, $I_2$, and adaptation index, $I_3$, can be found, but only under very restricted conditions. Without these restrictions some limiting distributions must be assumed.

For example, let selection be based on two traits only ($p = 2$) and assume $x_1$ and $x_2$, the two traits, are distributed lognormal with means, $\mu_1$ and $\mu_2$ and variances, $\sigma_1^2$ and $\sigma_2^2$ respectively. Then if one imposes the restrictions:

$k_1 = k_2 = 0$ (lower bound for $x_1$ and $x_2$ is zero) and $x_1$ and $x_2$ are independent then the index $I_2 = t = x_1x_2$ has the following p.d.f. (Appendix B)

$$g(t) = \frac{1}{\sqrt{2\pi} t \sqrt{\sigma_1^2 + \sigma_2^2}} e^{-\frac{1}{2}(\log t - (\mu_1 + \mu_2))^2/(\sigma_1^2 + \sigma_2^2)}, \quad 0 < t < \infty$$

If $\mu_1 = \mu_2 = 0$ and $\sigma_1^2 = \sigma_2^2 = 1$ then the above p.d.f. becomes

$$g(t) = \frac{1}{2t \sqrt{\pi}} e^{-\frac{1}{2}(\log t)^2}, \quad 0 < t < \infty$$
If $k_1 \neq k_2 \neq 0$ then the p.d.f. cannot be found analytically. Note that the restriction: $x_1$ and $x_2$ independent, has not been relaxed which is really the case with this study.

The next course of action would be to find the first and second moments of indices $I_2$ and $I_3$ assuming that the traits on which selection was to be based are say normally distributed with finite mean and variance. Then Monte Carlo techniques could be used to artificially construct indices $I_2$ and $I_3$ based on sampling procedures and frequency curves could be drawn. Next known distributions such as $t$ or $F$ would be used to approximate the p.d.f.'s of index $I_2$ and $I_3$ based on the previously calculated moments and frequency curves would again be drawn. Goodness-of-fit tests could then be used to determine how well the known distributions approximated the sample based p.d.f.'s of indices $I_2$ and $I_3$.

The most attractive method from a viewpoint of simplicity is the following one: Deming (1943) stated that the variance of a function $g$ of a number of correlated random variables $x_1, \ldots, x_n$ could be approximated by the expression

$$V(g) \approx \sum_{i=1}^{n} \sum_{j=1}^{n} \left[ \frac{\partial g}{\partial x_i} \right] \left[ \frac{\partial g}{\partial x_j} \right] \text{Cov}(x_i, x_j)$$

Now recall the Central Limit Theorem (Hogg and Craig, 1969) which states that if $x_1, \ldots, x_n$ denote the items of a random sample of size $n$ from any distribution having finite variance $\sigma^2$, then the random variable $\sqrt{n} (\bar{x} - \mu) / \sigma$ has a limiting
normal distribution with zero mean and unit variance. Utilizing this fact assume the expression

\[ \frac{I^\ast - I}{(I^\ast)} \sim N(0, 1) \quad \text{as } n \to \infty \]

Then confidence intervals of the form

\[ \text{Prob}(L < I_\ell < u) \geq 1 - \alpha \]

where \( L \) = some lower limit
\( u \) = some upper limit
\( 1 - \alpha \) = confidence coefficient
\( \alpha \) = significance level

can be constructed.

Likewise the variances of indices \( I_4 \) and \( I_5 \) can also be found.

It should be noted that a given index is more reliable if it fails to include a superior clone in the group ultimately selected than to include a bad clone.

In summation past research indicates that as photoperiod increased plant growth increased but as temperature increased growth increased to a maximum and then decreased.

Several methods of index construction have been taken from other science disciplines such as the H-S, weight-free, adaptation, curvature and Hamiltonian indices and appropriately modified as deemed necessary by myself. The distance
and canonical indices are visual displays of multivariate manipulations proposed by myself.

Objectives

The primary objective of this study was to develop indices that select for superior growth of poplar clones on an individual tree basis utilizing external morphology only. However the ultimate aim was to select clones with high fiber yield on an area basis using all important information.

I thus proposed to develop and test selection indices given existing information and to modify these indices or algorithms as more information became available. In this way, useful results were obtained earlier than if one waited until all the pertinent information was available.

To develop and test indices, an independent, new data set was necessary. Two studies, therefore, were carried out and are reported here.

The objective of Study I was to determine the effects of photoperiod, air temperature and their interaction on the vegetative growth of eight selected Populus clones.

The objective of Study II was to calculate selection indices based on the performance of clones grown under a number of different environments, and to evaluate or test the reliability of these indices using data collected in Study I.
STUDY I

Methods

Experimental design

The growth of eight Populus clones was observed in controlled-environment chambers. Two factors were considered each at four equally spaced levels (Table 1).

Each of the 16 possible treatment combinations was assigned at random to a growth chamber. A split plot design was used with chambers or environments as whole plots. Within each chamber the eight clones were located at random on three

Table 1. Description of the four levels of each of two factors, air temperature and photoperiod

<table>
<thead>
<tr>
<th>Air temperature (°C)</th>
<th>Photoperiod (hrs.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Intensity</td>
</tr>
<tr>
<td></td>
<td>Low^a</td>
</tr>
<tr>
<td></td>
<td>High^b</td>
</tr>
<tr>
<td>Day</td>
<td>Night</td>
</tr>
<tr>
<td>17</td>
<td>5</td>
</tr>
<tr>
<td>23</td>
<td>11</td>
</tr>
<tr>
<td>29</td>
<td>17</td>
</tr>
<tr>
<td>35</td>
<td>23</td>
</tr>
</tbody>
</table>

^aIncandescent light.

^bFluorescent light.
shelves which form an adjustable floor that can be raised or lowered. Therefore clones, one to each pot, were the split plots. The randomization procedure used to locate the clones within each chamber or environment was done to eliminate positional differences that exist within a chamber.

Since only 8 chambers were available at any one time, one repetition of the experiment of 128 pots took two separate runs. The whole experiment was replicated twice. This implied taking cuttings on four different occasions. Thus, in order to be able to analyze the data as coming from a split plot design it was assumed that the cuttings were physiologically similar on all four runs.

An estimate of the variation between the cuttings of replicate 1 (runs 1 and 2) and replicate 2 (runs 3 and 4) was obtained for each variate measured by looking at the replicate source of variation with one degree of freedom.

The potted plants remained in the growth chambers for six weeks at which time they were harvested. Certain measurements were recorded every week and at the end of the six week growth period (see Growth Chamber Procedures). The assumed underlying model was

\[ Y_{ijkl} = \mu + \rho_i + P_j + T_k + (PT)_{jk} + \eta_{ijk} + C_l + (PC)_{jl} + (TC)_{kl} + (PTC)_{jkl} + \epsilon_{ijkl} \]
where \( i = 1, 2 ; j = 1, \ldots, 4 ; k = 1, \ldots, 4 ; l = 1, \ldots, 8 \)

with assumptions (Federer, 1955; Kempthorne, 1952; Snedecor and Cochran, 1967)

\[
\sum_{i} \rho_i = \sum_{j} P_j = \sum_{k} T_k = \sum_{l} C_{kl} = 0
\]

\[
\sum_{j} (PT)_{jk} = \sum_{k} (PT)_{jk} = \sum_{j} (PC)_{jl} = \sum_{l} (PC)_{jl} = 0
\]

\[
\sum_{k} (TC)_{kl} = \sum_{l} (TC)_{kl} = \sum_{j} (PTC)_{jk l} = 0
\]

\[
\sum_{k} (PTC)_{jk l} = \sum_{l} (PTC)_{jk l} = 0
\]

\[
\eta_{ijk} \sim \text{NI}(0, \sigma^2_\eta) \quad \text{and} \quad e_{ijkl} \sim \text{NI}(0, \sigma^2_e)
\]

**Plant material**

Twenty tip cuttings from greenhouse stock plants of each of the eight clones were rooted in Jiffy-7 peat pellets under an alternating mist system in the greenhouse. Eight cuttings of each clone were selected for uniformity and placed in 8 inch diameter black plastic pots containing a 2:1 mixture of Jiffy-Mix and Perlite. At the beginning of replicate 2 (run 3) a new supply of Perlite from a different manufacturer was used. This Perlite was much finer in texture than the previous supply although it was labeled "coarse". Some greenhouse tests with stock plants potted in the original 2:1 mixture of Jiffy-Mix and Perlite indicated that water percolated about 2\(\frac{1}{2}\) times faster through the mixture using the
new Perlite as compared to the old. To avoid increasing
the frequency of fertilization the proportions were altered.
It was determined that percolation rate was a function of
the number of Perlite particles, not surface area. After
counting the number of particles in a fixed volume of the
'old' and 'new' Perlite, the proportion of Jiffy-Mix to
Perlite was changed to 4:1.

Pot moisture was maintained near field capacity by
frequent watering and the plants were fertilized weekly with
water soluble fertilizer plus a micronutrient and iron solu-
tion (Appendix C). The fertilizer solution was prepared by
adding 1 gram of Agrico 20:20:20 (NPK), 1 ml of Fe-EDTA and
1 ml of micronutrient solution to one liter of distilled
water. Two hundred mls of this final solution were applied
to each pot.

The eight clones used in this study were: 5321, 5323,
5326, 5328, 5377, 5260, 5339, and P. balsamifera (Appendix
E for origin and parentage).

The operation schedule is listed in Table 2.

<table>
<thead>
<tr>
<th>Run #</th>
<th>Date of operation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Taking cuttings</td>
</tr>
<tr>
<td>1</td>
<td>10-26-73</td>
</tr>
<tr>
<td>2</td>
<td>12-22-73</td>
</tr>
<tr>
<td>3</td>
<td>3-4-74</td>
</tr>
<tr>
<td>4</td>
<td>5-1-74</td>
</tr>
</tbody>
</table>
**Growth chamber procedures**

The experiment was conducted in Percival, Model PT-80, growth chambers. The average light intensity at the upper portion of the plant crowns was maintained at approximately 3,000 foot-candles for the duration of the experiment. The relative humidity was not controlled or monitored and probably varied considerably. At the time of watering it would be high and then drop at a rate varying from chamber to chamber depending on the air temperature. The plants were watered to the saturation point (water dripping out the pot bottom) once every two days. Each week every pot was flushed with demineralized water followed by 200 mls of the prepared nutrient-micronutrient solution.

The temperature was indicated by a thermometer placed in the center of the chamber above the plant crowns. The temperature was controlled to within ± 2°C and the photoperiod to within ± 15 minutes.

During the six weeks that the plants remained in the chambers, starting with week 0, the following quantities were recorded: total number of leaves, length and width of every leaf to the nearest 0.1 cm, total plant height to the nearest 0.1 cm (HT), and basal diameter to the nearest 0.1 mm (DIA).

When the plants were harvested at the end of six weeks the following measures were also recorded: leaf dry weight (LFWT), stem dry weight (STMWT), and root dry weight (RTWT).
Several additional variables were calculated from these latter three: total plant weight (TOTWT), stem to root ratio (SRR), top to root ratio (TRR), and leaf, stem, root weight ratios (LWR, SWR, RWR). The dry weights were recorded to the nearest 0.001 g. Leaf lengths and widths were measured with clear plastic 15 and 30 centimeter rulers, plant heights with a 100 centimeter wooden ruler placed on top of a flat wooden bar spanning the pot lip from one side to the other, and the basal diameters with a special plastic angle gauge constructed and calibrated by the author. To assist the leaf measurement process short lengths of yellow wool were loosely tied at the base of the petiole of every 5-th leaf starting from the bottom of the plant. The average height from the 'soil' line to the top of the above mentioned wooden bar was recorded at week 0 for each pot.

The direction of diameter measurement was determined at random and marked with a short piece of yellow embossed tape which was applied vertically to the inner wall of the pot. The location of the tape was defined by projecting an imaginary line through the main axis of the gauge unto the inner side of the pot just above the 'soil' line. The gauge was placed flat on the soil, perpendicular to the main stem, and one measurement was taken as opposed to the common practice of taking a second reading at right angles to the first and averaging these two measurements. This practice adjusts the diameter since most woody stem cross-sections are not
circular but elliptical.

**Leaf surface area relationships**

Many direct measurement methods which obtain leaf surface area with various precision levels are available (Sesták et al., 1971). All these methods, however, involve the destruction of the leaves to be measured and are tedious and time-consuming.

I used an indirect method that involved the development of regression equations using leaf length and width and their combination as independent variables and leaf area as the dependent variable.

At the end of run 1 enough plants were selected at random to yield a sample of at least 30 leaves for each of the eight clones. All the leaves, both juvenile and expanding, were taken from these plants and their circumference was traced on paper. The areas of these projections were obtained by using a planimeter which measured to the nearest 0.1 cm$^2$. Although the planimeter method is a slow one for leaf area measurements, it is the most precise of all the methods available excluding the costly electronic scanners. This latter group of devices is troublesome to calibrate and leaves wider than 10 to 12 cm usually must be cut in strips.

The independent variables, leaf length and width were obtained from the tally sheets of week 6 run 1. It was assumed for all clones that leaf shape was independent of the
environment in which the leaf was grown.

Various models were fitted to the data for each clone using ordinary least squares (Table 3).

Table 3. Regression models fitted to clonal data

<table>
<thead>
<tr>
<th>Partial models</th>
</tr>
</thead>
<tbody>
<tr>
<td>$y = b(LW)$; $y = b(W^2)$; $y = a + b(L)$;</td>
</tr>
<tr>
<td>$y = a + b(W)$; $y = a + b(LW)$; $y = a + b(W^2)$;</td>
</tr>
<tr>
<td>$y = b(LW) + c(W^2)$; $y = a + b(LW) + c(W^2)$;</td>
</tr>
<tr>
<td>$y = a + b(L) + c(W) + d(LW)$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Full model</th>
</tr>
</thead>
<tbody>
<tr>
<td>$y = a + b(L) + c(W) + d(LW) + e(W^2)$</td>
</tr>
</tbody>
</table>

where  
$L =$ leaf length  
$W =$ leaf width  
$LW =$ length x width  
$W^2 =$ width x width

Then the statistic

$$C_p = \frac{RSS_p}{s^2} - (N - 2p)$$

where  
$s^2 =$ error mean square for the full model  
$p =$ number of parameters in the model under consideration
N = number of observations

\( \text{RSS}_p = \) residual sum of squares for the model under consideration (with p parameters)

was calculated and \( C_p \) versus p was plotted (Daniel and Wood, 1971). The line \( C_p = p \) is drawn on the graph and the vertical distance from each point (one for each partial model) to this line is noted. Points above the line indicate a biased equation and below the line an equation with random error only. The model with the fewest terms and whose \( C_p \) statistic is closest to the line is chosen (Figure 4).

From these plots the model

\[
Y = a + b(LW) + c(W^2)
\]

was chosen for each clone. Parameter estimates and associated statistics were obtained for each clone (Table 4). To test the reliability of prediction of the above model some additional data was collected by Mr. Tim Max for four of the above clones, namely 5321, 5323, 5326, and 5377.

Four statistics were calculated using the observed and predicted leaf surface areas. The predicted areas were obtained by substituting the corresponding values of the independent variables associated with a particular observed area into the correct clonal prediction equation. The statistics were

\[
T_1 = \frac{(\hat{\beta} - \beta_0)' X'X (\hat{\beta} - \beta_0)}{ks^2} \sim F_{k,n-p}
\]
Figure 4. $C_p$ plot

to test the joint null hypothesis

$$H_0: \hat{\beta} = [0] = \beta_0$$

where

- $X = \text{matrix of observed leaf areas (n x 2)}$
- $\hat{\beta} = \text{vector of regression coefficients as a result of fitting the model } Y = a + bX \text{ where } Y = \text{predicted leaf areas and } X \text{ defined above}$
- $p = \text{number of parameters in the model}$
- $s^2 = \text{error mean square}$
Table 4. Regression coefficients and associated statistics for 8 clones

<table>
<thead>
<tr>
<th>Clone</th>
<th>Coefficient</th>
<th>S.E. of coefficient</th>
<th>n</th>
<th>( s^2 )</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>5321</td>
<td>0.50868</td>
<td>0.52286</td>
<td>37</td>
<td>3.184</td>
<td>.9972</td>
</tr>
<tr>
<td></td>
<td>0.54004</td>
<td>0.03332</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.09037</td>
<td>0.03587</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5323</td>
<td>0.43073</td>
<td>1.05231</td>
<td>40</td>
<td>10.389</td>
<td>.9977</td>
</tr>
<tr>
<td></td>
<td>0.52406</td>
<td>0.05146</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.14628</td>
<td>0.04666</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5326</td>
<td>-0.07917</td>
<td>1.32275</td>
<td>39</td>
<td>14.590</td>
<td>.9953</td>
</tr>
<tr>
<td></td>
<td>0.27336</td>
<td>0.04602</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.38605</td>
<td>0.04257</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5328</td>
<td>-3.48530</td>
<td>1.15573</td>
<td>36</td>
<td>12.001</td>
<td>.9982</td>
</tr>
<tr>
<td></td>
<td>0.64992</td>
<td>0.04883</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.12364</td>
<td>0.04511</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5377</td>
<td>1.26054</td>
<td>0.64691</td>
<td>50</td>
<td>7.383</td>
<td>.9975</td>
</tr>
<tr>
<td></td>
<td>0.29245</td>
<td>0.02778</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.36252</td>
<td>0.02795</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5260</td>
<td>-0.58338</td>
<td>0.73483</td>
<td>50</td>
<td>4.856</td>
<td>.9964</td>
</tr>
<tr>
<td></td>
<td>0.63068</td>
<td>0.05760</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.06288</td>
<td>0.07197</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5339</td>
<td>0.81738</td>
<td>0.85277</td>
<td>41</td>
<td>8.087</td>
<td>.9967</td>
</tr>
<tr>
<td></td>
<td>0.51805</td>
<td>0.04154</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.21589</td>
<td>0.05168</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Balsam</td>
<td>-0.06247</td>
<td>0.82671</td>
<td>39</td>
<td>6.448</td>
<td>.9945</td>
</tr>
<tr>
<td></td>
<td>0.69543</td>
<td>0.04729</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.01553</td>
<td>0.08489</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
\( k \) = number of parameters in joint null hypothesis under test

\( n \) = number of observations (Kempthorne, 1972)

\[
T_2 = \frac{1}{4n^2} \left\{ \sum_{i=1}^{n} [R(X(i)) - 2i]^2 + \sum_{j=1}^{m} [R(Y(j)) - 2j]^2 \right\}
\]

the Cramer-von Mises Two-Sample test to check

\( H_0: F(x) = G(x) \) for all \( x \)

vs \( H_1: F(x) \neq G(x) \) for at least one value of \( x \)

where \( n = m = \) number of observations in each sample

\( R(X^{(i)}) = \) the rank of the \( i \)-th smallest of the \( X \)'s in the combined ordered sample

\( R(Y^{(j)}) = \) the rank of the \( j \)-th smallest of the \( Y \)'s in the combined ordered sample (Conover, 1971).

\[
T_3 = \sum_{i=1}^{n} (y_i - \hat{y}_i)^2, \text{ sum of squares between observed and predicted leaf areas}
\]

\[
T_4 = \sum_{i=1}^{n} |y_i - \hat{y}_i|, \text{ sum of absolute deviations}
\]

These four statistics were calculated for the four clones of Mr. Max (Table 5). Test statistic, \( T_1 \), is significant at \( \alpha = 0.01 \) for all four clones implying that the joint null hypothesis: \( \beta = \begin{bmatrix} 0 \\ 1 \end{bmatrix} \) is rejected and one concludes that the equations do not fit the new data very well. The test statistic, \( T_2 \), is not significant at \( \alpha = 0.10 \) for all four clones. This implies the null hypothesis: \( F(x) = G(x) \) is
Table 5. Several statistics to show the reliability of prediction of leaf area model

\[ Y = a + b(LW) + c(W^2) \] for four clones

<table>
<thead>
<tr>
<th>Clone</th>
<th>n</th>
<th>( T_1 )</th>
<th>( T_2 )</th>
<th>( T_3 )</th>
<th>( T_4 )</th>
<th>Range of ( Y_i - Y_i ) (in ( \text{cms}^2 ))</th>
</tr>
</thead>
<tbody>
<tr>
<td>5321</td>
<td>32</td>
<td>26.12**</td>
<td>0.025 N.S.</td>
<td>548.63</td>
<td>97.25</td>
<td>-5.21 to 7.50</td>
</tr>
<tr>
<td>5323</td>
<td>25</td>
<td>7.58**</td>
<td>0.020 N.S.</td>
<td>248.56</td>
<td>63.89</td>
<td>-6.10 to 3.55</td>
</tr>
<tr>
<td>5326</td>
<td>28</td>
<td>10.82**</td>
<td>0.054 N.S.</td>
<td>1111.81</td>
<td>125.70</td>
<td>-15.94 to 2.11</td>
</tr>
<tr>
<td>5377</td>
<td>26</td>
<td>49.35**</td>
<td>0.067 N.S.</td>
<td>707.03</td>
<td>112.90</td>
<td>-8.99 to 1.61</td>
</tr>
</tbody>
</table>

**Significant at \( P < 0.01 \).

N.S. Not significant at \( P < 0.05 \).
accepted and one concludes that the equations do fit the new data.

These two statistics lead to opposing results but based on the fact that the leaves of these clones vary in shape to some degree the estimate, $s^2$, in the denominator of statistic $T_1$ may be difficult to estimate. Therefore I am inclined to trust test statistic $T_2$ more than $T_1$. From the beginning the goal has been to estimate leaf surface area to within $\pm 0.1 \text{ dm}^2$ or $\pm 10.0 \text{ cm}^2$ on a per leaf basis. With the exception of clone 5326 all the estimated leaf areas were within the specified tolerance of the actual leaf areas (Table 5). For clone 5326 only 5 out of the 28 areas calculated exceeded this tolerance.

Therefore I conclude that the model $Y = a + b(LW) + c(W^2)$ is satisfactory for estimating leaf surface areas for the four clones to within the tolerance $\pm 0.1 \text{ dm}^2$ (Table 5). From this and the knowledge that the remaining other four clones in this study are similar genetically and from the statistics, $s^2$ and $R^2$ (Table 4), I conclude that the above model is adequate for these remaining clones also.

In addition to the estimated leaf surface area (LFAREA), the specific leaf area (SLA), the leaf weight ratio (LWR), and the leaf area ratio (LAR), were calculated. The relationships are

$$\frac{LAR}{TOTWT} = \frac{LFAREA}{LFWT} \cdot \frac{LFWT}{TOTWT}$$
(SLA) = (LWR)  
where LFWT = leaf dry weight
TOTWT = total plant dry weight.

Results

Growth

Vegetative growth Since the three factor interaction, photoperiod by temperature by clone, was not significant at the 5% level for each of the three vegetative growth variables, DIA, HT and LFAREA it was appropriate to graph the mean response of each of the eight clones over levels of photoperiod and temperature for each of these variables.

With a few exceptions growth in basal stem diameter, height and leaf area increased rapidly as photoperiod increased from 12 to 16 hours for all eight clones although not at the same rate for each clone. The increase in growth was less rapid as photoperiod increased further to 18 hours. For clone 5321 growth with respect to all three variables decreased as photoperiod increased from 16 to 18 hours. The same decrease was observed for clone 5326 but for basal stem diameter only. Clone 5260 had the highest growth rate in height as photoperiod increased from 16 to 18 hours and attained the highest mean height of all 8 clones at 18 hour photoperiod. The same high growth rate in diameter and leaf area was observed for clone 5260 but the highest values of all 8 clones were not achieved by it.
Balsam poplar exhibited the poorest growth with respect to all three variables, DIA, HT and LFAREA while clone 5328 displayed the highest growth in diameter and leaf area over all photoperiod levels. Clone 5323 showed the greatest growth in height over all photoperiods (Figures 5, 6, and 7).

Clones 5339 and balsam poplar showed no rapid increase in either DIA or LFAREA as photoperiod increased from 12 to 14 hours.

The effect of temperature on growth in diameter and leaf area was quadratic in that DIA and LFAREA increased rapidly as the day-night temperature increased from 17-5°C to 29-17°C and then growth decreased as the day-night temperature was further increased to 35-23°C for all 8 clones. This trend was not so obvious in height growth. Generally height growth levelled off as the day-night temperature increased from 29-17°C to 35-23°C for all 9 clones with exceptions. The rate of growth over temperature levels was not the same for each clone.

Clone 5260 continued to increase in HT and LFAREA growth when the day-night temperature increased from 29-17°C to 35-23°C in contrast to the other clones although clones 5328, 5321, and 5377 also showed increased growth in HT over this temperature range.

\footnote{Figures 5 to 29 have been placed at the end of the discussion section for Study I so that the continuity of the text could be maintained.}
Balsam poplar exhibited the lowest growth in DIA, HT and LFAREA while clone 5328 showed the greatest growth in DIA and LFAREA over all temperature conditions. Clone 5323 displayed the greatest growth in HT over temperature (Figures 8, 9 and 10).

All main effects, experiment, photoperiod, temperature and clone sources of variation, were significant at the 1% level for all three growth variables as well as the temperature by clone interaction for the variables HT and LFAREA and the photoperiod by clone interaction for variable HT (Table 6). This meant that the clones responded significantly differently over temperature levels for the variables HT and LFAREA and for HT over photoperiod levels.

The significant effect due to experiments indicated that the mean response of experiment 1 was significantly different from that of experiment 2 for each of the three variables DIA, HT and LFAREA. Looking at the means revealed that the mean response for each variable of experiment 2 was much higher than that of experiment 1. This was probably due to the improved moisture and nutrient retention capabilities of the pot 'soil' when the proportions of Jiffy-Mix to Perlite, the two main ingredients forming the artificial soil, were changed from 2:1 to 4:1 in experiment 2.

Dry weight Again the three factor interaction, photoperiod by temperature by clone, was not significant at the 5%
Table 6. F-values for vegetative growth variables of eight *Populus* clones associated with eight major sources of variation

<table>
<thead>
<tr>
<th>Source</th>
<th>DIA</th>
<th>HT</th>
<th>LFAREA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expt</td>
<td>12.55**</td>
<td>9.62**</td>
<td>11.56**</td>
</tr>
<tr>
<td>Photo (P)</td>
<td>11.65**</td>
<td>31.34**</td>
<td>17.66**</td>
</tr>
<tr>
<td>Temp (T)</td>
<td>29.55**</td>
<td>51.08**</td>
<td>37.78**</td>
</tr>
<tr>
<td>P x T</td>
<td>2.35N.S.</td>
<td>2.59*</td>
<td>2.41N.S.</td>
</tr>
<tr>
<td>Clone (C)</td>
<td>24.16**</td>
<td>24.51**</td>
<td>32.23**</td>
</tr>
<tr>
<td>P x C</td>
<td>1.06N.S.</td>
<td>2.09**</td>
<td>1.25N.S.</td>
</tr>
<tr>
<td>T x C</td>
<td>1.55N.S.</td>
<td>2.31**</td>
<td>3.30**</td>
</tr>
<tr>
<td>P x T x C</td>
<td>1.21N.S.</td>
<td>1.22N.S.</td>
<td>1.00N.S.</td>
</tr>
</tbody>
</table>

* Significant at P < 0.05.

** Significant at P < 0.01.

N.S. Not significant at P < 0.05.

level for each of the four dry weight variables, LFWT, STMWT, RTWT and TOTWT.

With the exception of clone 5339 and balsam poplar dry weights of leaves, stem, and total plant increased rapidly with increase in photoperiod from 12 to 16 hours and less rapidly from 16 to 18 hours of light for all clones although not at the same rate for each clone. Dry weight of roots decreased rapidly with increase in photoperiod from 12 to 14
hours and then increased rapidly when the photoperiod was increased further from 14 to 18 hours for all clones. The rate of decrease in root dry weight was greatest for clone 5339 and balsam poplar. For the dry weights of leaves, stem and total plant these two clones either decreased or increased slightly in growth as photoperiod increased from 12 to 14 hours and then increased sharply as photoperiod increased further from 14 to 18 hours. Again the dry weight of leaves, stem and total plant decreased for clone 5321 as photoperiod increased from 16 to 18 hours. Clone 5260 attained the highest rate of dry weight accumulation as photoperiod increased from 16 to 18 hours for leaves, stem, roots and total plant. The largest mean stem dry weight was attained by clone 5260 at a photoperiod of 18 hours.

Balsam poplar yielded the lowest dry weight accumulation with respect to leaves, stem, roots and total plant while clones 5328 and 5323 yielded the highest dry weight production for all the dry weight variables except STMWT over all photoperiod levels. Clones 5377 and 5326 produced the highest STMWT over all photoperiods except when the photoperiod increased from 16 to 18 hours (Figures 11, 12, 13 and 14).

The dry weight of leaves, stem, roots and total plant increased sharply as the day-night temperature increased from 17-5°C to 29-17°C and decreased as the temperature increased from 29-17°C to 35-23°C. Again the classic quadratic response to temperature was exhibited by all eight clones.
With the exception of stem dry weight clones 5328 and 5323 yielded the largest dry weights and balsam poplar the smallest dry weight over all temperature conditions (Figures 15, 16, 17 and 18).

Clones 5323 produced the largest stem dry weight followed closely by clones 5326 and 5377 over all temperature levels. However, clone 5326 decreased very sharply in stem dry weight as the day-night temperature increased from 29-17°C to 35-23°C.

The photoperiod, temperature and clone sources of variation were all significant at the 1% level for all four dry weight variables except the photoperiod source of variation for RTWT. The effect of photoperiod on RTWT was not even significant at 10% (Table 7). A trend, however, was observed as described earlier.

The temperature by clone interaction was significant at the 1% level for LFWT and TOTWT and at the 5% level for STMWT and RTWT. This indicated that the response of each clone over temperature was significantly different, one from another. In fact the differential response of clones over temperature with respect to LFWT was much more pronounced than the response with respect to either STMWT or RTWT.

The experiment effect was significant at the 1% level for STMWT only and significant at the 5% level for the other dry weight variables. This possibly indicates that stem
Table 7. F-values for dry weight variables of eight Populus clones associated with eight major sources of variation

<table>
<thead>
<tr>
<th>Source</th>
<th>LFWT</th>
<th>STMWT</th>
<th>RTWT</th>
<th>TOTWT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expt</td>
<td>5.96*</td>
<td>9.39**</td>
<td>6.01*</td>
<td>7.91*</td>
</tr>
<tr>
<td>Photo (P)</td>
<td>9.91**</td>
<td>13.30**</td>
<td>0.97 N.S.</td>
<td>6.61**</td>
</tr>
<tr>
<td>Temp (T)</td>
<td>26.98**</td>
<td>22.16**</td>
<td>15.78**</td>
<td>25.96**</td>
</tr>
<tr>
<td>P x T</td>
<td>1.69 N.S.</td>
<td>1.60 N.S.</td>
<td>0.89 N.S.</td>
<td>1.37 N.S.</td>
</tr>
<tr>
<td>Clone (CL)</td>
<td>25.82**</td>
<td>13.80**</td>
<td>22.04**</td>
<td>20.73**</td>
</tr>
<tr>
<td>P x C</td>
<td>1.00 N.S.</td>
<td>1.36 N.S.</td>
<td>0.62 N.S.</td>
<td>0.94 N.S.</td>
</tr>
<tr>
<td>T x C</td>
<td>2.60**</td>
<td>1.66*</td>
<td>1.67*</td>
<td>2.06**</td>
</tr>
<tr>
<td>P x T x C</td>
<td>0.91 N.S.</td>
<td>1.08 N.S.</td>
<td>1.01 N.S.</td>
<td>0.96 N.S.</td>
</tr>
</tbody>
</table>

*S Significant at P < 0.05.

**Significant at P < 0.01.

N.S. Not significant at P < 0.05.

dry weight production was altered to a greater degree than either leaf or root dry weight production by the change in 'soil' composition from experiment 1 to experiment 2.

**Distribution of assimilate**

The distribution of assimilate was expressed in dry weight stem to root and top to root ratios as well as leaf, stem and root dry weights as proportions of total dry weight.
With the exception of SWR the photoperiod by temperature by clone interaction was again not significant at the 5% level for all the other assimilate distribution variables.

Only the variables SRR and TRR were plotted for each clone over photoperiod and temperature levels. More meaningful information about the other three proportions was obtained by plotting the average dry weight of leaves, stem and roots over all clones versus environment (photoperiod by temperature combination) which caused information about each individual clone to be lost (Figure 19).

The SRR and TRR increased rapidly as photoperiod increased from 12 to 16 hours for all clones with the exception of balsam poplar with respect to TRR only. For this clone the TRR increased as photoperiod increased from 12 to 14 hours but remained constant as photoperiod increased further from 14 to 16 hours. As photoperiod continued to increase from 16 to 18 hours clones 5260, 5339 and balsam poplar continued to increase in SRR and TRR at a high rate. Clones 5377, 5323 and 5328 continued to increase at a low rate and clones 5321 and 5326 decreased in SRR and TRR.

Balsam poplar yielded the highest SRR and TRR of all the clones over all photoperiod levels. Clones 5321 and 5328 yielded the lowest SRR and clones 5260 and 5321 the lowest TRR over all photoperiod levels (Figures 20 and 21).

Although balsam poplar was not a superior clone in terms of total dry weight accumulation (it was the poorest) pro-
portionately more assimilate was deposited in the top and stem as opposed to the roots compared to the other clones.

As the day-night temperature increased from 17-5°C to 35-23°C most of the clones increased rapidly in SRR and TRR. No quadratic response of these variables to temperature was observed for any of the eight clones. Clones 5323 and 5326 increased at a slower rate in SRR as the temperature increased from 29-17°C to 35-23°C while balsam poplar exhibited a slow increase in SRR and a sharp decrease in TRR only when the day-night temperature increased from 23-11°C to 29-17°C.

Balsam poplar yielded the highest SRR and TRR over all temperature levels while clone 5321 yielded the lowest SRR and clones 5321 and 5260 the lowest TRR (Figures 22 and 23). Again the main effects, photoperiod, temperature and clone were significant at the 1% level except for the variable LWR. Here the photoperiod effect was only significant at the 5% level and the temperature effect was not significant at all. Possibly photoperiod affects LWR more than temperature.

The experiment effect was not significant at the 5% level for any of the assimilate distribution variables except SWR for which it was highly significant at the 1% level (Table 8).

The changes in pot soil proportions of the two ingredients composing the 'soil' from experiment 1 to experiment 2 did not significantly affect SRR, TRR, LWR or RWR. SWR,
Table 8. F-values for assimilate distribution variables of eight *Populus* clones associated with eight major sources of variation

<table>
<thead>
<tr>
<th>Source</th>
<th>Dependent variables</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>SRR</td>
</tr>
<tr>
<td>Expt</td>
<td>2.81&lt;sup&gt;N.S.&lt;/sup&gt;</td>
</tr>
<tr>
<td>Photo (P)</td>
<td>33.27**</td>
</tr>
<tr>
<td>Temp (T)</td>
<td>30.73**</td>
</tr>
<tr>
<td>P x T</td>
<td>1.67&lt;sup&gt;N.S.&lt;/sup&gt;</td>
</tr>
<tr>
<td>Clone (C)</td>
<td>22.43**</td>
</tr>
<tr>
<td>P x C</td>
<td>2.13**</td>
</tr>
<tr>
<td>T x C</td>
<td>1.74*</td>
</tr>
<tr>
<td>P x T x C</td>
<td>1.31&lt;sup&gt;N.S.&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup>These proportions were transformed by the function arcsin √P. The analyses of variance were performed on these transformed variables.

* Significant at P < 0.05.

** Significant at P < 0.01.

N.S. Not significant at P < 0.05.
However, was significantly different and higher in experiment 2 than experiment 1.

The photoperiod by clone interaction was significant at the 1% level for all the variables except TRR. For this variable the above interaction was not significant at the 5% level. This implied that there was no significant difference in response with respect to TRR from one clone to another over levels of photoperiod. Similarly the temperature by clone interaction was significant at the 1% level for TRR and RWR, at the 5% level for SRR and not significant at the 5% level for LWR and SWR. The response with respect to RWR from one clone to another, therefore, was significantly different over temperature but that of LWR and SWR was not.

The combined action of photoperiod and temperature produced noticeable shifts in the average dry weight distribution of all eight clones combined (Figure 19) even though the P x C interaction for LWR, SWR and RWR was not significant at the 5% level (Table 8).

At a photoperiod of 12 hours approximately 32% of the total dry weight was located in the roots and 68% in the top as the day-night temperature increased from 17-5°C to 29-17°C. From the portion of the total dry weight located in the top about 75% resided in the leaves and 25% in the stem.

When the temperature increased further to 35-23°C at the above photoperiod 19% of the total dry weight was located
in the roots and 81% in the top. The proportions of the top dry weight allocated to the leaves and stem stayed about the same.

At a photoperiod of 14 hours the proportion of the total dry weight located in the roots and in the top oscillated from a low of 24% and 76% to a high of 15% and 85% respectively as temperature increased from 17-5°C to 35-23°C. At the same time the proportions of the top allocated to leaves and stem changed from 76% and 24% to 67% and 33% respectively.

At photoperiods of 16 and 18 hours the percentage of the total dry weight located in the roots and top changed from 21% and 79% to about 14% and 86% respectively as the day-night temperature increased from 17-5°C to 35-23°C. Concurrently the percentages of the top allocated to leaves and stem changed from 75% and 25% to 64% and 36% respectively at the 18 hour photoperiod as temperature increased from 17-5°C to 35-23°C. Similarly at the 16 hour photoperiod the portions of the top dry weight residing in the leaves and stem changed from 73% and 27% to 64% and 36% as the temperature increased from 17-5°C to 29-17°C and to 66% and 34% as the temperature further increased to 35-23°C (Table 9; Figure 19).

**Relative size of assimilatory apparatus**

The photoperiod by temperature by clone interaction was not significant at the 5% level so it was appropriate to plot leaf area ratio (LAR) and specific leaf area (SLA) versus
Table 9. Average dry weight distribution of all clones combined over levels of photoperiod and temperature (environments) expressed in percentages of total plant and top dry weight

<table>
<thead>
<tr>
<th>Photo (hrs.)</th>
<th>Temp (°C)</th>
<th>Component</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Root %</td>
<td>Top %</td>
<td>Leaf %</td>
<td>Stem %</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>17-5</td>
<td>33.04</td>
<td>66.96</td>
<td>72.43</td>
<td>27.57</td>
<td></td>
</tr>
<tr>
<td></td>
<td>23-11</td>
<td>35.31</td>
<td>64.69</td>
<td>77.02</td>
<td>22.98</td>
<td></td>
</tr>
<tr>
<td></td>
<td>29-17</td>
<td>28.72</td>
<td>71.28</td>
<td>74.36</td>
<td>25.64</td>
<td></td>
</tr>
<tr>
<td></td>
<td>35-23</td>
<td>19.13</td>
<td>80.87</td>
<td>73.00</td>
<td>27.00</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>17-5</td>
<td>23.57</td>
<td>76.43</td>
<td>76.37</td>
<td>23.63</td>
<td></td>
</tr>
<tr>
<td></td>
<td>23-11</td>
<td>17.92</td>
<td>82.08</td>
<td>73.73</td>
<td>26.27</td>
<td></td>
</tr>
<tr>
<td></td>
<td>29-17</td>
<td>19.53</td>
<td>80.47</td>
<td>67.45</td>
<td>32.55</td>
<td></td>
</tr>
<tr>
<td></td>
<td>35-23</td>
<td>14.61</td>
<td>85.39</td>
<td>66.56</td>
<td>33.44</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>17-5</td>
<td>20.77</td>
<td>79.23</td>
<td>72.87</td>
<td>27.13</td>
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</tr>
<tr>
<td></td>
<td>23-11</td>
<td>16.60</td>
<td>83.40</td>
<td>67.06</td>
<td>32.94</td>
<td></td>
</tr>
<tr>
<td></td>
<td>29-17</td>
<td>14.63</td>
<td>85.37</td>
<td>63.85</td>
<td>36.15</td>
<td></td>
</tr>
<tr>
<td></td>
<td>35-23</td>
<td>14.37</td>
<td>85.63</td>
<td>65.74</td>
<td>34.26</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>17-5</td>
<td>21.20</td>
<td>78.80</td>
<td>75.31</td>
<td>24.69</td>
<td></td>
</tr>
<tr>
<td></td>
<td>23-11</td>
<td>16.68</td>
<td>83.32</td>
<td>65.82</td>
<td>34.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>29-17</td>
<td>14.58</td>
<td>85.42</td>
<td>65.96</td>
<td>34.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td>35-23</td>
<td>13.38</td>
<td>86.62</td>
<td>64.18</td>
<td>35.82</td>
<td></td>
</tr>
</tbody>
</table>
levels of photoperiod and temperature separately for all eight clones.

Generally the relative size of the leaves on a square decimeter per gram basis yields information about leaf density. The magnitude of the variables SLA (=LFAREA/LFWT) and LAR (=LFAREA/TOTWT) indicates the degree to which assimilation rate and efficiency are affected by changes in photoperiod and temperature.

SLA was definitely more sensitive to changes in environment than LAR. The former varied from 1.6 to 2.6 and the latter from 0.8 to 1.5.

Clone 5339 had the densest leaves (large SLA) and balsam poplar had the least dense leaves (small SLA) over all temperature levels.

Only the main effects, photoperiod, temperature and clone sources of variation were significant at the 1% level. The remaining sources were not significant at the 5% level (Table 10).

The nonsignificance of the experiment source indicated that SLA and LAR did not change significantly from experiment 1 to experiment 2. Specifically soil composition changes in experiment 2 did not significantly alter the relative size and thickness of leaves compared to that of experiment 1.

As photoperiod increased from 12 to 14 hours LAR increased rapidly for all clones except 5328 which increased moderately while SLA increased sharply for all clones except
Table 10. F-values for relative leaf size variables of eight Populus clones associated with eight major sources of variation

<table>
<thead>
<tr>
<th>Source</th>
<th>Dependent variables</th>
<th>LAR</th>
<th>SLA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expt</td>
<td>0.88 N.S.</td>
<td>3.90 N.S.</td>
<td></td>
</tr>
<tr>
<td>Photo (P)</td>
<td>10.69**</td>
<td>7.74**</td>
<td></td>
</tr>
<tr>
<td>Temp (T)</td>
<td>14.12**</td>
<td>17.16**</td>
<td></td>
</tr>
<tr>
<td>P x T</td>
<td>0.57 N.S.</td>
<td>1.40 N.S.</td>
<td></td>
</tr>
<tr>
<td>Clone (C)</td>
<td>8.46**</td>
<td>20.24**</td>
<td></td>
</tr>
<tr>
<td>P x C</td>
<td>1.23 N.S.</td>
<td>1.40 N.S.</td>
<td></td>
</tr>
<tr>
<td>T x C</td>
<td>1.39 N.S.</td>
<td>1.23 N.S.</td>
<td></td>
</tr>
<tr>
<td>P x T x C</td>
<td>0.82 N.S.</td>
<td>1.02 N.S.</td>
<td></td>
</tr>
</tbody>
</table>

**Significant at P < 0.01.
N.S. Not significant at P < 0.05.

5321, 5328 and 5377. SLA decreased for clone 5377 and increased moderately for clone 5321 and 5328 (Figures 24 and 25). When photoperiod increased from 14 to 16 hours SLA and LAR continued to increase for most of the clones. Clone 5339 decreased sharply, clone 5321 remained constant and clone 5260 increased sharply for both SLA and LAR. Clone 5377 remained constant for the variable LAR.

Except for clone 5260 which decreased sharply all clones increased in SLA and LAR as photoperiod increased from 16 to 18 hours.
Clone 5339 yielded the highest SLA and LAR over all photoperiod levels and balsam poplar the lowest.

Again as temperature increased LAR and SLA generally increased for all clones and no quadratic response was observed. With the exception of clones 5323 and 5377 all clones increased rapidly then moderately and finally very sharply as the day-night temperature increased from 17-5°C to 35-23°C for SLA. Clone 5377 decreased initially as the temperature increased from 17-5°C to 23-11°C and then followed the above pattern. On the other hand clone 5323 increased slowly as the temperature increased from 17-5°C to 29-17°C and then followed the above pattern. LAR responded in a similar pattern as SLA over increasing temperature with some clonal variation. Clones 5377 and 5321 increased slower than the other clones as the temperature increased from 17-5°C to 23-11°C and remained constant from 23-11°C to 29-17°C. The increase in LAR as the temperature increased from 29-17°C to 35-23°C was rapid for all clones except clones 5339 and 5323. These clones increased at a more modest rate (Figures 26 and 27).

Discussion

Growth

Dry weight, as an expression of growth, is directly related to net photosynthesis. That is, as net photosynthesis
increases or decreases depending on the environment so does dry weight. Increases in dry weight and changes in its distribution result in increases in basal diameter, height and leaf surface area. The rate of increase is clone dependent.

Optimum growth for all clones, as expressed by the variables DIA, HT, LFWT, STMWT, RTWT, TOTWT and LFAREA, occurred at certain photoperiod and temperature combinations. In this study the optimum conditions were 29-17°C day-night temperature and 14 hour photoperiod for clone 5321, the same temperature and 16 hour photoperiod for clones 5377 and balsam poplar and the same temperature and 18 hour photoperiod for the remaining five clones 5323, 5326, 5328, 5260 and 5339. Maximum growth occurred in clone 5323 at 29-17°C day-night temperature and 18 hour photoperiod.

Growth takes place over a wide temperature range and within this range there are temperatures which yield optimum growth (Hellmers, 1962). These optimal temperatures vary with species and even with different plant parts. In this study all seven growth variables peaked at 29-17°C. The classic quadratic response to temperature was exhibited by all clones for all growth variables except height. Height growth continued to increase sharply as the day-night temperature increased from 29-17°C to 35-23°C for clone 5260. Over the same temperature range height increased slightly for clones 5321, 5328 and 5377, decreased slightly for clones
5323, 5326 and balsam poplar and decreased sharply for clone 5339. Apparently the high temperatures which usually lead to net reductions in photosynthate were not severe enough to have an adverse effect on height growth of any of these clones except clone 5339. This behavior of clone 5339 corresponds with the findings of other authors (Domingo, 1971). The cause of the response in height of clone 5260 to high temperatures is not obvious to me. Possibly this clone respires relatively less than the other clones leading to a net gain in photosynthate production even at these high temperatures.

Usually enzymes that catalyze the component reactions in both photosynthesis and respiration begin to denature and the rates of both processes are reduced when temperature is much higher than the optimum. Likewise, at temperatures lower than the optimum, component reactions slow down and lead to inadequate photosynthate production and translocation. This inadequate photosynthate supply leads to increased competition between various plant parts and differential growth reduction results. With the exception of RTWT, growth as expressed by the remaining six variables increased steadily with increasing photoperiod from 12 to 18 hours for all eight clones. Although RTWT was not found to differ significantly from one photoperiod to another (in the analysis of variance at the 5%), trends were observed when RTWT was plotted against photoperiod for each clone. With the exception of
clones 5326 and 5260 RTWT decreased as photoperiod increased from 12 to 14 hours and increased as photoperiod increased further to 16 and 18 hours. Clones 5326 and 5260 decreased as photoperiod increased from 12 to 16 hours and increased as photoperiod increased to 18 hours. Balsam poplar exhibited the lowest root weight and clones 5328 and 5323 the highest over all photoperiods. The reduction in root weight for all clones as photoperiod increases from 12 to 14 hours can probably be explained by the improved photosynthate production. Under the abnormal condition of 12 hour photoperiod more photosynthate is stored in the roots than under the more normal 14 hour photoperiod even though the photosynthesis process is reduced also. At photoperiods of 14 hours or more the distribution of assimilate shifts to one where more photosynthate is deposited in the stem than the roots.

No optimum photoperiod was observed. However, the rate of increase in growth was reduced as photoperiod increased from 16 to 18 hours compared to that when photoperiod increased from 12 to 16 hours.

Clone 5321 was the only *Populus* hybrid in this study that decreased in growth for all variables except RTWT as photoperiod increased from 16 to 18 hours. This net reduction in photosynthate production as photoperiod increased from 16 to 18 hours may be due to genetic controls related to photoperiod which cause growth to cease. The original
source of this clone may have been a location at a higher latitude and hence with shorter photoperiod. From this study a 16 hour photoperiod yields optimum growth for clone 5321.

Another possibility is the quality and intensity of light available to the clones under controlled-environment conditions. This light is approximately 1/4 the intensity of natural light and is low in radiation in the ultraviolet and infrared ranges. Clone 5321 may be more sensitive to this type of light than the other seven clones.

The interaction between photoperiod and temperature averaged over all clones was found not to be significant at the 5% level for any of the seven growth variables. A preliminary scanning of the data in Study I, however, revealed that, for example, clone 5321 grew in DIA and HT approximately the same for several combinations of photoperiod and temperature. In other words the increase of one factor compensated for the decrease of the other (Figures 28 and 29). Further analyses of the controlled-environment data should reveal similar patterns for the other growth variables and other clones.

Balsam poplar revealed itself as distinctly inferior in growth with respect to the other seven Populus hybrids. This points out clearly the differences in growth between a naturally occurring species such as balsam poplar and specifically chosen hybrids.
The effect due to experiment was significant at the 1% level for all growth variables except LFWT, RTWT and TOTWT. For these variables the experiment effect was significant at the 5% level. This information indicated that the mean response of experiment 1 was significantly different from that of experiment 2. In fact, the mean response for each growth variable of experiment 2 was much higher than that of experiment 1. Nevertheless, growth response trends were closely similar between the two experiments.

The two main ingredients forming the artificial soil, namely Jiffy-Mix and Perlite, were changed from a proportion of 2:1 in experiment 1 to 4:1 in experiment 2. This change in 'soil' composition probably improved the moisture and nutrient retention capabilities of the pot soil and led to better growth in experiment 2 than experiment 1.

**Distribution of assimilate**

Both SRR and TRR increased with temperature. This indicates a differential response of various plant parts to increases in temperature. As temperature increased STMWT and LFWT + STMWT (top dry weight) responded more than RTWT.

Under favorable temperature conditions an adequate distribution of assimilate exists. With decreasing temperature the top and the roots may compete for decreased supplies of photosynthate, water, and minerals. Since the top is further from the source of water uptake than the roots, water
becomes more limiting to top growth than to root growth. Similarly since the roots are further from the photosynthate source than the top, photosynthate becomes more limiting to root growth than top growth. Due to the reduced water uptake top growth is checked and photosynthate consumption in the top is reduced, and relatively more photosynthate becomes available to the roots. As a result the roots are less affected than the top by decreased temperature and SRR and TRR decrease with decreasing temperature.

Under cold conditions only 20% of the top dry weight is located in the stem and 80% in the leaves. In addition, a larger percentage, 33%, of the total plant dry weight resides in the roots under low temperature conditions as opposed to 20% under warm temperature conditions. Under favorable conditions 35% of the top dry weight is located in the stem and 64% in the leaves (Kursanov, 1961).

In the present study these same phenomena occurred. The distribution of assimilate averaged over all eight clones was as described above when conditions were abnormal (short photoperiod and low temperature) and normal (14 hour photoperiod and 29-17°C temperature).

LWR, the ratio of leaf weight to total plant weight, was not significantly different from one temperature level to another at the 5% level but SWR and RWR were significantly different at the 1% level. These ratios, averaged over all clones, showed that LWR was approximately constant at 0.55
while SWR increased from 0.18 to 0.27 and RWR decreased from 0.26 to 0.16 as temperature increased from 17-5°C to 35-23°C.

This was probably due to increased photosynthate supplies. Although the active apex takes precedence over other meristems in photosynthate distribution (Wardlaw, 1968) the surplus photosynthate produced by the leaves as temperature increases is translocated down to the stem and roots. But because the stem is physically closer to the photosynthate source more is usually deposited here than in the roots.

SRR and TRR increased with increasing photoperiod with two exceptions. Balsam poplar had a constant TRR when photoperiod increased from 14 to 16 hours and SRR and TRR decreased for clones 5321 and 5326 as photoperiod increased from 16 to 18 hours. Apparently both LFWT and STMWT decreased for clone 5321 as photoperiod increased from 16 to 18 hours. Again, the only explanation is genetic controls acting on the photosynthesis-related processes that are photoperiod dependent.

LWR, averaged over all clones, jumped from 0.52 at a 12 hour photoperiod to 0.57 at a 14 hour photoperiod and then remained constant, whereas SWR increased from 0.18 to 0.27 and RWR decreased from 0.29 to 0.16. Proportions are deceiving, however, in the sense that a quantity may be increasing in absolute terms but relative to the whole it may be decreasing. This was the case with RTWT.

Balsam poplar exhibited the largest SRR and TRR over
all temperature and photoperiod levels. Although this clone had the smallest LFWT, STMWT and RTWT under all environmental conditions the percentage of the total weight located in the roots was generally 5 to 10% less than that of the other hybrids. The clones of the seven *Populus* hybrids allocated more photosynthate to their roots both in quantity and percentage of total weight than did naturally occurring balsam poplar.

It was found that the variability associated with most of the variables in this study increased with an increasing mean. For the proportions LWR, SWR and RWR, however, the arcsine square root transformation was used to render independent the means and variances. Analyses on the transformed data indicated that LWR exhibits the least variation, followed by SWR and finally RWR. This indicates that RWR is much more sensitive to environmental changes and clonal differences than LWR.

For the five variables associated with the distribution of assimilate only SWR had a significant effect due to experiment at the 1% level. This suggests that only the proportion of total weight located in the stem was significantly affected by changes in soil composition from experiment 1 to experiment 2. The improved water and nutrient retention capabilities of the soil had differential effects on various plant parts and the stem received the greatest benefit.
The combined effects of photoperiod and temperature on the distribution of assimilate are complex. Generally, temperature modifies the effects of increased photoperiod (Wareing, 1956). Basically as day-night temperature increased from 17-5°C to 35-23°C with increasing photoperiod the magnitude of the shift in the assimilate distribution decreased. That is, at a short photoperiod (12 hours) the distribution shifted from 33% of total plant weight in the roots and 67% in the top to 19% and 81% respectively as temperature increased from 17-5°C to 35-23°C. However, at a photoperiod of 18 hours the distribution shifted from 21% in the roots and 79% in the top to 13% and 87% respectively as temperature increased over the same range as above. The effect of increasing temperature seemed to decrease with increasing photoperiod. Photosynthesis conditions were probably favorable enough at photoperiods of 16 and 18 hours that increases in temperature did not cause large shifts in assimilate distribution although absolute dry weight values of plant parts did change markedly.

**Relative size of assimilatory apparatus**

Relative leaf size gives information about leaf density and thickness. Changes in specific leaf area (SLA) and leaf area ratio (LAR) due to photoperiod and temperature lead to changes in assimilation rate and efficiency.

Generally LAR and SLA increased with increasing tempera-
ture. For most clones the rate of increase was moderate as temperature increased from 17-5°C to 23-11°C, stationary or slight as temperature increased further to 29-17°C, and high as temperature increased to 35-23°C.

Clones 5339 and 5328 increased continuously in SLA and LAR as temperature increased but clone 5339 leveled off somewhat in both SLA and LAR as the temperature increased from 29-17°C to 35-23°C. Statistically there was no significant interaction between clones and temperature implying there was no evidence that the clones did not all behave the same as temperature increased.

LAR and SLA increased with increasing photoperiod. The rate of increase generally decreased as photoperiod increased. There was no significant interaction between clones and photoperiod implying that the clones exhibited similar behavior over increasing photoperiod. Some clones, however, such as 5339 and 5260, responded differently to increased photoperiod. Clone 5339 decreased sharply as photoperiod lengthened from 14 to 16 hours as did clone 5260 when photoperiod lengthened from 16 to 18 hours.

Balsam poplar had the lowest SLA and hence the least dense leaves over all photoperiod and temperature levels. Clone 5339 yielded the highest SLA and hence the densest leaves.

SLA is more sensitive to changes in environment than LAR for all clones. These results support those of other
researchers (Sesták et al., 1971).

Also both SLA and LAR averaged over all clones did not change significantly from experiment 1 to experiment 2. This indicates that the improved water and nutrient retention capabilities of the pot soil used in experiment 2 versus that of experiment 1 did not affect relative leaf size.
Figure 5. Diameter response (in mms) of eight Populus clones over increasing photoperiod.
DURATION OF HIGH AND LOW INTENSITY LIGHT, HRS.

DIA, mm
Figure 6. Height response (in cms) of eight *Populus* clones over increasing photoperiod.
DURATION OF LOW AND HIGH INTENSITY LIGHT, HRS.
Figure 7. Estimated leaf surface area response (in dms$^2$) of eight *Populus* clones over increasing photoperiod.
Figure 8. Diameter response (in mms) of eight *Populus* clones over increasing day-night temperature
Figure 9. Height response (in cms) of eight *Populus* clones over increasing day-night temperature.
Figure 10. Estimated leaf surface area response (in $\text{dms}^2$) of eight Populus clones over increasing day-night temperature
Figure 11. Leaf dry weight response (in gms) of eight *Populus* clones over increasing photoperiod.
LFMI, gms

DURATION OF HIGH AND LOW DENSITY LIGHT, HRS.
Figure 12. Stem dry weight response (in gms) of eight *Populus* clones over increasing photoperiod
Figure 13. Root dry weight response (in gms) of eight *Populus* clones over increasing photoperiod
Figure 14. Total plant dry weight response (in gms) of eight Populus clones over increasing photo-period
DURATION OF HIGH AND LOW INTENSITY LIGHT, HRS.
Figure 15. Leaf dry weight response (in gms) of eight *Populus* clones over increasing day-night temperature.
Figure 16. Stem dry weight response (in gms) of eight Populus clones over increasing day-night temperature
Figure 17. Root dry weight response (in gms) of eight Populus clones over increasing day-night temperature.
Figure 18. Total plant dry weight response (in gms) of eight *Populus* clones over increasing day-night temperature.
Figure 19. Average dry weight distribution over all clones in each of 16 environments (numbers in brackets along the x-axis represent photoperiod and temperature levels respectively)
ENVIRONMENT: PHOTOPERIOD x TEMPERATURE LEVELS

1:1 (1:2 (1:3 (2:1 (2:3) (3:4) (4:2) (4:3) (4:1)))

Dry Weight, gms

105a

Root Weight

Leaf Weight

Stem Weight
Figure 20. Shoot-to-root ratio response of eight *Populus* clones over increasing photoperiod.
Figure 21. Top-to-root ratio response of eight *Populus* clones over increasing photoperiod
DURATION OF HIGH AND LOW INTENSITY LIGHT, HRS.
Figure 22. Shoot-to-root ratio response of eight *Populus* clones over increasing day-night temperature.
Figure 23. Top-to-root ratio response of eight *Populus* clones over increasing day-night temperature
Figure 24. The effect of increasing photoperiod on leaf area ratio (in dm$^2$/gm) for eight *Populus* clones
DURATION OF HIGH AND LOW INTENSITY LIGHT, HRS.

LAR, dm²/gm

5339
5328
5326
5377
5323
5321
5260
BALSAM
Figure 25. The effect of increasing photoperiod on specific leaf area (in dms²/gm) for eight Populus clones.
DURATION OF HIGH AND LOW INTENSITY LIGHT, HRS.
Figure 26. The effect of increasing day-night temperature on leaf area ratio (in $\text{dm}^2/\text{gm}$) for eight Populus clones
DAY AND NIGHT TEMPERATURE, °C

LAR, dm²/gm

1.5 - 1.0

5328
5326
5339
5377
5260
5321
BALSAM
5323
Figure 27. The effect of increasing day-night temperature on specific leaf area (in dms²/gm) for eight *Populus* clones.
Figure 28. The effect of increasing photoperiod and day-night temperature on basal diameter for clone 1 (5321)
CLONE #1
Y-AXIS (TEMPERATURE)
X-AXIS (PHOTOPERIOD)
Z-AXIS DIAMETER (mms)
Figure 29. The effect of increasing photoperiod and day-night temperature on height for clone 1 (5321)
CLONE #1

Y-AXIS (TEMPERATURE)
X-AXIS (PHOTOPERIOD)
Z-AXIS HEIGHT (CMS)
STUDY II
Methods

Data collected by Mr. Paul Wray in 1972 (experiment I) were used to evaluate the seven indices proposed earlier. One growth chamber and two greenhouse environments were utilized to assess the juvenile growth potential of 25 Populus clones. The data set was constructed so that there were four replications in each environment. There were a total of three hundred observations with the variables measured being total plant height (HT), stem and leaf dry weights (STMWT and LFWT).

Data from Study I (experiment II) were also used to evaluate the seven selection indices. Eight clones were grown twice under 16 environments yielding 256 observations, each consisting of six variables of interest: basal diameter (DIA), total plant height (HT), leaf surface area (LFAREA), leaf, stem and root dry weight (LFWT, STMWT, RTWT).

Results

Introduction

H-S index Before estimating the coefficients of this index, the P and G matrices had to be obtained. The elements of these variance-covariance matrices were procured by performing all possible analyses of variance (ANOVA) and cross-
produce analyses for the traits of interest (three traits for experiment I and six traits for experiment II). Assuming all factors as random, except replicates within environments for experiment I, the expected mean squares were determined (Table 11).

Assuming the model

\[ P = G + E + EG \]

and

\[ \sigma^2_p = \sigma^2_G + \sigma^2_E + \sigma^2_{EG} \]

where

- \( P \) = phenotypic value
- \( G \) = genotypic value
- \( E \) = environment component
- \( EG \) = genotype by environment interaction component
- \( \sigma^2_p \) = phenotypic variance
- \( \sigma^2_G \) = genotypic variance
- \( \sigma^2_E \) = environmental variance
- \( \sigma^2_{EG} \) = genotype by environment variance

the component of variance estimates, \( \hat{G}_{ij} \) and \( \hat{P}_{ij} \) were obtained (Table 12).

Elements of the vector, \( a \), of economic weights were set equal to 1. Coefficients for index \( I_1 \) associated with each trait were obtained for the original data and the data transformed by means of logarithms to the base ten.

From the signs and magnitudes of the coefficients, index
Table 11. ANOVA table structure from which component of variance estimates were obtained for the traits of interest by experiment

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>E.M.S.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reps/Envir</td>
<td>9</td>
<td>$\sigma^2 + 25 \sigma^2_{R(E)}$</td>
</tr>
<tr>
<td>Envir (E)</td>
<td>2</td>
<td>$\sigma^2 + 4\sigma^2_{EC} + 100 \sigma^2_E$</td>
</tr>
<tr>
<td>Clone (C)</td>
<td>24</td>
<td>$\sigma^2 + 4\sigma^2_{EC} + 12 \sigma^2_C$</td>
</tr>
<tr>
<td>E x C</td>
<td>48</td>
<td>$\sigma^2 + 4\sigma^2_{EC}$</td>
</tr>
<tr>
<td>Error</td>
<td>216</td>
<td>$\sigma^2$</td>
</tr>
<tr>
<td>Total</td>
<td>299</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
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<th>Source</th>
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<th>E.M.S.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expt</td>
<td>1</td>
<td>$\sigma^2_S + 8 \sigma^2_W + 128 \sigma^2_{R}$</td>
</tr>
<tr>
<td>Envir (E)</td>
<td>15</td>
<td>$\sigma^2_S + 8 \sigma^2_W + 2\sigma^2_{EC} + 16 \sigma^2_E$</td>
</tr>
<tr>
<td>Error (a)</td>
<td>15</td>
<td>$\sigma^2_S + 8 \sigma^2_W$</td>
</tr>
<tr>
<td>Clone (C)</td>
<td>7</td>
<td>$\sigma^2_S + 2 \sigma^2_{EC} + 32 \sigma^2_C$</td>
</tr>
<tr>
<td>E x C</td>
<td>105</td>
<td>$\sigma^2_S + 2 \sigma^2_{EC}$</td>
</tr>
<tr>
<td>Error (b)</td>
<td>112</td>
<td>$\sigma^2_S$</td>
</tr>
<tr>
<td>Total</td>
<td>255</td>
<td></td>
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</tbody>
</table>
Table 12. Formulas to obtain component of variance estimates by experiment

<table>
<thead>
<tr>
<th>Component</th>
<th>Experiment I</th>
<th>Experiment II</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\hat{G}<em>{ij} = \sigma^2</em>{C_{ij}}$</td>
<td>$\frac{M.S.(Clone)<em>{ij} - M.S.(E \times C)</em>{ij}}{12}$</td>
<td>$M.S.(Clone)<em>{ij} - M.S.(E \times C)</em>{ij}$</td>
</tr>
<tr>
<td>$\hat{\sigma}^2_{EG_{ij}} = \sigma^2_{EC_{ij}}$</td>
<td>$\frac{M.S.(E \times C)<em>{ij} - M.S.(Error)</em>{ij}}{4}$</td>
<td>$M.S.(E \times C)<em>{ij} - M.S.(Error (b))</em>{ij}$</td>
</tr>
<tr>
<td>$\hat{\sigma}^2_{E_{ij}}$</td>
<td>$\frac{M.S.(Envir)<em>{ij} - M.S.(E \times C)</em>{ij}}{100}$</td>
<td>$\frac{[M.S.(Envir)<em>{ij} - M.S.(Error (a))</em>{ij} - M.S.(E \times C)<em>{ij} + M.S.(Error (b))</em>{ij}]}{16}$</td>
</tr>
</tbody>
</table>

for $i, j = 1, 2, 3$, (number of variables) for $i, j = 1, \ldots, 6$ (number of variables)

---

*aThe three components listed were used to obtain the quantity

$$\hat{\sigma}^2_{ij} = \hat{\sigma}^2_{C_{ij}} + \hat{\sigma}^2_{EC_{ij}} + \hat{\sigma}^2_{E_{ij}}$$
Index $I_1$ appeared to be a contrast between LFWT and STMWT in experiment I (Table 13). For experiment II, however, index $I_1$ appeared to be a comparison of LFWT and STMWT versus RTWT and LFAREA, and DIA, HT and RTWT versus STMWT and LFAREA for the original and transformed data respectively (Table 13).

Index $I_1$ was evaluated by environment for experiment I for both the original and transformed data. Ranks were assigned to the index values within each group. The ranking of the clones within each environment varied substantially from one environment to another for both the original and transformed data (Table 14). However, within each environment the ranks were approximately the same for both the original and transformed data. Since the three environments were independent of each other these index values were summed for each clone and ranks were assigned to these values for both the original and transformed data.

Index $I_1$ was not evaluated for each environment in experiment II because the main objective was to select clones exhibiting rapid juvenile growth over all 16 environments. Marked variation in the ranking of the clones was found from one environment to the next.

For experiment I, clones 5266, 5334, 5265, 5264, and 5323 were selected when the original data was considered and clones 5266, 5265, 5334, 5264, and 5328 when the transformed data was used (Table 23). This selection was based on the
Table 13. Estimated coefficients for index I, associated with the appropriate traits by data base and experiment

<table>
<thead>
<tr>
<th>Trait</th>
<th>Experiment I</th>
<th></th>
<th></th>
<th>Experiment II</th>
<th></th>
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<tr>
<td></td>
<td>Data base</td>
<td></td>
<td></td>
<td>Data base</td>
<td></td>
<td></td>
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<tr>
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<td>Original</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DIA</td>
<td>--</td>
<td>--</td>
<td>6.8974</td>
<td>27.4666</td>
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<td></td>
</tr>
<tr>
<td>HT</td>
<td>0.3137</td>
<td>0.6631</td>
<td>1.0832</td>
<td>9.8186</td>
<td></td>
<td></td>
</tr>
<tr>
<td>LFWT</td>
<td>2.1883</td>
<td>1.9500</td>
<td>118.9613</td>
<td>1.9062</td>
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<td></td>
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<tr>
<td>STMWT</td>
<td>-3.3192</td>
<td>-1.1332</td>
<td>66.0984</td>
<td>-4.4460</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RTWT</td>
<td>--</td>
<td>--</td>
<td>-35.5430</td>
<td>8.0979</td>
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<tr>
<td>LFAREA</td>
<td>--</td>
<td>--</td>
<td>-61.9364</td>
<td>-15.7343</td>
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</table>
Table 14. Ranks associated with index I_1 values by environment for both the original and transformed data in experiment I

<table>
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<th>Environment</th>
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<td></td>
<td>O^a</td>
<td>T^b</td>
<td>O</td>
<td>T</td>
</tr>
<tr>
<td>4877</td>
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<tr>
<td>5322</td>
<td>24</td>
<td>24</td>
<td>14</td>
<td>11</td>
</tr>
<tr>
<td>5323</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>5324</td>
<td>17</td>
<td>15</td>
<td>19</td>
<td>13</td>
</tr>
<tr>
<td>5325</td>
<td>6</td>
<td>6</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>5326</td>
<td>8</td>
<td>11</td>
<td>21</td>
<td>15</td>
</tr>
<tr>
<td>5327</td>
<td>14</td>
<td>13</td>
<td>11</td>
<td>17</td>
</tr>
<tr>
<td>5328</td>
<td>21</td>
<td>9</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>5331</td>
<td>15</td>
<td>16</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>5332</td>
<td>18</td>
<td>21</td>
<td>16</td>
<td>19</td>
</tr>
<tr>
<td>5334</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>5260</td>
<td>23</td>
<td>23</td>
<td>24</td>
<td>23</td>
</tr>
<tr>
<td>5377</td>
<td>12</td>
<td>10</td>
<td>23</td>
<td>21</td>
</tr>
</tbody>
</table>

^aOriginal data.

^bTransformed data.
assumption that the top 20% of the group of clones under consideration was to be chosen. Essentially the same clones were chosen, regardless of the data base (original or transformed). The data, therefore, need not have been transformed from a selection criteria viewpoint.

In experiment \( \text{II} \), clone 5323, balsam poplar, and clones 5339 and 5321 were selected based on the original and transformed data respectively (Table 24). The results of this index are rather puzzling and unexpected since clone 5339 and balsam poplar are definitely not superior.

One critical assumption associated with this index states that index \( I_1 \) is effective as a discriminator only when the genotypic correlations between the traits included in the index are high. The following statistics were calculated from the relationship

\[
\hat{r}_g = \frac{\hat{\sigma}_{G_{ij}}}{\sqrt{\hat{\sigma}_{G_{ii}} \cdot \hat{\sigma}_{G_{jj}}}}, \quad i,j = 1, \ldots, 3 \quad (\text{Falconer, 1960})
\]

for both the original and transformed data.

All the correlations between the three traits of interest in experiment I were high with the exception of the genotypic correlation between LFWT and HT for both the original and transformed data. Those correlations based on the transformed data were slightly higher than those based on the original data (Table 15). Index \( I_1 \), therefore, is an effec-
Table 15. Genotypic correlations between 3 traits based on original and transformed data (n=300) for experiment I

<table>
<thead>
<tr>
<th>Trait</th>
<th>LFWT</th>
<th>STMWT</th>
<th>HT</th>
</tr>
</thead>
<tbody>
<tr>
<td>LFWT</td>
<td>1.0000a</td>
<td>0.8490</td>
<td>0.5139</td>
</tr>
<tr>
<td></td>
<td>1.0000</td>
<td>0.8464</td>
<td>0.5574</td>
</tr>
<tr>
<td>STMWT</td>
<td>1.0000</td>
<td>1.0000</td>
<td>0.7513</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.0000</td>
<td>0.7974</td>
</tr>
<tr>
<td>HT</td>
<td></td>
<td>1.0000</td>
<td>1.0000</td>
</tr>
</tbody>
</table>

\(^{a}\)Upper figure is based on original data and lower figure on transformed data.

tive discriminator for experiment I. In experiment II, however, there are low genotypic correlations between the traits DIA and HT, and LFWT and HT for both the original and transformed data (Table 16). This may indicate that index $I_1$ is not an effective discriminator in experiment II and possibly the reason for this is the large number of traits being considered.

**Weight-free index** Before evaluating this index the assumptions, that the distributions of the traits are similar (at least unimodal) and that the selection of individuals with large measurements on each trait is desired, were verified. These assumptions were satisfied although no evidence
Table 16. Genotypic correlations (over all clones) for six traits based on the original and transformed data (n = 256) for experiment II

<table>
<thead>
<tr>
<th>Trait</th>
<th>DIA</th>
<th>HT</th>
<th>LFWT</th>
<th>STMWT</th>
<th>RTWT</th>
<th>LFAREA</th>
</tr>
</thead>
<tbody>
<tr>
<td>DIA</td>
<td>1.0000^a</td>
<td>0.3267</td>
<td>0.9256</td>
<td>0.7143</td>
<td>0.8512</td>
<td>0.9619</td>
</tr>
<tr>
<td></td>
<td>1.0000</td>
<td>0.2764</td>
<td>0.9031</td>
<td>0.6923</td>
<td>0.7879</td>
<td>0.9222</td>
</tr>
<tr>
<td>HT</td>
<td>1.0000</td>
<td>0.4451</td>
<td>0.8644</td>
<td>0.6731</td>
<td>0.6060</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.0000</td>
<td>0.4730</td>
<td>0.8251</td>
<td>0.6724</td>
<td>0.6056</td>
<td></td>
</tr>
<tr>
<td>LFWT</td>
<td>1.0000</td>
<td></td>
<td>0.7774</td>
<td>0.9192</td>
<td>0.9707</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.0000</td>
<td></td>
<td>0.8248</td>
<td>0.8921</td>
<td>0.9620</td>
<td></td>
</tr>
<tr>
<td>STMWT</td>
<td></td>
<td></td>
<td>1.0000</td>
<td>0.8588</td>
<td>0.8676</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1.0000</td>
<td>0.9132</td>
<td>0.9048</td>
<td></td>
</tr>
<tr>
<td>RTWT</td>
<td></td>
<td></td>
<td></td>
<td>1.0000</td>
<td>0.9455</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.0000</td>
<td>0.9569</td>
<td></td>
</tr>
<tr>
<td>LFAREA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.0000</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.0000</td>
<td></td>
</tr>
</tbody>
</table>

^aUpper figure based on original data and lower figure based on transformed data.
is presented.

For experiment I, the trait HT was found not to be as important as the traits LFWT and STMWT so HT was omitted. Lower bounds for the remaining two traits were obtained for each environment and then ranks were assigned to the index values within each environment.

The lower bounds for both traits increased from environment 1 to environment 3 indicating improved growing conditions from the growth chambers to the greenhouse environments (Table 17).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>LFWT</td>
<td>7.223</td>
</tr>
<tr>
<td>STMWT</td>
<td>2.580</td>
</tr>
</tbody>
</table>

Ranks associated with index $I_2$ showed marked variation from one environment to another. For example, clones 5260, 5326, 5258, 5266 and 5377 were selected in environment 1 while clones 5266, 4879, 5258, 5334 and 5265, and clones 5334, 5258, 5266, 5326 and 5377 were selected in environments 2 and 3 respectively. The only clones selected in all three
environments were 5266 and 5258 (Table 18). This index appeared to be less consistent than index $I_1$ from one environment to another.

Index values were also summed over environments for each clone and ranks were assigned. Clones 5334, 5266, 5258, 5326 and 4879 were chosen (Table 23). For both index $I_1$ and $I_2$ only clones 5334 and 5266 were chosen by each index.

For experiment II, index $I_2$ was not evaluated for each of the 16 environments. Based on the ranks associated with index $I_2$ values over all environments, clones 5323 and 5326 were selected (Table 24). For both index $I_1$ and $I_2$ only clone 5323 was chosen by each index.

**Adaptation index** Regression analyses of the clone by environment means on the environment means (over all clones) were performed for each trait. Only the transformed data was used since the logarithmic transformation helped to linearize the data as well as decrease the dependence existing between means and variances.

By definition a clone is stable across all environments for a particular trait if the slope of the straight line fitted through the above mentioned means is near 1.0 (Finlay and Wilkinson, 1963). Via the method of simple least squares these lines were fitted and regression coefficients were obtained. Considering experiment I and the trait LFWT, clones 5258, 5325, 5326, 5327 and 5377 are stable while clones 5321,
Table 18. Ranks associated with index $I_2$ values based on 2 traits by environment for experiment I

<table>
<thead>
<tr>
<th>Clone</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>4877</td>
<td>9</td>
<td>24</td>
<td>13</td>
</tr>
<tr>
<td>4878</td>
<td>21</td>
<td>22</td>
<td>16</td>
</tr>
<tr>
<td>4879</td>
<td>11</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>5258</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>5262</td>
<td>14</td>
<td>6</td>
<td>11</td>
</tr>
<tr>
<td>5263</td>
<td>8</td>
<td>20</td>
<td>15</td>
</tr>
<tr>
<td>5264</td>
<td>12</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>5265</td>
<td>13</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>5266</td>
<td>4</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>5267</td>
<td>23</td>
<td>23</td>
<td>23</td>
</tr>
<tr>
<td>5271</td>
<td>24</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td>5272</td>
<td>19</td>
<td>13</td>
<td>17</td>
</tr>
<tr>
<td>5321</td>
<td>20</td>
<td>21</td>
<td>24</td>
</tr>
<tr>
<td>5322</td>
<td>25</td>
<td>16</td>
<td>14</td>
</tr>
<tr>
<td>5323</td>
<td>10</td>
<td>7</td>
<td>10</td>
</tr>
<tr>
<td>5324</td>
<td>17</td>
<td>11</td>
<td>19</td>
</tr>
<tr>
<td>5325</td>
<td>6</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>5326</td>
<td>2</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>5327</td>
<td>18</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>5328</td>
<td>22</td>
<td>14</td>
<td>12</td>
</tr>
<tr>
<td>5331</td>
<td>15</td>
<td>12</td>
<td>20</td>
</tr>
<tr>
<td>5332</td>
<td>16</td>
<td>15</td>
<td>21</td>
</tr>
<tr>
<td>5334</td>
<td>7</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>5260</td>
<td>1</td>
<td>19</td>
<td>22</td>
</tr>
<tr>
<td>5377</td>
<td>5</td>
<td>17</td>
<td>5</td>
</tr>
</tbody>
</table>
5322, 5334 and 5260 are highly unstable. Likewise for the trait STMWT, clones 4878, 5324, 5325, 5326, 5327 and 5377 are stable while clones 5271, 5322, 5334 and 5260 are unstable (Table 19). Lastly for the trait HT, clones 5258, 5262, 5264, 5265, 5272, 5323, 5325 and 5377 are stable while clones 5271, 5334 and 5260 are unstable. All three traits considered jointly revealed clones 5325 and 5377 as stable and clones 5334 and 5260 as unstable.

To assist data interpretations scatter diagrams were formed by plotting clonal regression coefficients (slopes) against clone means (over all environments) for each of the tree traits in experiment I only. Utilizing Figure 30 the general significance of the location of the points on these scatter diagrams was obtained. For the trait LFWT, clones 5258(4), 5265(8) and 5266(9) appear well adapted to all environments; for the trait STMWT, clones 4879(3), 5258(4), 5266(9) and 5326(18); and for the trait HT, clones 4879(3), 5262(5), 5263(6) and 5266(9) (Figures 31, 32 and 33).

Within experiment II the slopes of the fitted lines indicated that balsam poplar was unstable for all traits while clone 5326 was stable for all traits except DIA (Table 20).

Index $I_3$ (adaptation index) has a form similar to index $I_2$ because individuals are selected on the basis of large values of clone means (over all environments). In addition, individuals are to be selected on the basis of
Table 19. Estimated regression coefficients associated with the simple linear regression of clone by environment means on environment means for three traits based on the transformed data

<table>
<thead>
<tr>
<th>Clone</th>
<th>LFWT a</th>
<th>STMWT b</th>
<th>HT a</th>
<th>STMWT b</th>
</tr>
</thead>
<tbody>
<tr>
<td>4877</td>
<td>0.044</td>
<td>0.915</td>
<td>0.128</td>
<td>0.798</td>
</tr>
<tr>
<td>4878</td>
<td>-0.206</td>
<td>1.126</td>
<td>-0.034</td>
<td>0.989</td>
</tr>
<tr>
<td>4879</td>
<td>-0.322</td>
<td>1.287</td>
<td>0.029</td>
<td>1.108</td>
</tr>
<tr>
<td>5258</td>
<td>0.166</td>
<td>0.981</td>
<td>0.096</td>
<td>1.083</td>
</tr>
<tr>
<td>5262</td>
<td>-0.252</td>
<td>1.206</td>
<td>0.000</td>
<td>1.088</td>
</tr>
<tr>
<td>5263</td>
<td>0.148</td>
<td>0.862</td>
<td>0.123</td>
<td>0.907</td>
</tr>
<tr>
<td>5264</td>
<td>-0.371</td>
<td>1.340</td>
<td>-0.162</td>
<td>1.157</td>
</tr>
<tr>
<td>5265</td>
<td>-0.106</td>
<td>1.190</td>
<td>-0.092</td>
<td>1.127</td>
</tr>
<tr>
<td>5266</td>
<td>0.063</td>
<td>1.099</td>
<td>0.037</td>
<td>1.097</td>
</tr>
<tr>
<td>5267</td>
<td>0.239</td>
<td>0.675</td>
<td>-0.207</td>
<td>0.934</td>
</tr>
<tr>
<td>5271</td>
<td>0.184</td>
<td>0.583</td>
<td>0.078</td>
<td>0.598</td>
</tr>
<tr>
<td>5272</td>
<td>0.077</td>
<td>0.929</td>
<td>-0.117</td>
<td>1.112</td>
</tr>
<tr>
<td>5321</td>
<td>0.797</td>
<td>0.308</td>
<td>0.163</td>
<td>0.695</td>
</tr>
<tr>
<td>5322</td>
<td>-1.118</td>
<td>1.804</td>
<td>-0.658</td>
<td>1.510</td>
</tr>
<tr>
<td>5323</td>
<td>-0.172</td>
<td>1.189</td>
<td>-0.023</td>
<td>1.089</td>
</tr>
<tr>
<td>5324</td>
<td>0.187</td>
<td>0.846</td>
<td>-0.029</td>
<td>1.014</td>
</tr>
<tr>
<td>5325</td>
<td>0.049</td>
<td>1.022</td>
<td>0.062</td>
<td>1.018</td>
</tr>
<tr>
<td>5326</td>
<td>0.091</td>
<td>0.993</td>
<td>0.202</td>
<td>0.956</td>
</tr>
<tr>
<td>5334</td>
<td>0.049</td>
<td>1.009</td>
<td>-0.007</td>
<td>0.960</td>
</tr>
<tr>
<td>5332</td>
<td>0.349</td>
<td>0.722</td>
<td>0.163</td>
<td>0.848</td>
</tr>
<tr>
<td>5333</td>
<td>0.379</td>
<td>0.649</td>
<td>0.092</td>
<td>0.905</td>
</tr>
<tr>
<td>5334</td>
<td>0.673</td>
<td>1.590</td>
<td>-0.245</td>
<td>1.341</td>
</tr>
<tr>
<td>5260</td>
<td>0.785</td>
<td>0.363</td>
<td>0.705</td>
<td>0.353</td>
</tr>
<tr>
<td>5377</td>
<td>-0.036</td>
<td>1.054</td>
<td>0.060</td>
<td>1.051</td>
</tr>
</tbody>
</table>

a Intercept.

b Slope.
Figure 30. General interpretation of the scatter diagram when clonal regression coefficients are plotted against clone means.
Figure 31. Clonal regression coefficients (slopes plotted against clone means (over all environments) for the trait LFWT based on the transformed data
REGRESSION COEFFICIENT

[Graph with labeled axes and data points]
Figure 32. Clonal regression coefficients (slopes) plotted against clone means (over all environments) for the trait STMWT based on the transformed data.
Figure 33. Clonal regression coefficients (slopes) plotted against clone means (over all environments) for the trait HT based on the transformed data.
REGRESSION COEFFICIENT
Table 20. Estimated slopes of the straight lines fitted by regressing the clone by environment means on the environment means for six traits based on the transformed data

<table>
<thead>
<tr>
<th>Clone</th>
<th>Trait</th>
<th>DIA</th>
<th>HT</th>
<th>LFWT</th>
<th>STMWT</th>
<th>RTWT</th>
<th>LFAREA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>DIA</td>
<td>0.942</td>
<td>0.926</td>
<td>0.881</td>
<td>0.942</td>
<td>1.019</td>
<td>0.872</td>
</tr>
<tr>
<td>2</td>
<td>HT</td>
<td>1.008</td>
<td>1.111</td>
<td>0.999</td>
<td>1.093</td>
<td>1.132</td>
<td>1.034</td>
</tr>
<tr>
<td>3</td>
<td>LFWT</td>
<td>0.970</td>
<td>0.992</td>
<td>0.990</td>
<td>0.983</td>
<td>1.028</td>
<td>1.020</td>
</tr>
<tr>
<td>4</td>
<td>STMWT</td>
<td>1.028</td>
<td>1.097</td>
<td>1.241</td>
<td>1.171</td>
<td>1.155</td>
<td>1.233</td>
</tr>
<tr>
<td>5</td>
<td>RTWT</td>
<td>1.243</td>
<td>1.087</td>
<td>1.243</td>
<td>1.159</td>
<td>1.164</td>
<td>1.142</td>
</tr>
<tr>
<td>6</td>
<td>LFAREA</td>
<td>1.039</td>
<td>1.225</td>
<td>0.959</td>
<td>1.016</td>
<td>0.823</td>
<td>1.018</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>1.189</td>
<td>0.983</td>
<td>1.047</td>
<td>1.071</td>
<td>1.037</td>
<td>1.061</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td>0.546</td>
<td>0.703</td>
<td>0.525</td>
<td>0.556</td>
<td>0.687</td>
<td>0.614</td>
</tr>
</tbody>
</table>
small values of the squared deviations of the slope about the mean slope, 1.0 (i.e., \( \min (b_i - 1.0)^2 \)). These requirements led to the form of index \( I_3 \) which was

\[
I_3 = (\hat{\mu}_i - \mu)^2 (k_2 - (b_i - 1.0)^2)
\]

The lower bounds for the expressions \( \hat{\mu}_i \) and \( (b_i - 1.0)^2 \) were obtained for the traits used in experiment I and II (Table 21) and index \( I_3 \) values and associated ranks were calculated. For experiment I clones 5266, 5258, 5265, 5326 and 5325 were chosen based on the trait LFWT; clones 5258, 5326, 5266, 4879 and 5377 for the trait STMWT; and clones 5262, 5263, 4879, 5266 and 5332 for the trait HT (Table 23). When all three traits were considered jointly only clone 5266 was selected. What other clones might be selected was not clear since the index values could not be summed over all traits for each clone due to the dependence between traits.

Within experiment II, clones 5323 and 5326 were chosen when each of the six traits were considered separately, even though clone 5326 ranked low with respect to the trait DIA. Balsam poplar ranked last for all six traits (Table 22). This is understandable since this clone is a naturally occurring \textit{Populus} species and not a purposely chosen hybrid like the other seven clones.

An alternative procedure was to construct index \( I_{3}^{(2)} \) utilizing the \( \ell \)-th canonical variable associated with the clone source of variation in the MANOVA table (see Canonical
Table 21. Lower bounds for two expressions which form index $I_3$ for the appropriate traits by experiment based on transformed data

<table>
<thead>
<tr>
<th>Trait</th>
<th>Expression</th>
<th>Experiment</th>
<th>Expression</th>
<th>Experiment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\hat{\mu}_i.$</td>
<td>$(b_i - 1.0)^2$</td>
<td>$\hat{\mu}_i.$</td>
<td>$(b_i - 1.0)^2$</td>
</tr>
<tr>
<td>DIA</td>
<td>--</td>
<td>--</td>
<td>0.7623</td>
<td>0.2601</td>
</tr>
<tr>
<td>HT</td>
<td>1.9385</td>
<td>0.2116</td>
<td>1.5492</td>
<td>0.0882</td>
</tr>
<tr>
<td>LFWT</td>
<td>0.9522</td>
<td>0.6464</td>
<td>0.5170</td>
<td>0.2256</td>
</tr>
<tr>
<td>STMWT</td>
<td>0.6838</td>
<td>0.4186</td>
<td>0.1258</td>
<td>0.1971</td>
</tr>
<tr>
<td>RTWT</td>
<td>--</td>
<td>--</td>
<td>-0.0954</td>
<td>0.0980</td>
</tr>
<tr>
<td>LFAREA</td>
<td>--</td>
<td>--</td>
<td>0.7687</td>
<td>0.1490</td>
</tr>
</tbody>
</table>
Table 22. Ranks associated with values of index $I_3$ for six traits based on the transformed data in experiment II

<table>
<thead>
<tr>
<th>Clone</th>
<th>Trait</th>
<th>DIA</th>
<th>HT</th>
<th>LFWT</th>
<th>STMWT</th>
<th>RTWT</th>
<th>LFAREA</th>
</tr>
</thead>
<tbody>
<tr>
<td>5321</td>
<td>Trait</td>
<td>4</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>5323</td>
<td>Trait</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>5326</td>
<td>Trait</td>
<td>7</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>5328</td>
<td>Trait</td>
<td>1</td>
<td>7</td>
<td>3</td>
<td>6</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>5377</td>
<td>Trait</td>
<td>3</td>
<td>3</td>
<td>5</td>
<td>4</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>5260</td>
<td>Trait</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>3</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>5339</td>
<td>Trait</td>
<td>5</td>
<td>4</td>
<td>7</td>
<td>7</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>Balsam</td>
<td>Trait</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
</tr>
</tbody>
</table>

The canonical variable $Y^{(2)} = 0.02016(LFWT) - 0.03383(STMWT) + 0.00455(HT)$ was chosen for experiment I and the canonical variable $Y^{(2)} = -0.03020(DIA) + 0.00437(HT) - 0.07773(LFWT) -0.05162(STMWT) + 0.11780(RTWT) + 0.03984(LFAREA)$ was chosen for experiment II.

Through this canonical variable the clone, environment and clone by environment means were transformed to produce new canonical means. Slopes were obtained by fitting lines
Table 23. Ranks associated with the values of five different indices in experiment I

<table>
<thead>
<tr>
<th>Clone #</th>
<th>Index</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>O</td>
<td>T</td>
<td>O</td>
<td>TLF</td>
<td>TST</td>
</tr>
<tr>
<td>4877</td>
<td></td>
<td>14</td>
<td>19</td>
<td>17</td>
<td>18</td>
<td>19</td>
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<tr>
<td>4878</td>
<td></td>
<td>9</td>
<td>13</td>
<td>18</td>
<td>16</td>
<td>17</td>
</tr>
<tr>
<td>4879</td>
<td></td>
<td>18</td>
<td>12</td>
<td>5</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>5258</td>
<td></td>
<td>17</td>
<td>7</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>5262</td>
<td></td>
<td>6</td>
<td>9</td>
<td>11</td>
<td>11</td>
<td>6</td>
</tr>
<tr>
<td>5263</td>
<td></td>
<td>13</td>
<td>20</td>
<td>15</td>
<td>15</td>
<td>10</td>
</tr>
<tr>
<td>5264</td>
<td></td>
<td>4</td>
<td>4</td>
<td>8</td>
<td>9</td>
<td>16</td>
</tr>
<tr>
<td>5265</td>
<td></td>
<td>3</td>
<td>2</td>
<td>6</td>
<td>3</td>
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<td>5266</td>
<td></td>
<td>1</td>
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<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>5267</td>
<td></td>
<td>22</td>
<td>22</td>
<td>24</td>
<td>21</td>
<td>23</td>
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<td>22</td>
</tr>
<tr>
<td>5323</td>
<td></td>
<td>5</td>
<td>6</td>
<td>10</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>5324</td>
<td></td>
<td>16</td>
<td>16</td>
<td>16</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>5325</td>
<td></td>
<td>7</td>
<td>8</td>
<td>9</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>5326</td>
<td></td>
<td>21</td>
<td>10</td>
<td>4</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>5327</td>
<td></td>
<td>10</td>
<td>14</td>
<td>20</td>
<td>14</td>
<td>18</td>
</tr>
<tr>
<td>5328</td>
<td></td>
<td>8</td>
<td>5</td>
<td>12</td>
<td>10</td>
<td>20</td>
</tr>
<tr>
<td>5331</td>
<td></td>
<td>12</td>
<td>17</td>
<td>19</td>
<td>17</td>
<td>11</td>
</tr>
<tr>
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<td></td>
<td>19</td>
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<td>20</td>
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<tr>
<td>5334</td>
<td></td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>12</td>
<td>15</td>
</tr>
<tr>
<td>5260</td>
<td></td>
<td>24</td>
<td>24</td>
<td>21</td>
<td>22</td>
<td>25</td>
</tr>
<tr>
<td>5377</td>
<td></td>
<td>23</td>
<td>18</td>
<td>7</td>
<td>7</td>
<td>5</td>
</tr>
</tbody>
</table>

a Original data based on three traits.

b Transformed data based on three traits.

c Original data based on two traits.

d Transformed data based on LFWT.

e Transformed data based on STMWT.

f Transformed data based on HT.

g Original data utilizing a canonical variable.
through these new means, i.e., regressing the canonical clone by environment means on the canonical environment means.

Table 24. Ranks associated with the values of seven different indices in experiment II

<table>
<thead>
<tr>
<th>Clone Number</th>
<th>Index 1</th>
<th>Index 2</th>
<th>Index 3</th>
<th>Index 4</th>
<th>Index 5</th>
<th>Index 6</th>
<th>Index 7</th>
</tr>
</thead>
<tbody>
<tr>
<td>5321</td>
<td>3</td>
<td>2</td>
<td>5</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>5323</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>5326</td>
<td>4</td>
<td>7</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>5328</td>
<td>7</td>
<td>5</td>
<td>4</td>
<td>7</td>
<td>6</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>5377</td>
<td>6</td>
<td>6</td>
<td>3</td>
<td>6</td>
<td>3</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>5260</td>
<td>5</td>
<td>3</td>
<td>6</td>
<td>3</td>
<td>5</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>5339</td>
<td>8</td>
<td>1</td>
<td>7</td>
<td>2</td>
<td>7</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Balsam</td>
<td>2</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
</tr>
</tbody>
</table>

\(^{a}\)Original data based on six traits.

\(^{b}\)Transformed data based on six traits.

\(^{c}\)Original data utilizing a canonical variable.

\(^{d}\)Canonical variables associated with Photo * Clone interaction.

\(^{e}\)Canonical variables associated with Temp * Clone interaction.
Index \( I_3^{(2)} \) was of the form

\[
I_3^{(2)} = (\bar{y}_i^{(2)} - 0.4258)(0.8604 - (b_i^{(2)} - 1.0)^2)
\]

for experiment I and

\[
I_3^{(2)} = (\bar{y}_i^{(2)} - 0.00272)(0.4009 - (b_i^{(2)} - 1.0)^2)
\]

for experiment II, where

\[
\bar{y}_i^{(2)} = \text{clone mean of canonical variable 2}
\]

\[
b_i^{(2)} = \text{slope of line fitted through canonical variable 2 means.}
\]

From the ranks associated with the values of index \( I_3^{(2)} \), clones 5266, 5262, 5323, 5325 and 5264 were selected for experiment I and clones 5326 and 5339 for experiment II (Tables 23 and 24).

For experiment I there seems to be no consistency between this index and the previous two indices. Perhaps another canonical variable should have been chosen although the signs and magnitudes of the coefficients of \( y^{(2)} \) are acceptable from a selection viewpoint. In experiment II, the lack of a consistency between the indices may be due to the large number of traits on which selection is based.

**Curvature index** Like the adaptation index this index selects clones on the basis of one trait at a time over the range of some independent environmental measure. Because none of the clonal responses over environments in experiment
I were quadratic, this index was not evaluated. In experiment II, this index was evaluated but an interpretation problem existed when the ranks associated with the index values for each of the six traits were considered simultaneously.

Consequently the canonical variable 2 given in the previous subsection was used to obtain a linear combination of all six traits. For each clone the quadratic

\[ Y_{ij}^{(2)} = a + bT_i + cT_i^2 \]

where \( T_i = \) day temperature (17, 23, 29, 35°C) and \( i = 1, \ldots, 4; \ j = 1, \ldots, 8. \)

was fitted as well as the quadratic over all clones. The curvature parameter, \( \rho \), for each clone and over all clones was evaluated by setting \( T = \bar{T} = 26 \). Clones with a curvature near the average were considered stable and those with a curvature much above or below the average curvature exhibited below and above average stability respectively. Clone 5326 exhibited average stability while clone 5339 and balsam poplar showed below and above average stability respectively (Table 25).

Index \( I_4 \) was of the form

\[ I_4 = (Y_i^{(2)} - 0.00272)(0.00205 - |\rho_i - .00304|) \]

where \( Y_i^{(2)} \) has previously been defined.
\[ \rho_i = \text{i-th clonal curvature} \]
and the constant inside the absolute value signs is \( \bar{\rho} \).

From the ranks associated with the values of index \( I_4 \) clones 5326 and 5323 were selected (Table 24). These results are consistent with those obtained via index \( I_2 \) and are inconsistent with the results obtained via indices \( I_1 \) and \( I_3 \).

**Hamiltonian index** Using only the data from experiment II and the estimated coefficients of the quadratic equations developed for the curvature index, the parameter \( H \) was calculated for each clone and over all clones. Clone 5377 exhibited average stability while clone 5339 and balsam poplar showed below and above average stability respectively (Table 25). The interpretation of \( H \) is the same as that for parameter \( \rho \).

From the ranks associated with the values of index \( I_5 \) which has the form

\[ I_5 = (\bar{\nu}_i^{(2)} - 0.00272)(0.00101 - |H_i - 0.00104|) \]

with the constant inside the absolute value signs denoting \( \bar{H} \), clones 5377 and 5260 were selected (Table 24).

The results obtained by this index were completely different from those obtained by any of the other indices. Possibly the principle of conservation of energy does not hold and the function \( H = f(g(x), h(x)) \) is not constant for different values of \( x \) (see Literature Review: Selection indices).
Table 25. Regression coefficients for the model $Y_{ij} = a + bT_i + cT_i^2$ and the parameters $p$ and $H$ for each clone and the overall average

<table>
<thead>
<tr>
<th>Clone</th>
<th>Regression coefficients</th>
<th>$\rho$</th>
<th>$H$</th>
</tr>
</thead>
<tbody>
<tr>
<td>5321</td>
<td>-1.26370 0.10552 -0.00170</td>
<td>0.00340</td>
<td>0.00127</td>
</tr>
<tr>
<td>5323</td>
<td>-1.26032 0.10678 -0.00173</td>
<td>0.00346</td>
<td>0.00134</td>
</tr>
<tr>
<td>5326</td>
<td>-1.04387 0.09194 -0.00147</td>
<td>0.00294</td>
<td>0.00115</td>
</tr>
<tr>
<td>5328</td>
<td>-1.57985 0.12965 -0.00217</td>
<td>0.00434</td>
<td>0.00154</td>
</tr>
<tr>
<td>5377</td>
<td>-1.08102 0.08832 -0.00132</td>
<td>0.00264</td>
<td>0.00104</td>
</tr>
<tr>
<td>5260</td>
<td>-0.87136 0.07313 -0.00102</td>
<td>0.00203</td>
<td>0.00090</td>
</tr>
<tr>
<td>5339</td>
<td>-1.66792 0.14504 -0.00254</td>
<td>0.00509</td>
<td>0.00203</td>
</tr>
<tr>
<td>Balsam</td>
<td>-0.29345 0.01662 -0.00019</td>
<td>0.00038</td>
<td>0.00003</td>
</tr>
<tr>
<td>Avg.</td>
<td>-1.13267 0.09462 -0.00152</td>
<td>0.00304</td>
<td>0.00104</td>
</tr>
</tbody>
</table>
Distance index A discriminant analysis was performed on the original data and the generalized squared distance between each possible pair of clones was calculated considering the three traits LFWT, STMWT and HT. A pooled covariance matrix was used to ensure consistency with the standard analysis of variance assumption of equality of variance. Although a test for the equality of a group of variance-covariance matrices was made and resulted in the rejection of the null hypothesis $H_0: \Sigma_1 = \Sigma_2 = \ldots = \Sigma_p = \Sigma$ where $p$ equals the number of clones, this test is not a good one. Even if one element of one of these matrices is different from the corresponding elements in the other matrices $H_0$ will be rejected.

A better plan is to look at the correlation matrices, one for each clone, and see if the signs and magnitude of the coefficients are similar from one clone to the next. This was done and the correlation matrices were found to be quite similar.

Next a cluster analysis was performed on these clonal distances and a dendrograph was constructed to display the results. From this graph clones 5266, 5334, 5265, 5264 and 5326 were chosen for experiment I (Figure 34). Within experiment II, clone 5328 and balsam poplar were selected (Figure 35). Recall that this technique, however, separates very poor clones also. Based on the clonal means over all
Figure 34. Dendrograph displaying the results of a cluster analysis performed on the generalized squared distances between 25 clones based on 3 traits.
Figure 35. Dendrograph displaying the results of a cluster analysis performed on the generalized squared distances between 8 clones based on 6 traits.
environments for each of the six traits balsam poplar was the poorest overall performer of the group of eight clones. Balsam poplar, therefore, was rejected and clone 5323 was selected instead (Figure 35). With the exception of index \( I_1 \) based on the original data, balsam poplar was ranked the lowest of all the eight clones by all the other indices considered so far. The mean clonal response over all environments for the traits of interest must be considered if widely different clones are present so that the dendrogram will be interpreted correctly.

The results obtained via index \( I_6 \) agree closely with those obtained by index \( I_1 \) for experiment I but are inconsistent with all the other indices for experiment II.

**Canonical index** A multivariate analysis of variance was performed on the combined data over all environments with all traits considered jointly for both experiment I and II. The form of the univariate analysis of variance associated with each trait prior to the multivariate analysis was identical to that assumed for the H-S index in experiment I and II (Table 11).

Canonical variables were derived from the partial sums of squares and crossproducts matrix due to the clone by environment interaction for experiment I. For experiment II, canonical variables associated with both the partial sums of squares and crossproducts matrices due to the photoperiod by
clone and temperature by clone interactions respectively were calculated.

Generally the first two canonical variables account for 80% or more of the total variation in the data and thus are good for data condensation and description purposes (Table 26). These first two canonical variables, however, are poor discriminators. The means of canonical variable 1 (one for each clone) within each environment tend to cluster around the overall mean. This is not true for the means of canonical variable 2 and 3. As a result the plotting of canonical variable 1 means versus canonical variable 2 means yielded no good clonal separation but the plotting of the means of canonical variables 2 against 3 did.

Table 26. Coefficients of each canonical variable (CANVAR) and the percentage of the total variation explained by each CANVAR for experiment I

<table>
<thead>
<tr>
<th>Canonical variable</th>
<th>Trait</th>
<th>Trait</th>
<th>Trait</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LFWT</td>
<td>STMWT</td>
<td>HT</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>-0.01614</td>
<td>0.04589</td>
<td>-0.00257</td>
<td>59.12</td>
</tr>
<tr>
<td>2</td>
<td>0.01842</td>
<td>-0.02041</td>
<td>0.00257</td>
<td>24.57</td>
</tr>
<tr>
<td>3</td>
<td>-0.00804</td>
<td>-0.00979</td>
<td>0.00709</td>
<td>16.31</td>
</tr>
</tbody>
</table>
For experiment I, three distinct clusters of points appeared, one for each environment, and the superior clones stood out clearly. Clones 5266(9), 5334(23), 5265(8), 5262(5) and 5263(6) were selected (Figure 36). And the results of this index compare favorably with those obtained by the H-S index, $I_1$, and the distance index, $I_6$.

For experiment II, four distinct groups of points were exhibited by both plots, one for each photoperiod or temperature level.

Considering the means of canonical variables 2 and 3 associated with the photoperiod by clone interaction clones 5323(2) and 5328(4) were chosen (Figure 37). When the means of $Y^{(2)}$ and $Y^{(3)}$ associated with the temperature by clone interaction were considered the question of which clones should be selected was not so obvious. Definitely balsam poplar (8) was the poorest performer while clones 5260(6) and 5339(7) were the 'best' at two out of the four temperature levels (Figure 38). One reason for this dilemma might be the magnitude and signs associated with the coefficients of the canonical variables. For example, the signs of the coefficients associated with the traits LFWT and RTWT of canonical variable 3 associated with the temperature by clone interaction are reversed as compared to those coefficients associated with the same traits of the corresponding canonical variable related to the photoperiod by clone interaction.
Figure 36. Plot of the means of canonical variable 2 versus the means of canonical variable 3 for each environment based on 3 traits for experiment I ($Y^{(2)}$ and $Y^{(3)}$ are associated with $H_{CE}$).
Figure 37. Plot of the means of canonical variable 2 versus the means of canonical variable 3 for each photoperiod level based on 6 traits in experiment II. (Y(2) and Y(3) are associated with $H_{PC}$.)
Figure 38. Plot of means of canonical variable 2 versus the means of canonical variable 3 for each temperature level based on 6 traits in experiment II

\(Y^{(2)}\) and \(Y^{(3)}\) are associated with \(H_{TC}\)
Another reason was that the elements of the partial sums of squares and crossproducts matrix associated with the temperature by clone interaction were much larger than those elements of the corresponding matrix related to the photoperiod by clone interaction. Thus the temperature by clone means were more variable than the photoperiod by clone means.

The results of index $I_7$ based on the photoperiod by clone interaction agreed with those obtained by index $I_6$ but not with any of the other index results.

**Appraisal of the reliability of indices**

The construction of confidence intervals about the values of indices $I_2$ through $I_5$ was begun.

Due to the large variances and positive covariances between traits, however, the approximated variances associated with various index values were so large that confidence intervals were meaningless. A more useful approach was to apply an index with coefficients estimated from existing data to new data and vice versa. This was done for indices $I_1$ through $I_3$.

Index $I_1$ with coefficients derived from experiment I was applied to both the original and transformed data from experiment II and ranks were assigned to the resulting index values. Clones 5323 and 5328 were chosen. These results agreed with those obtained by index $I_6$ and $I_7$ based on the data from
experiment II only.

To apply index $I_1$ with coefficients, $b$, derived from experiment II to experiment I the coefficients had to be recalculated because not all traits were present in both data sets. From the ranks associated with the values of this latter index, clones 5326, 5377, 5334, 5266 and 5325 were selected. With the original index $I_1$ clones 5334 and 5266 were chosen. Apparently the index derived from an experiment involving few environments and many clones gave more reliable results than one obtained from an experiment involving many environments and few clones.

Similarly index $I_2$ with coefficients derived from experiment II was applied to experiment I, and clones 5334, 5266, 5258, 5326 and 4879 were chosen. These results compared favorably with those obtained by index $I_2$ when it was derived from and used in experiment I. When index $I_2$ with coefficients derived from experiment I was applied to experiment II clones 5323 and 5326 were selected. Lower bounds derived from experiment I, however, could not be used in experiment II since these bounds were too high. These bounds, therefore, were set equal to zero because 2 of the 3 environments in experiment I were greenhouse environments with significantly higher means for all traits as compared to experiment II which consisted of only growth chamber environments. Consequently, no valid comparisons could be made for index $I_2$ other than those already mentioned.
Similar problems with lower bounds arose when index $I_3$ based on experiment I was applied to experiment II. Also index $I_3$, with coefficients derived from experiment II, could not be evaluated for all clones when applied in experiment I. Only those clones common to both experiments could be evaluated.

The above results demonstrate the data dependence of all the proposed indices and their coefficients. In other words, two experiments could not be combined if the clones associated with experiment II were grown under conditions which were different from those under which the previously-tested clones of experiment I were grown.

The number of traits on which selection is based appears to influence the reliability of an index. For example, when the number of traits associated with index $I_2$ in experiment II was reduced from six to two, namely STMWT and SLA, and individuals were selected on the basis of large values of STMWT and small values of SLA, clones 5323 and 5328 were selected. When all six original traits were considered clones 5323 and 5326 were chosen.

As a further extension index $I_1$ with coefficients derived from experiment I was applied to first year field data composed of clones 5321, 5326, 5323 and 5377 only. Clone 5323 was chosen after assigning ranks to the index values. This compares favorably with results obtained by indices $I_6$ and $I_7$ applied to experiment II.
The computations associated with indices $I_6$ and $I_7$ must be executed again whenever a new group of clones is to be tested.

Discussion

Indices and their reliability

Five of the seven proposed selection indices were evaluated using data obtained from experiment I. This experiment was conducted by Mr. Paul Wray to determine the effect of three environments on the vegetative growth of 25 Populus clones in 1972. The curvature and Hamiltonian indices were not evaluated because none of the clonal responses over environments were quadratic and no independent environmental measure could be associated with each environment.

All seven selection indices were evaluated using data obtained from Study I (experiment II).

In experiment I reasonable consistency was exhibited by indices $I_1$, $I_2$, $I_6$ and $I_7$ which selected clones 5265, 5266 and 5334 in the top group of five superior clones. These results compare favorably with those obtained by Wray (1974).

In experiment II indices $I_1$ through $I_7$ produced less consistent results than the corresponding indices based on experiment I. For example, out of nine cases (7 indices of which indices $I_1$ and $I_2$ were based on both original and transformed data) clone 5323 was selected 5 times in the top 20% chosen each time and clones 5326 and 5328 were each
included 3 times. Which two clones should be selected as superior in growth is not clear although from personal observations I would select clones 5323 and 5328. The reliability of an index apparently decreases as the number of traits on which selection is based increases.

In experiment I and II the coefficients of index $I_1$ were estimated from both original and transformed data. Since the variances associated with the traits of interest tended to increase with increasing mean and since the coefficients of index $I_1$ were based on estimated phenotypic and genotypic variances the transformed data was thought to improve the reliability of index $I_1$. A comparison of index $I_1$ in experiment I based on both the original and transformed data revealed identical results. In experiment II the results of index $I_1$ based on both types of data were dissimilar. The data transformation (logarithms to the base ten), therefore, did not improve the reliability of index $I_1$.

Unlike the other indices, index $I_1$ has the built-in facility of assigning weights, either economic or biological, to the traits on which selection is to be based. The sign and magnitude of these weights depend on the goals of clonal selection. In Study II equal weights were assumed for lack of any other information. As information about the relative importance of these traits, consistent with the selection goals, becomes available it can be incorporated into the index and a new set of coefficients will be formed.
Kempthorne and Nordskog (1959) point out that index $I_1$ is reliable only when the genotypic correlations between the traits forming the index are high. These correlations were high for the traits in experiment I and most, but not all, traits in experiment II.

Bridgwater (1972) used different weights and various combinations of six traits (height, diameter, total dry weight, specific gravity, volume and number of limbs per foot) to construct many indices. The form of these indices was the same as index $I_1$ in this present study. The expected gain (Falconer, 1960) was employed as a means of deciding which index was best according to the selection goals. The expected gain was found to be high only when the traits height, diameter and total dry weight were incorporated into the index.

Bridgwater (1972) found that a reliable index was one which contained traits with high genotypic correlations between them. Such an index was one containing the above three traits. My results tend to support these findings.

Index $I_1$ with coefficients estimated from experiment I was applied to experiment II and clones 5323 and 5328 were selected. This procedure produced good results compared to other indices.

After some additional calculations indices $I_1$ and $I_2$ based on data from experiment II were applied to experiment I and clones 5334 and 5266 were chosen as part of the top
group of five superior clones. These results are acceptable when compared to the results of other indices.

Index $I_1$ when derived from an experiment involving few environments and many clones, therefore, gave more reliable results than one obtained from an experiment involving many environments and few clones.

Index $I_2$ is a desirable index from an ease-of-calculation viewpoint. Unlike index $I_3$ which bases selection on one trait at a time over several environments, index $I_2$ bases selection on several traits at a time over one environment. The latter index is preferred because an average value over all environments can be calculated (environments are assumed independent). This cannot be done with index $I_3$ because the traits measured on the same plant are correlated with each other. Index $I_3$ must, therefore, be evaluated for each trait separately which leads to interpretation problems if there are many traits. Even if a canonical variable is used to evaluate index $I_3$ its reliability is totally dependent on the canonical variable. A canonical variable which 'explains' a large percentage of the total variation in the data, say 50 to 80% is not desirable. Canonical variable 2 was usually a better discriminator even though it 'explained' only 10 to 30% of the total variation.

Wu (1973) originally proposed the use of the curvature of a quadratic equation which was a function of some independent environmental variable as a measure of adaptation.
in contrast to the procedure outlined by Finlay and Wilkinson (1963).

Wu (1973), however, stated that a variety was stable when its curvature approached zero. I, on the other hand, thought that a clone was stable across all temperatures if the curvature of a particular clonal response was near the overall average curvature. This idea was incorporated into index $I_4$.

Likewise index $I_5$ was evaluated based on data from experiment II but this index did not perform as well as index $I_4$. Possibly the assumption of the existence of a function, formed by the product of a growth and growth rate function, which remains constant over increasing temperature does not hold. Indices $I_4$ and $I_5$ were not evaluated in experiment I because some necessary information was absent. Index $I_4$ performed as well as index $I_2$ when both were based on data from experiment II. Clones 5323 and 5326 were selected in both cases.

Indices $I_6$ and $I_7$ are constructed by methods which involve complex computations but existing computer programs, in part, help to solve the problem. Since final selection is a visual subjective process no mathematical functions are needed. Only the plotting of the computer results is required to produce a pleasing visual display which simplifies interpretation.
The computations associated with index $I_6$ can easily be performed on any computer accepting FORTRAN. The computations associated with index $I_7$ are performed by an IBM dependent package called SAS which is not available for use on an non-IBM computer. A procedure REGR, a subprogram of the SAS package was used to perform MANOVAs and produce the canonical variables associated with various sources of variation of the assumed model. There is the limitation that the degrees of freedom associated with the source of variation due to regression must be 80 or less. Otherwise the procedure REGR breaks down and the plot of canonical means cannot be constructed.

In summary, an index based on an existing data can be used reliably to select clones from a new data set or a combined data set of new and previously-tested clones provided that the new clones are grown under environmental conditions similar to those under which the previously-tested clones were grown. Given the present state of development the indices evaluated in Study II cannot be used directly on any new set of clones if these new clones are not grown under conditions comparable to those under which the previously-tested clones were grown.
SUMMARY AND CONCLUSIONS

Study I

Eight Populus clones were grown in 16 different growth chamber environments in order to determine the effects of photoperiod and temperature on their vegetative growth. Study I (experiment II) was replicated twice and six traits DIA, HT, LFWT, STMWT, RTWT and LFAREA were measured and another eight quantities were calculated from them. The trait LFAREA was estimated via regression equations which were formed by the author, one for each of the eight clones. These equations met the criterion that leaf surface area be estimated within ± 0.1 dms² of the true value.

The following conclusions were deduced:

1. Optimum growth as expressed by the variables DIA, HT, LFWT, STMWT, RTWT, TOTWT and LFAREA occurred at 29-17°C day-night temperature and 14 hour photoperiod for clone 5321, the same temperature and 16 hour photoperiod for clones 5377 and balsam poplar and the same temperature and 16 hour photoperiod for clones 5323, 5326, 5328, 5260 and 5339.

2. Growth as depicted by all variables either measured or synthesized, with the exception of RTWT, increased with increasing photoperiod from 12 to 18 hours for all eight Populus clones.
3. Growth rate was clone dependent with balsam poplar exhibiting a much slower growth rate than the other seven hybrids for all variables.

4. For all eight clones RTWT decreased as photoperiod increased from 12 to 14 hours and then increased steadily as photoperiod increased further from 14 to 18 hours.

5. The classic quadratic response of growth, as expressed by the traits DIA, LFWT, STMWT, RTWT, TOTWT and LFAREA, to increasing day-night temperature was exhibited by all clones. That is, growth increased with increasing temperature to a maximum and then decreased as temperature continued to increase.

6. Growth in HT increased sharply with increasing temperature and then levelled off as temperature continued to increase.

7. SRR, RTT, SLA and LAR increased continuously as temperature increased from 17.5°C to 35-23°C.

8. With one or two exceptions the photoperiod by temperature and photoperiod by temperature by clone interactions were not significant at the 5% level for any of the variables considered in this study.

9. The source of variation due to experiments was significant at the 5% level for the variables LFWT, STMWT, RTWT, TOTWT, DIA, HT, LFAREA and SWR. Growth
as expressed by these eight variables was significantly greater for the clones of replicate 2 than for those of replicate 1. This growth increase was thought to be due to the improved moisture and nutrient retention capabilities of the pot soil used in replicate 2. These soil improvements were brought about when the proportions of Jiffy-Mix to Perlite, the two main ingredients forming the artificial soil, were changed from 2:1 to 4:1 in replicate 2.

10. Under abnormal conditions (low temperature and short photoperiod) 33% of total plant dry weight resided in the roots and 67% in the top. Of the latter percentage 80% of the top dry weight was located in the leaves and 20% in the stem. Under normal conditions (medium temperature and long photoperiod) 20% of total plant dry weight resided in the roots and 80% in the top. Of the latter percentage 64% of the top dry weight was located in the leaves and 36% in the stem.

11. Balsam poplar exhibited a larger SRR and TRR over increasing temperature and photoperiod than the seven hybrids.

12. SLA (specific leaf area) was found to be more sensitive to changes in environment than LAR (leaf area ratio) for all eight clones.
13. The rate of increase in SLA and SRR for superior clones was much more gradual over increasing temperature and photoperiod than nonsuperior clones.

14. In order of increasing variability LWR exhibited the least variation followed by SWR and RWR.

Study II

Seven selection indices were evaluated and their reliability and ease of application were investigated.

Indices I₁ through I₅ were mathematical functions where index I₁ was a weighted function and indices I₂ through I₅ were unweighted. Indices I₆ and I₇ were graphical displays. These indices were applied to both an existing and a newly-collected data set. The existing data set (experiment I) was obtained from Mr. Paul Wray who conducted an experiment to determine the effect of three different environments (one growth chamber plus two greenhouse environments) on the vegetative growth of 25 Populus clones. The experiment was replicated four times and three traits LFWT, STMWT, and HT were measured.

The newly-collected data set (experiment II) was obtained from the experiment conducted by myself and discussed in Study I.

The following conclusions were deduced:

1. Clones 5334, 5266 and 5265 were selected as part of the top group of five clones when five of the seven
indices were evaluated based on experiment I.

2. Clone 5323 was selected as part of the top group of two clones when all seven indices were evaluated based on experiment II.

3. Index $I_1$ when derived from an experiment involving few environments and many clones gave more reliable results than one obtained from an experiment involving many environments and few clones.

4. The reliability of an index decreased as the number of traits on which selection was based increased.

5. The coefficients associated with the indices outlined in this study are data dependent and must be calculated for each new group of clones.

6. An index based on an existing data set can be used to select clones from an expanded population consisting of new and previously-tested clones provided that the new clones are grown under environmental conditions similar to those under which the previously-tested clones were grown.

7. Indices $I_4$ and $I_5$ can only be computed when there exists an underlying quadratic response to some independent environmental measure with at least four levels.

8. Index $I_2$ is preferred if computational ease is important; index $I_1$ is recommended if the selection of individuals is to be based on unequally weighted
traits; indices $I_6$ and $I_7$ are preferred if a graphical display is more meaningful to the user than ranks.
ACKNOWLEDGEMENTS

I wish to thank Dr. John Gordon for suggesting this research and being willing to answer my questions and make helpful suggestions.

I am grateful to Dr. Kenneth Ware (former staff member of the Dept. of Forestry, I.S.U.) and several staff members of the Dept. of Statistics who pointed me in the right direction early in my career as a graduate student and gave me confidence during the years when I was building up my statistical skills.

I also appreciate the help of Rich Faltonson who prepared the necessary cuttings in the greenhouses for this study.

I thank also the many people who assisted in the data collection phase of this research, especially Tom Burk.

Finally, I thank my wife, Barbara for helping me with some of the watering and potting work, and for her patience, endurance and understanding during our five years of graduate student life.
LITERATURE CITED


Hanson, W. D. and H. W. Johnson. 1957. Methods for calculating and evaluating a general selection index obtained by pooling information from two or more experiments. Genetics 42: 421-432.


Kramer, P. J. 1957. Some effects of various combinations of day and night temperatures and photoperiod on the height growth of loblolly pine seedlings. For. Sci. 3: 45-55.


APPENDIX A

Now $H = a'X$ and we wish to find $I = b'Y$ so the correlation, $\rho_{IH}$, between $H$ and $I$ is maximum.

Now let $V(Y) = P = \text{matrix of phenotypic variances and covariances}$ and $V(X) = G = \text{matrix of genotypic variances and covariances}$. Then

$$V(I) = V(b'Y) = b'V(Y)b = b'Pb$$

and

$$V(H) = V(a'X) = a'V(X)a = a'Ga$$

Also

$$\rho_{IH} = \frac{\text{Cov}(I,H)}{\sqrt{V(I) \cdot V(H)}}$$

and assuming $Y = X + E$ (any $XE$ term is pooled with $E$) and $\text{Cov}(X,E) = 0$

this implies $\text{Cov}(I,H) = \text{Cov}(b'(X+E),a'X)$

$$= \text{Cov}(b'X,a'X) + \text{Cov}(b'E,a'X)$$

$$= a'V(X)b = a'Gb$$

Therefore

$$\rho_{IH} = \frac{a'Gb}{\sqrt{(a'Ga)(b'Pb)}}$$

Now let

$$K = \sqrt{a'Ga} \cdot \left(\rho_{IH}\right) = \frac{a'Gb}{\sqrt{b'Pb}}$$

and square both sides.

Then we must find

$$\max (a'Gb)^2 - K^2(a'Ga)(b'Pb)$$
Let $\frac{\partial K}{\partial b} = 0$ then we obtain

$$2(a'Gb)Ga - 2K \frac{\partial K}{\partial b} (b'Pb) - K^2.2Pb$$

and finally $P \left\{ \frac{K^2}{a'Gb} \right\} = Ga$

or $Pb' = Ga$
APPENDIX B

If $x_1 \sim \lognormal(\mu_1, \sigma_1^2)$ and $x_2 \sim \lognormal(\mu_2, \sigma_2^2)$ and $x_1$ and $x_2$ are independent then the joint density of $x_1$ and $x_2$ is

$$f(x_1, x_2) = f_1(x_1) \cdot f_2(x_2)$$

$$= \frac{1}{2\pi x_1 x_2 \sigma_1 \sigma_2} e^Q, \quad x_1 \text{ and } x_2 > 0$$

where

$$Q = -\frac{1}{2} \left\{ \frac{(\log x_1 - \mu_1)^2}{\sigma_1^2} + \frac{(\log x_2 - \mu_2)^2}{\sigma_2^2} \right\}$$

Now define the transformation

$$t = x_1 x_2 \text{ and } u = x_2$$

then

$$x_1 = \frac{t}{u} \text{ and } x_2 = u$$

and

$$J = \begin{vmatrix} \frac{\partial x_1}{\partial t} & \frac{\partial x_1}{\partial u} \\ \frac{\partial x_2}{\partial t} & \frac{\partial x_2}{\partial u} \end{vmatrix} = \begin{vmatrix} \frac{1}{u} & -\frac{t}{u^2} \\ 0 & 1 \end{vmatrix} = \frac{1}{u}$$
We have mapped $A = \{(x_1, x_2) | 0 < x_1, x_2 < \infty\}$ into $B = \{(t, u) | 0 < t, u < \infty\}$.

Then $g(t, u) = f_1\left(\frac{t}{u}\right) \cdot f_2(u). |J|$

$$= \frac{1}{2\pi\sigma_1\sigma_2} e^R, \quad t \text{ and } u > 0$$

where $R = -\frac{1}{2} \left\{ \frac{(\log \frac{t}{u} - \mu_1)^2}{\sigma_1^2} + \frac{(\log u - \mu_2)^2}{\sigma_2^2} \right\}$

Manipulation of the $R$ term yields

$$R = -\frac{1}{2} \left\{ K + \frac{\sigma_1^2 + \sigma_2^2}{\sigma_1^2 \cdot \sigma_2^2} \left[ \log u - \frac{A}{\sigma_1^2 + \sigma_2^2} \right]^2 \right\}$$

where $K = \frac{[\log t - (\mu_1 + \mu_2)]^2}{\sigma_1^2 + \sigma_2^2}$

and $A = \sigma_2^2 (\log t - \mu_1) + \sigma_1^2 \mu_2$
Now let \( \log u = \frac{\sigma_1 \sigma_2}{\sqrt{\sigma_1^2 + \sigma_2^2}} z \)

then \( \frac{1}{u} \frac{du}{dz} = \frac{\sigma_1 \sigma_2}{\sqrt{\sigma_1^2 + \sigma_2^2}} \), \( -\infty < z < \infty \)

and \( g(t) = \int_{-\infty}^{\infty} \frac{1}{2\pi \sqrt{\sigma_1^2 + \sigma_2^2}} e^{-\frac{1}{2} U(z)} \, dz \)

where \( U(z) = K + [z - A/\sigma_1 \sigma_2 \sqrt{\sigma_1^2 + \sigma_2^2}]^2 \)

Then \( g(t) = \frac{1}{2\pi \sqrt{\sigma_1^2 + \sigma_2^2}} e^{-K/2} \int_{-\infty}^{\infty} e^{-\frac{1}{2} p^2} \, dp \)

where \( p = z - A/\sigma_1 \sigma_2 \sqrt{\sigma_1^2 + \sigma_2^2} \)

and finally \( g(t) = \frac{1}{\sqrt{2\pi} t \sqrt{\sigma_1^2 + \sigma_2^2}} e^{-K/2} \)

If \( \mu_1 = \mu_2 = 0 \) and \( \sigma_1^2 = \sigma_2^2 = 1 \) then

\[ g(t) = \frac{1}{2t\sqrt{\pi}} e^{-(\log t)^2/4} , 0 < t < \infty \]
APPENDIX C

Fe-EDTA Solution Recipe

<table>
<thead>
<tr>
<th>Compound</th>
<th>Grams</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fe $\text{SO}_4 \cdot 7\text{H}_2\text{O}$</td>
<td>24.9</td>
</tr>
<tr>
<td>EDTA</td>
<td>26.1</td>
</tr>
<tr>
<td>NaOH</td>
<td>10.3</td>
</tr>
</tbody>
</table>

Dissolve first two compounds in one liter of distilled $\text{H}_2\text{O}$ and mix well. Add NaOH next and aerate solution vigorously overnight. Solution will be cloudy lime green but should be clear reddish-brown after aeration. Add 1 ml of this solution for each liter of nutrient solution.

<table>
<thead>
<tr>
<th>Element</th>
<th>ppm (mg/liter)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fe</td>
<td>5</td>
</tr>
</tbody>
</table>
Micronutrient Solution Recipe

<table>
<thead>
<tr>
<th>Compound</th>
<th>Grams</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\text{H}_3\text{BO}_3$ (boric acid)</td>
<td>2.86</td>
</tr>
<tr>
<td>$\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$ (Manganese chloride)</td>
<td>1.81</td>
</tr>
<tr>
<td>$\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ (zinc sulfate)</td>
<td>0.22</td>
</tr>
<tr>
<td>$\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ (cupric sulfate)</td>
<td>0.08</td>
</tr>
<tr>
<td>$\text{H}_2\text{MoO}_4 \cdot \text{H}_2\text{O}$ (Molybdic acid)</td>
<td>0.02</td>
</tr>
<tr>
<td>$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ (Magnesium sulfate)</td>
<td>0.20</td>
</tr>
</tbody>
</table>

Dissolve the above compounds in one liter of distilled $\text{H}_2\text{O}$.

Add 1 ml of this solution for each liter of nutrient solution.

<table>
<thead>
<tr>
<th>Element</th>
<th>ppm</th>
<th>mg/liter</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>.50</td>
<td></td>
</tr>
<tr>
<td>Mn</td>
<td>.50</td>
<td></td>
</tr>
<tr>
<td>Zn</td>
<td>.05</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Mg</td>
<td>.02</td>
<td></td>
</tr>
</tbody>
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APPENDIX D

Field Experiment Structure

In the discussion of Study II I suggested that the methods of index construction could be applied to field data. This field data could be collected via an experiment based on a design which takes advantage of all pertinent information gathered from Study I.

The author proposes a study which could run from one to three years. Sixteen clones would be grown at four different locations in a two-replicate randomized block layout. The experimental plots would each contain 4 clones spaced 6 feet apart. Each block would be bordered by two rows of whatever clone the experimenter desires to eliminate border effects. Basal diameter, total height and top dry weight should be the variables of interest from a selection standpoint. Plot averages would be analyzed so that the analysis would be balanced even if some mortality occurred in some of the experimental plots.

Having determined the ANOVA table analyses could be carried out for each year separately and then a combined analysis could be performed over all years if the experiment continued for more than one year (Table 27; Cochran and Cox, 1957).

A number of authors have examined the analysis of repeated-measurements experiments (Cole and Grizzle, 1966;
Table 27. ANOVA structure for the proposed field experiment based on plot averages

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blks/Locs</td>
<td>4</td>
</tr>
<tr>
<td>Locations (L)</td>
<td>3</td>
</tr>
<tr>
<td>Clones (C)</td>
<td>15</td>
</tr>
<tr>
<td>L x C</td>
<td>45</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>127</strong></td>
</tr>
</tbody>
</table>

Danford et al., 1960; and Patterson and Bridget, 1970). Generally analyses are kept simple if equal subclass numbers can be maintained. By utilizing plot averages the experimenter has greater assurance of a balanced experiment.

The problem of plot size has also been investigated by some authors (Wright and Freeland, 1960). These researchers state that if most of the total cost is assignable on a per-plot basis a small number of trees should be assigned to each plot. However, if the plot is too small the problem of missing plots arises. Finally, the authors suggest that the biological adequacy of data collected from small plots depends on the magnitude of the correlation between the performance of varieties grown in mixture and that of the same varieties
grown in pure stands. Four clones per experimental plot, therefore, appears adequate for the proposed field study.
<table>
<thead>
<tr>
<th>NCFES&lt;sup&gt;1&lt;/sup&gt; number</th>
<th>Name and parentage</th>
<th>Source recent (original)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4877</td>
<td><em>Populus alba</em> L.</td>
<td>-</td>
</tr>
<tr>
<td>4878</td>
<td><em>Populus</em> × <em>euramericana</em>&lt;sup&gt;2&lt;/sup&gt; (Dode) Guinier</td>
<td>-</td>
</tr>
<tr>
<td>4879</td>
<td><em>Populus</em> × <em>euramericana</em> (Dode) Guinier</td>
<td>-</td>
</tr>
<tr>
<td>5258</td>
<td><em>Populus</em> spp.</td>
<td>Indian Head, Sask.</td>
</tr>
<tr>
<td>5262</td>
<td><em>Populus candicans</em>&lt;sup&gt;3&lt;/sup&gt; Ait.&lt;sup&gt;4&lt;/sup&gt; × <em>Populus berolinensis</em> Dipp.</td>
<td>Upper Darby, Pa., U.S.A.</td>
</tr>
<tr>
<td>5263</td>
<td><em>Populus candicans</em> Ait.&lt;sup&gt;4&lt;/sup&gt; × <em>Populus berolinensis</em> Dipp.</td>
<td>Upper Darby, Pa., U.S.A.</td>
</tr>
<tr>
<td>5264</td>
<td><em>Populus angulata</em> Michx. × <em>Populus plantierensis</em> Schneid.</td>
<td>Upper Darby, Pa., U.S.A.</td>
</tr>
</tbody>
</table>

<sup>1</sup>North Central Forest Experiment Station, Rhinelander, Wisc.

<sup>2</sup>*Populus x euramericana* (Dode) Guinier = *Populus deltoides* Marsh. × *Populus nigra* L.

<sup>3</sup>*Populus candicans* Ait. = *Populus alba* L. × *Populus balsamifera* L.

<table>
<thead>
<tr>
<th>Page</th>
<th>Plant Name</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>5266</td>
<td>Populus angulata Michx. x Populus trichocarpa Torr. et Gray</td>
<td>Upper Darby, Pa., U.S.A.</td>
</tr>
<tr>
<td>5267</td>
<td>Populus deltoides Marsh. x Populus caudina</td>
<td>Upper Darby, Pa., U.S.A.</td>
</tr>
<tr>
<td>5271</td>
<td>Populus charkoviensis Schroed. x Populus deltoides Marsh</td>
<td>Upper Darby, Pa., U.S.A.</td>
</tr>
<tr>
<td>5272</td>
<td>Populus nigra L. x Populus laurifolia Ledeb.</td>
<td>Upper Darby, Pa., U.S.A.</td>
</tr>
<tr>
<td>5321</td>
<td>Populus x euramericana 'Negrito de Granada' (Dode) Guinier</td>
<td>Maple, Ont., (Spain)</td>
</tr>
<tr>
<td>5322</td>
<td>Populus x euramericana 'Jacometti 78B' (Dode) Guinier</td>
<td>Maple, Ont., (Germany)</td>
</tr>
<tr>
<td>5323</td>
<td>Populus x euramericana 'Canada Blanc' (Dode) Guinier</td>
<td>Maple, Ont., (Italy)</td>
</tr>
<tr>
<td>5324</td>
<td>Populus x euramericana 'B-56' (Dode) Guinier</td>
<td>Maple, Ont.,</td>
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<tr>
<td>5325</td>
<td>Populus x euramericana 'Ostia' (Dode) Guinier</td>
<td>Maple, Ont., (Italy)</td>
</tr>
<tr>
<td>5326</td>
<td>Populus x euramericana 'Eugenii' (Dode) Guinier</td>
<td>Maple, Ont., (France)</td>
</tr>
<tr>
<td>5327</td>
<td>Populus x euramericana 'I-214' (Dode) Guinier</td>
<td>Maple, Ont., (Italy)</td>
</tr>
<tr>
<td>5328</td>
<td>Populus x euramericana 'I-45/51' (Dode) Guinier</td>
<td>Maple, Ont., (Italy)</td>
</tr>
<tr>
<td>5331</td>
<td>Populus betulafolia Dipp. x Populus trichocarpa Torr. et Gray</td>
<td>Upper Darby, Pa., U.S.A.</td>
</tr>
<tr>
<td>5332</td>
<td>Populus betulafolia Dipp. x Populus trichocarpa Torr. et Gray</td>
<td>Upper Darby, Pa., U.S.A.</td>
</tr>
</tbody>
</table>
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5334  \textbf{Populus angulata} Michx.  \\
\textit{x} \textbf{Populus trichocarpa}  \\
Torr. et Gray  \\
Upper Darby, Pa.,  \\
U.S.A.

5260  \textbf{Populus tristis} Fish.  \\
\textit{x} \textbf{Populus balsamifera} L.  \\
Indian Head,  \\
Sask.

5377  \textbf{Populus x euramericana}  \\
\textit{'W-5'} (Dode) Guinier  \\
Madison, Wisc.

5339  \textbf{Populus alba} L.  \\
\textit{x} \textbf{Populus grandidentata}  \\
Michx.  \\
Central Iowa

--  \textbf{Populus balsamifera} L.  \\
--
5334  \( \text{Populus angulata Michx.} \times \text{Populus trichocarpa Torr. et Gray} \)

5260  \( \text{Populus tristis Fish.} \times \text{Populus balsamifera L.} \)

5377  \( \text{Populus} \times \text{euroamericana 'W-5' (Dode) Guinier} \)

5339  \( \text{Populus alba L.} \times \text{Populus grandidentata Michx.} \)

--  \( \text{Populus balsamifera L.} \)