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Genetic variation in traits affecting the water relations of balsam poplar along a latitudinal transect in Northwestern Ontario

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GENETIC VARIATION IN TRAITS AFFECTING THE WATER RELATIONS OF BALSAM POPLAR ALONG A LATITUDINAL TRANSECT IN NORTHWESTERN ONTARIO

by

Cameron S. Penfold ©

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Major Advisor Reader

A CAUTION TO THE READER

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ABSTRACT

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Key Words: *Populus balsamifera* L., water relations, genetic variation, clones, field and greenhouse conditions.

Genetic variation in traits potentially affecting the water relations of balsam poplar (*Populus balsamifera* L.) clones from four provenances along a transect from northern Wisconsin to Pickle Lake in northwestern Ontario was examined both in the field and in the greenhouse. Traits measured were transpiration rates, stomatal conductance, internode length, average single-leaf abaxial area and oven-dry weight, specific leaf weight, and stomatal density and length. Additional traits measured in the greenhouse provenance trial were shoot length, number of leaves per plant, total abaxial leaf area per plant, total oven-dry root, shoot and leaf weight, and oven-dry root/shoot weight ratio. Most of the observed variation in traits was attributable to clones within provenances and to ramets within clones. As much as eighty-five percent of the observed variation was attributable to variation among and within clones within provenances. The provenance effect had a significant influence on leaf size and morphology traits, with an apparent north-south clinal trend. Leaves from northern sources were smaller in area, lighter in weight, and were thicker than leaves from southern sources. As expected stomatal conductance was positively correlated with measured transpiration rates. The only other trait significantly correlated with transpiration rates was stomatal length, and this only occurred in the greenhouse provenance trial. Larger stomata were associated with higher rates of transpiration.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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I. INTRODUCTION

As an introduction to the phenomenon commonly referred to as the photosynthesis-transpiration compromise, Salisbury and Ross (1978) cite an experiment conducted by Hanks in 1974. Hanks (1974) found that approximately 600 kg of water evaporated from corn plants for every kilogram of *Zea mays* L. (corn) grain produced. Moreover, for every kilogram of dry plant material produced, including roots, shoots, leaves and reproductive structures, 225 kg of water passed from the plants to the surrounding air. Water loss by terrestrial plants is unavoidable and, in fact, is essential for growth.

The principle function of a plant's leaves, or more precisely the chloroplasts located within the leaves, is to produce food for the entire plant via photosynthesis. To maximize photosynthesis, the plant's leaves must capture an optimal amount of sunlight. However, sunlight is not the only requirement for photosynthesis; a source of carbon is also needed. The plant's source of carbon is carbon dioxide present in the surrounding air. Gaseous carbon dioxide must enter the intercellular spaces of the plant's leaves by the process of diffusion through stomatal pores, but before the carbon dioxide can enter the leaf's cells, it must go into solution. The plasma membrane of the mesophyll cells is virtually impermeable to carbon dioxide gas (Raven *et al*, 1981). Thus,

moisture must be present on the cell surface if carbon is to be absorbed, and this gives rise to the photosynthesis-transpiration compromise.

Just as there is a concentration gradient favoring the diffusion of carbon dioxide from the surrounding air into the intercellular spaces of the leaf, there is a moisture concentration gradient favoring the diffusion of water from the leaf to the air. The diffusion of water vapor from the leaf, or any other plant part, to the atmosphere is termed transpiration.

Transpiration can be extremely harmful to plants, having the potential to produce water deficits and injury caused by dehydration (Kramer, 1983). Consequently, the plant must balance carbon dioxide accumulation with water loss. For this reason, transpiration appears to be a hindrance to carbon assimilation, and ultimately, photosynthesis. However, transpiration is such a wide spread phenomena that it must serve some adaptive function. If not, natural selection would, in theory, eliminate the maladaptive feature if a viable alternative exists.

Salisbury and Ross (1978) propose several possible advantages of transpiration to plants. The first proposal could be best thought of as a consequence rather than an advantage. Plants have evolved a system to extract carbon from the atmosphere and transpiration may merely be a by-product of this system. This could be possible, but under certain conditions it appears that transpiration may be of some benefit to the plant. Transpiration may aid in the absorption of minerals from the soil, and in the subsequent movement of the minerals in the plant. Another

advantage may involve the concept of optimum cell turgidity. Transpiration may be involved in maintaining and optimum turgidity at which the cell functions best. Finally, transpiration may aid in the moderation of leaf temperatures. Evaporation of water from the leaf often plays an important role in cooling the leaf.

Whatever the advantages of transpiration, plants have evolved many processes to balance water loss with carbon dioxide accumulation, and such adaptations may include variations in plant morphology and/or physiology. Furthermore, intraspecific variation in characters affecting the photosynthesis-transpiration balance might be expected for terrestrial plant species occupying large geographic ranges. Species with large geographic ranges generally possess the ability to grow in differing climatic regions, often with distinct moisture conditions. Thus, intraspecific variation could arise due to the varying environments exerting different selection pressures (Pallardy, 1981). Balsam poplar (*Populus balsamifera* L.) is such a species, growing in moist, nutrient-rich soils on valley bottoms, stream banks, sandbars and flood plains throughout the Boreal, Great Lakes-St. Lawrence, and Acadia forest regions (Figure 1) (Hosie, 1979; Little, 1980).

Different forms of balsam poplar have been noted throughout its range. In the prairies, one form of balsam poplar has been classified as *Populus balsamifera* var. *subcordata* Hylander (Heartleaf Balsam Poplar) (Hosie, 1979). It has leaves that are broader at the base (heart-shaped) and distinctly hairy on the

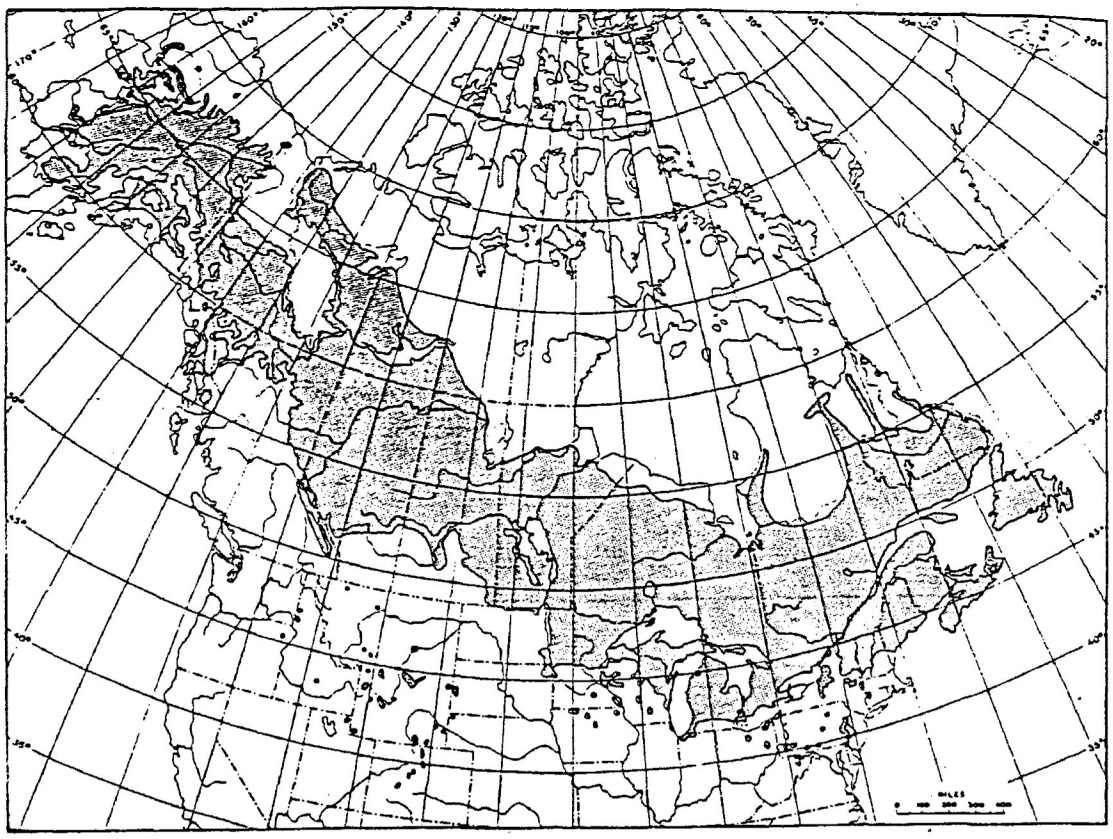


Figure 1. The range of balsam poplar (Fowells, 1965).

abaxial surface. Further to the west where the range of balsam poplar meets that of black cottonwood (*Populus trichocarpa* Torr. et Gray), individuals intermediate to the two species are abundant. Some botanists suggest that the observed variation is a response to differences in geography, rather than the interbreeding of two different species. Thus, black cottonwood is also refered to as a subspecies (*Populus balsamifera* var. *trichocarpa* (Torr. et Gray) Bradshaw) of balsam poplar.

To date, variation in physiological and morphological traits potentially affecting the water relations of balsam poplar have not been examined within the context of a provenance investigation. It is the purpose of this study to investigate the

following questions:

1) What is the extent and pattern of genetic variation in balsam poplar, with particular reference to adaptations affecting the control of transpiration?
2) How are the observed variations in traits correlated to each other and to measured transpiration rates?

II. LITERATURE REVIEW

Plants have not evolved a process or membrane that allows the assimilation of carbon dioxide while preventing transpiration. Thus, transpiration is inevitable. However, plants have evolved many adaptations to control transpiration, but no matter what the adaptation, the strategy of the plant is still the same: to assimilate carbon dioxide rapidly when atmospheric conditions promote minimal rates of transpiration or when water supply is adequate to meet the transpirational demand, and to assimilate slowly, or not at all under all other conditions (Cowan, 1977).

In essence, plants growing under conditions of frequent drought have developed one of three methods to survive the periods of water stress (Beweley, 1979). These are drought evasion, drought tolerance, and drought avoidance. Drought evaders complete the vegetative and reproductive phases of their life cycle while there is adequate moisture. Drought tolerators have the ability to endure periods of protoplasmic desiccation. Finally, drought avoiders or desiccation avoiders resist desiccation by either retarding water loss or increasing water absorption. Most woody plants are classified as drought or desiccation avoiders and, to a lesser extent, drought tolerators (Levitt, 1972).

In a review of studies pertaining to intraspecific genetic

variation in physiological and morphological traits affecting the water relations of woody plants, Pallardy (1981) proposes three major classes of adaptations. The first concerns variation in the capacity of a plant to absorb water in relation to the transpirational demand; the second, variation in plant resistance to liquid-phase water transport; and the third, variation in the control of transpiration.

Due to the complexity of the energy and matter exchange in the soil-plant-atmosphere continuum, Pallardy (1981) further divides genetic variation in the control of transpiration into the following components: variation in shoot growth, leaf size and morphology, leaf abscission, leaf cuticle, and stomatal anatomy and control.

It is beyond the scope of this study to research all possible adaptations presented by Pallardy (1981); therefore, the study and literature review will focus on variations in selected aspects of shoot and root growth, leaf size and morphology, stomatal size and frequency, stomatal conductance and transpiration rates. Furthermore, unless stated otherwise, all studies presented will have been conducted under uniform growth conditions to ensure that the reported variation is genetic in nature.

A. VARIATIONS IN SHOOT AND ROOT GROWTH

Adaptations which alter the plant's capacity to absorb water in relation to potential water loss will greatly affect the water balance of the plant (Pallardy, 1981). The relationship between

absorption and potential transpiration can be best evaluated by comparing the root absorbing surface area to the surface area of potential transpiration, but measurement of the absorptive surface area of the root is a difficult task. The mere size and delicacy of the root system makes measurement of root surface area virtually impossible. For example, a four-month-old rye (*Secale cereale*) plant had an estimated 626 km of roots (not including root hairs) with a surface area of 233 m^2 (Salisbury and Ross, 1978). Including root hairs, the estimated total length of roots and accompanying surface area increased to 11,300 km and 638 m^2, respectively. Moreover, the absorptive capacity of the root is thought to differ with root age, the transpirational demand for water, and the spacial pattern of rooting in the soil profile (Raven *et al*, 1981). To avoid many of these problems, the root/shoot weight ratio often has been used as an approximation for the relationship between water absorption and potential water loss.

The root/shoot ratio has been shown to vary intraspecifically, and furthermore, the pattern of variation is often associated with the moisture conditions at the seed source or correlated with the geographic trends in precipitation and potential evaporation. Brown (1969) studied the root systems of forty-eight provenances of Scotch pine (*Pinus sylvestris* L.), representing thirteen different locations throughout Europe. On the basis of root form and growth, the provenances were divided into three main types: Northern, Central European, and Southern.

Within the Northern (Scandanavian) type, root development and annual growing season precipitation were not correlated, possibly because temperature, not moisture, was the critical environmental factor affecting the growth and development of seedlings. However, one provenance (mongolica) from an area that had a high "Index of Aridity" (low levels of precipitation combined with relatively high growing season temperatures) had minimal root and shoot development and a higher root/shoot weight ratio than other Northern provenances. The root system was characterized by a shallow tap root with an extremely well developed network of lateral roots. It appears that the shallow depth of rooting could have been an adaptive character associated with the occurrence of permafrost at a shallow depth in the soils of the region. The large lateral root extension and the higher root/shoot ratio may be an adaptive response to the dry growing season.

Unlike the Northern provenances, the root characteristics of the Central European sources could not be related, at any level, to the climate of the seed source. Brown (1969) hypothesizes that the lack of correlation between seedling morphology and climate could be a result of free interchange of genes in the more-or-less continuous range of the species in central Europe and/or due to the climatic fluctuations of post-Pleistocene time. Brown (1969) states that there is usually a lag between climatic change and evolutionary response to that change, so that modern genotypes may not be perfectly adapted to their present environments.

Within the Southern type, the root systems of seedlings of

Spanish and Turkish origin (areas with a high "Index of Aridity") had root/shoot weight ratios higher than those of other provenances located in southern and central Europe. The root systems of the seedlings from Spain had a narrow, columnar appearance, while the Turkish seedlings had a similar appearance, but with a more extensive lateral root system. Both root systems may have developed in response to the warm, dry climatic conditions which prevail in the areas of seed collection.

Hermann and Lavender (1968) collected seed of Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco.) from north and south slopes along an elevational gradient on the western slopes of the Cascades in southern Oregon. In a growth room study, Hermann and Lavender (1968) found that the root/shoot weight ratio was higher for seedlings from populations located on the more xeric southern slopes. As elevation of the seed source increased, differences between the aspects became less, and more so for roots than for shoots. A possible explanation for the decrease in differences is that, elevation and its associated climatic variables, mainly temperature, increasingly became the dominant environmental factor, while aspect, and its associated climatic variables, mainly moisture, became less prominant as the altitude of the seed source increased. Lavender and Overton (1972) reported similar results. Grown under various temperature treatments, the seedlings from the xeric seed sources generally had higher root/shoot weight ratios. In an earlier study (Ferrell and Woodward, 1966), Douglas-fir seedlings grown from seed collected from drier, interior and moister, coastal sources were

subjected to severe drought to see if any relation between survival and root or shoot characteristics existed. Regression analysis indicated that there was no significant relationship between the number of days of survival under drought conditions and the weights of roots and shoots and the root/shoot weight ratio. However, the number of actively growing root tips showed a positive relationship with the number of days of survival. Comparisons of root weights, leaf weights, root/shoot weight ratios, and the number of actively growing root tips revealed no significant differences between coastal and interior seed sources, but only a small number of seedlings from each source were examined. In another study, Heiner and Lavender (1972) found that survival under drought conditions was positively correlated to the ability of the seedling's roots to penetrate deeply into the soil. Heiner and Lavender (1972) used seed collected from a xeric inland site and a mesic coastal site.

Cannell *et al.* (1978) studied the root and shoot relationships of loblolly pine (*Pinus taeda* L.) from nine families located on the north Coastal Plain and seven families located on the south Coastal Plain in North Carolina. They found that the superior (in terms of height growth) northern families, which grew well when under water stress, may have avoided stress by producing greater root masses and lengths proportional to their shoot weights. South Coastal families grew well only under well-watered conditions. South Coastal collection sites were characterized as being very moist, with the soil being virtually water-logged during the winter and the water table being very close to the

surface during the growing season. Other studies concerning loblolly pine have revealed similar relationships, in that seedlings from the more xeric sources exhibit greater survival under drought conditions and produce deeper root systems with a more extensive network of lateral roots (Bilan *et al*, 1978; van Buijtenen *et al*, 1976; Youngman, 1965).

This morphological trend is also apparent for silver maple (*Acer saccharinum* L.) (Kriebel, 1963; Kriebel and Gabriel, 1969). Four-year-old seedlings grown from seed collected from the drier southeastern United States possessed a large primary root with a dense mass of lateral roots. Seedlings from the wetter northeastern United States were characterized as having a shallow root system with a poorly developed primary root. Seedlings from the xeric sources had higher levels of survival when subjected to severe water stress.

Just as moisture may be limited due to climatic or geographic factors, available moisture may be limited by competing vegetation. Sands *et al* (1984) recognized from previous studies that certain families of radiata pine (*Pinus radiata* D. Don) performed better than others depending on whether or not competing vegetation was controlled. Three families were isolated for study: Family A grew well only when weeds were controlled, Family B grew poorly under both weeded and non-weeded conditions, and Family C grew well under both conditions. Root/shoot weight ratios were significantly higher for Family C when compared to both Family A and B. However, actual measurement of the surface area of the roots and needles

for each family indicated that the root/shoot surface area ratios were similar for all three families. Sands *et al* (1984) indicated that the surface area measurement was more representative of the relationship between potential water absorption and transpiration and postulated that the inherent differences in family response to weed control (moisture and availability) were more likely attributable to contrasting tissue sensitivities to moisture status, and hence, gas exchange characteristics rather than relative differences in absorbing and transpiring surface areas. This may be so; however, differences in gross and internal morphologies of the needles and roots, as indicated by the differing root/shoot weight ratios and similar root/shoot surface areas, were not investigated.

From the previous discussion, it can be postulated that many plants growing in areas of frequent drought have adapted to limited moisture availability by altering root morphology and growth to maximize soil-water availability, thereby, improving the photosynthesis-transpiration balance. However, not only has the root system been altered to increase moisture availability, but in many instances, the growth and morphology of the shoot has also been altered to decrease the transpirational demand for water.

Upon studying two populations of *Potentilla glandulosa* Lindl., a long-lived herbaceous perennial, Teeri (1978) found that field collected plants had different phenotypic responses to drought following simulated winter conditions. The inland population, which is native to an inland climate with

unpredictable droughts occurring at any time during the year, produced a compact rosette of small leaves and shed the larger summer leaves in response to low autumn temperatures, thereby reducing total plant leaf area. Consequently, the inland plants could begin growth in the spring in the compact rosette phenotype, which is much less sensitive to drought than the larger-leaved summer phenotype. The coastal population, located in a coastal mediterranean climate with highly predictable annual cycles of winter rain and summer drought, did not exhibit the low temperature induced change in shoot morphology and were relatively more sensitive to drought.

Roy and Mooney (1987) also found that the morphology of the shoot also differed for individuals of *Heliotropium curassavicum* L. collected from coastal and desert areas in California. Plants were vegetatively propogated and grown under two humidity regimes. Coastal plants grew more prostrate, with an average leaf height of 5 cm. Desert plants grew more erect, with an average leaf height of 15 cm. Results appear to contradict the findings of Roy and Mooney (1982), in that the morphology of the individuals from the more xeric desert populations appear to favor higher transpiration rates (larger, more erect plants). However, upon closer examination of the desert individuals, it was found that leaf angle, as measured from the horizontal plane, of the desert plants were almost twice that of the coastal plants; an adaptation which should decrease leaf temperature, and subsequently, decrease transpiration rates. Furthermore, it was found that the desert plants only grew in the vicinity of spring or

irrigation drains where water is continuously available in the soil, and thus, an adequate supply of moisture would be available to meet the higher transpirational demand. Hence, the peculiarity of the adaptive characteristics probably results from temperature being the predominant selective force (Roy and Mooney, 1982).

In many provenance studies, it has been observed that individuals or populations from xeric sites exhibit less shoot growth than individuals from mesic locations. This has been reported for red maple (*Acer rubrum* L.) (Townsend and Roberts, 1973), balsam fir (*Abies balsamea* (L.) Mill.) (Lester, 1970; Lowe *et al*, 1977), red ash (*Fraxinus pennsylvanica* Marsh.) (Meuli and Shirley, 1937), western white pine (*Pinus monticola* Dougl.) (Squillace and Bingham, 1958), black pine (*Pinus nigra* Arnold) (Wright and Bull, 1962; Lee, 1968), yellow pine (*Pinus ponderosa* Dougl. ex Laws.) (Squillace and Silen, 1962), loblolly pine (Wells and Wakeley, 1966; Woessner, 1972a), eastern cottonwood (*Populus deltoides* Bartr.) (Kelliher and Tauer, 1980), Douglas-fir (Griffin and Ching, 1977) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) (Eickmeier *et al*, 1975).

In the above studies, actual rate of growth or the length of growing season was not measured, but from other studies it is apparent that individuals from xeric habitats tend to have slower growth rates and shorter growing seasons relative to individuals from mesic habitats when grown under conditions of adequate moisture. Slower growth rates have been noted for more xeric populations or individuals of *Diplacus aurantiacus* (Curtis) Jeps. (Mooney and Chu, 1983), *Heliotropium curassavicum* (Mooney,

1980), black spruce (*Picea mariana* (Mill.) B.S.P.) (Morgenstern, 1969), radiata pine (Bennett and Rook, 1978; Sands *et al*, 1984), loblolly pine (Woessner, 1972b; Cannell *et al*, 1978), eastern cottonwood (Drew and Bazzaz, 1978) and Douglas-fir (Zavitkovski and Ferrell, 1970). Hermann and Lavender (1968) noted that not only did the seedlings of the more mesic north slope populations of Douglas-fir grow faster, but that the length of the growing season was also longer than that of the seedlings from the more xeric south slope populations. Slower shoot growth will decrease the amount of surface area exposed to the atmosphere, thereby, decreasing potential transpiration (Grime, 1979) and a shorter period of shoot growth will also allow for longer periods of root growth (Cannell and Willet, 1976). Thus, in areas of limited moisture, the relationship between the plant's capacity to absorb water as compared to potential transpiration will be optimized.

B. VARIATIONS IN LEAF SIZE AND MORPHOLOGY

Genetic variation in leaf size and shape have been detected and correlated with differing moisture conditions for a variety of species. Smaller leaves have been associated with more xeric seed origins for many species. Ying and Bagely (1976), studying eastern cottonwood, found that seedlings of provenances collected from the drier western portions of the species' range in the United states had smaller leaves. Smaller single leaf areas were also noted for xeric provenances of yellow birch (*Betula allenghensis* Britton) (phenotypic study) (Dancik and Barnes, 1975), eastern

redbud (*Cercis canadensis* L.) (Donselmann, 1976; Abrams, 1986, 1988), *Heliotropium curassavicum* (Mooney, 1980; Roy and Mooney, 1987), *Pinus caribaea* Morelet. (Venator, 1976) and Scotch pine (Wright and Bull, 1963; Ruby, 1967). Ladiges (1974) reported that seedlings from populations of *Eucalyptus viminalis* Labill. growing in xeric habitats produced narrower leaves than those from populations growing in mesic environments. Similar results were reported by Phillips and Ried (1980), who found a clinal trend in the shape of *Eucalyptus viminalis* leaves as provenances extended inland from the coast. Seedlings from the xeric coastal provenances were characterized as having long, lanceolate leaves, and as one moved inland to more mesic habitats, the leaves became more broad and cordate.

Salazar (1983) found that needle width did not vary significantly among populations of *Pinus caribaea*; however, needle length and thickness was greater for seedlings from xeric provenances. Differences in thickness were partially attributed to the presence of more cells (transfusion tissue) around the resin ducts and to a greater number of hypodermal cells, both adaptations thought to conserve moisture. Studies of a xeric ecotype of loblolly pine (Thames 1963; Knauf and Bilan, 1977) indicated adaptations similar to those reported by Salazar (1983) for *Pinus carabaea*. Thames (1963) noted that extra hypodermal cells were packed between rows of stomata and that the epidermal cell layer was significantly thicker. Additionally, results from Knauf and Bilan's 1977 study indicate that the xeric ecotype seedlings have significantly greater volumes of mesophyll

tissue and a thicker cuticle. Thicker leaves and/or greater specific leaf weights (leaf weight divided by leaf area) have been observed for seedlings of xeric provenances of eastern redbud (Donselmann and Flint, 1982; Abrams, 1986, 1988), lodgepole pine (*Pinus contorta* Dougl. ex Loud.) (Jeffers and Black, 1963), black pine (Lee, 1968) and eastern cottonwood (Drew and Bazzaz, 1978).

In addition to variations in leaf length, width, and thickness, there may be variation in the form of the leaf margin. A phenotypic study conducted by Baranski (1975) showed that leaves of seedlings of white oak (*Quercus alba* L.) from xeric habitats were more dissected than those of seedlings growing in mesic environments. Leaves of black pine from xeric provenances also had a higher number of leaf serrations per unit length of leaf margin (Lee, 1968).

There appears to be two general adaptations of leaf shape and size that function to limit transpiration rates: firstly, seedlings from drier habitats tend to have smaller leaves; and secondly, the leaves tend to be thicker. Thicker leaves may contain more mesophyll tissue, as well as thicker epidermal and hypodermal cell layers and a thicker cuticle. The additional mesophyll cells may permit greater carbon dioxide assimilation at times of favorable moisture conditions, while the presence of the other thicker cell layers and cuticle may impede water loss from the leaf (Raven *et al*, 1981). Although the needles or leaves were thicker, studies by Thames (1963), Knauf and Bilan (1977) and Donselmann and Flint (1982) indicate that the ratio of surface area to volume can be significantly lower. Thus, the potential

evaporative surface in contact with the surrounding air is minimized for a given leaf volume. In conclusion, both thicker protective layers (hypoderm, epiderm and cuticle), more photosynthesizing tissue and a decreased surface area to volume ratio will tend to decrease the potential transpirational demand for water.

Smaller, narrower, and/or more highly dissected leaves will also decrease potential rates of transpiration under certain environmental conditions (Pallardy, 1981). Smaller leaves will have a smaller boundary layer, and hence, a lower boundary layer resistance to sensible heat transfer from the leaf to the air (Campbell, 1977). At times when the temperature of the air is higher, smaller leaves will be cooler than larger leaves due to the smaller boundary layer resistance to heat transfer. The cooler leaf temperature will decrease the vapor pressure difference between the intercellular spaces of the leaf and the surrounding air, consequently lowering transpiration rates. However, one problem exists, the smaller boundary layer will also have a lower resistance to movement of water vapor from the leaf to the air (Kramer, 1983). The two effects seem to compensate for each other: one decreases potential transpiration, while the other increases potential transpiration. Although the mechanics are not fully understood, it is known that a reduction in leaf size will reduce transpiration rates in drier environments (Pallardy, 1981).

C. VARIATIONS IN STOMATAL ANATOMY AND CONTROL

The majority of water transpired by a plant passes through the stomata. Therefore, any adaptation affecting the density, distribution, size and/or control of the stomata might affect both the quantity and the pattern of water loss (Pallardy, 1981).

Studies by Thames (1963) and Knauf and Bilan (1974, 1977) have shown that loblolly pine needles from seedlings of more xeric provenances have fewer stomata per unit needle surface area and volume. This is due to larger distances between stomatal rows and fewer stomata per unit length of row. In a phenotypic study of several populations of *Pinus caribaea*, Salazar (1983) noted that two of the populations that grew in areas with a long, dry growing season were also characterized as having lower stomatal densities. However, Donselmann and Flint (1982) found that stomatal density decreased and stomatal size (mean perimeter) increased for seedlings of eastern redbud as net precipitation for the seed source increased. Moreover, the total perimeter of stomata per unit leaf area increased as values of net precipitation increased. Further studies of eastern redbud by Abrams (1986, 1988) also showed that the seedlings from more xeric provenances had significantly more stomata per unit leaf area. Higher stomatal densities and smaller stomata (as indicated by measurement of guard cell length) were also found for seedlings from xeric provenances of *Heliotropium curassavicum* (Roy and Mooney, 1987). Seedlings of southern slope populations of grand fir (*Abies grandis* (Dougl. ex D. Don)

Lindl.) also had more stomata per unit leaf area (Zobel, 1973) (phenotypic study). Variations in stomatal density and dimensions have also been observed among populations for several oak species (*Quercus mongolica*, *serrata*, *variabilis* and *acutissima*) (Kim *et al*, 1986), black walnut (*Juglans nigra* L.) (Carpenter, 1974) and longleaf pine (*Pinus palustris* Mill.) (Snyder *et al*, 1977), but information pertaining to correlations with moisture characteristics were not provided. To conclude, there appear to be conflicting observations, in that stomatal density both decreases and increases, depending upon the species, in response to a drier environment. However, the study by Donselmann and Flint (1982) hints that stomatal pore area (a function of both stomatal density and size) may be a more important factor, and may be smaller for populations from drier habitats, despite increased or decreased stomatal density.

Intraspecific variation in stomatal responses to experimentally manipulated environmental factors have been reported for a number of species. In an earlier study by Pharis and Ferrell (1966), it was shown that seedlings from drier, interior populations of Douglas-fir survived for longer periods of time when placed under conditions of extreme soil moisture deficites. Moreover, among interior and coastal populations, south slope (more xeric) seedlings were more drought-hardy than north-slope (more mesic) seedlings. Subsequent studies by Zavitkovski and Ferrell (1968, 1970) revealed that seedlings from mesic populations of Douglas-fir had higher rates of transpiration than seedlings from xeric populations at comparable soil moisture

contents. Similar patterns of variation were also observed for seedlings of red maple from mesic and xeric sites (Townsend and Roberts, 1973).

Under conditions of increasing moisture stress, Jackson *et al.* (1973) noted large differences in transpiration rates among seven randomly selected clones of radiata pine. Although transpiration rates followed much the same trends over the drying cycle, the range of differences in overall rates of transpiration was 50 percent (i.e. clone 457 had transpiration rates 50 percent higher than that of clone 456). Closer examination of clones 456 and 457 by Bennett and Rook (1978) verified the findings of Jackson *et al.* (1973) and also revealed that the stomatal resistance to water vapor diffusion was approximately twice as great for clone 456 than clone 457 under conditions of increasing vapor pressure deficits (decreasing humidity). In another study with radiata pine, Sands *et al.* (1984) observed patterns and values of stomatal resistances for seedlings of three open -pollinated families which differed in response to weed control, and hence, differences in root-zone moisture status. Seedlings from family A (good growth only when weeds are controlled) had higher stomatal resistances under adequate soil moisture conditions than seedlings from both family B (poor growth under all conditions) and family C (good growth under all conditions), which had similar stomatal resistances. During a drying cycle, stomatal resistance increased, in response to decreasing needle water potentials, at a greater rate for seedlings from family A than for seedlings from families B and C. However, needle water

potentials, for any given soil water potential, were more negative for seedlings from family C, than family B and family A, in that order. Thus, information suggests that seedlings from family A are well adapted to conserve limiting supplies of moisture, but are at a disadvantage when competing with more freely transpiring weed species. Seedlings from family B and C have lower stomatal resistances under conditions of moisture stress; however, it appears that family C seedlings are more sensitive to decreasing levels of moisture than family B seedlings due to the relation between soil water potential and needle water potential. Seedlings of families B and C had similar needle water potentials at higher soil water potentials, but as soil water potentials decreased, the needle water potentials of family C seedlings decreased at a more rapid rate. Thus, seedlings of family C were more sensitive to changes in the moisture status of the soil.

Variation in stomatal response to increasing moisture stress has been observed among provenances in a number of other woody species. Transpiration rates were found to be similar under conditions of high soil and plant water potentials for two contrasting seed sources of Douglas-fir: a humid coastal source and a drier inland source (Unterscheutz *et al*, 1974). However, as the soil water potentials decreased, the plant water potentials decreased and the transpiration rates for seedlings from the xeric inland source decreased more rapidly. Unlike the seedlings from the xeric source, the seedlings from the mesic coastal provenance continued to transpire at higher rates and the plant water potentials decreased slightly. Only when soil water potentials

reached significantly lower levels, did the transpiration rates of the mesic source seedlings begin to decrease. Moreover, at the lower water potentials the transpiration rates of the seedlings from the mesic seed source decreased at a more rapid rate. Transpiration rates for seedlings from both sources were similar at very low soil and plant water potentials. Thus, seedlings from the xeric seed source were more sensitive to changes in internal water potentials.

For a more xeric provenance of loblolly pine, seedling transpiration rates and percentage of open stomata showed a greater decline over a drying phase when compared to the results obtained from seedlings of a more mesic provenance (Bilan *et al*, 1977). Average needle moisture contents were significantly higher in the mesic than the xeric provenance seedlings.

Kelliher and Tauer (1980) measured stomatal resistances of four clones of eastern cottonwood: two from a xeric site and two from a mesic site. The clones were subjected to three moisture stress treatments: no stress, moderate stress and severe stress. Differences in stomatal resistances between plants from the two sites were discernable with or without stress. In contrast to the previous studies that measured transpiration rates and/or stomatal resistance, stomatal resistances were greatest for the wet-site plants under all treatments. Furthermore, stomatal resistances of the wet-site clones increased with increasing moisture stress, while stomatal resistances of the dry-site plants did not increase substantially. Similar results were found for seedlings grown from eastern redbud seed collected from

three contrasting environments in Kansas (Abrams, 1988). Seedlings from the xeric provenances maintained significantly lower leaf resistances under drought conditions than did the seedlings from the other seed sources. By the end of the drying phase, stomatal resistance had increased by 70 and 60 percent, respectively, for seedlings from the mesic and the xeric provenances.

In another study, Eickmeier *et al.* (1975) collected eastern hemlock seed from two sites in Wisconsin. Seedlings were established in a hydroponic solution and twenty-eight weeks after germination, the seedlings were subjected to two temperature and two water stress preconditioning treatments. In the absence of water stress preconditioning treatments, transpiration rates were comparable for both sources. However, high levels of water stress killed most northern provenance (mesic) seedlings and reduced transpiration rates by 75-80 percent for the surviving seedlings. Most of the southern provenance (xeric) seedlings survived the high levels of water stress and transpiration rates were only reduced by 25 percent. Stomatal resistance to water vapor loss was greater for seedlings from the southern provenance under non-stressed conditions. Increases in moisture stress had little effect on stomatal resistances for seedlings of the more xeric southern provenance, but caused a large increase for the mesic northern provenance seedlings.

Intraspecific variation in stomatal responses to atmospheric environmental factors have also been reported. Mooney and Chu (1983) collected cuttings from a high-humidity

coastal population and a low-humidity interior population of *Diplacus aurantiacus*. Cuttings were vegetatively propagated and grown at either 35 or 90 percent humidity and then exposed to different water vapor concentration gradients. Plants from both populations reacted to increases in water vapor concentration gradients by increasing stomatal resistance. Populations did not differ in response to varying water vapor concentration gradients when the seedlings received the low humidity preconditioning treatment. However, when preconditioned at 90 percent humidity, coastal seedlings had lower stomatal resistances and higher transpiration rates at all water vapor concentration gradients. A phenotypic study by Korner and Bannister (1985) also found that *Nothofagus menziesii* (Hook. f.) Oerst. seedlings from more humid environments increased stomatal resistance at lower vapor pressure deficits and closure was more rapid as concentration gradients increased. A growth chamber study of a desert and a coastal population of *Heliotropium curassavicum* showed that stomatal resistances were similar for the two populations regardless of the drastic air humidities of their habitats (Roy and Mooney, 1982). Thus desert plants, growing in their natural habitat, would have much higher transpiration rates due to higher water vapor concentration gradients and the lower stomatal resistances to water vapor diffusion. Further analysis of internal plant water potentials and the plant's micro-habitat revealed that possible lethal injuries due to dehydration were avoided because internal resistances to water flow were very low and the plants only grew in habitats with adequate soil moisture availability.

Thus, lethal or injurious internal water potentials were avoided because adequate moisture was available to meet the high transpirational demand.

D. CONCLUDING REMARKS

In summary, intraspecific variation in the water relations of woody plants is very complex, reflecting the complexity of the energy and matter exchange in the soil-plant-atmosphere continuum. Often it appears that the results for one species conflict with those of another, but this is the result of having incomplete information. If all information concerning the water relations of a particular plant species could be gathered and synthesized, a virtually impossible task, the end product would, in all likelihood, point towards the optimization of growth and survival by balancing carbon assimilation with water loss: the photosynthesis-transpiration compromise.

III. MATERIALS AND METHODS

From 1982 to 1984, shoot cuttings were collected from approximately fifty trees in each of four provenances located on a latitudinal transect from northern Wisconsin (45°N latitude) to Bearskin Lake, Ontario (54°N latitude) (Table 1). Sample trees in each provenance were selected without bias and were located at least one kilometer apart, so as to minimize the probability of selecting ramets of a single, naturally-occurring clone.

Table 1. Name, longitude and latitude of the sampled provenances.

Provenance	Longitude	Latitude
Northern Wisconsin	90°W	45-46°N
Thunder Bay	90°W	48-49°N
Pickle Lake	90°W	50-51°N
Bearskin Lake	90°W	53-54°N

Collected cuttings were vegetatively propagated and maintained in a nursery near Lakehead University in Thunder Bay, Ontario. In 1984, a provenance trial was established using cuttings from the nursery material. The provenance trial was installed using a split-plot design. There were five blocks, with provenances (whole-plots) randomly located in each block, and clones (split-plots), which were represented by three ramets,

randomly located within each provenance block.

A. DATA COLLECTION

1. Field Provenance Trial

Three of the five blocks from the field provenance trial established in 1984 were used in this study. One ramet per clone was observed per block. Originally, clones were to be randomly selected from the fifty clones collected from each provenance, but this was not possible. Survival in the field provenance trial was low in some of the blocks. Furthermore, to eliminate the possible confounding effects of disease and insects, clones and ramets were selected from relatively disease- and pest-free material only. Nine clones per provenance were selected and are listed in Table 2.

Table 2. Selected clones for study from each of the four provenances of balsam poplar.

Clone	Provenance			
	Northern Wisconsin	Thunder Bay	Pickle Lake	Bearskin Lake
1	201	001	102	303
2	219	006	112	308
3	222	008	119	314
4	229	015	122	319
5	233	024	135	322
6	238	034	137	326
7	240	037	141	330
8	242	043	142	337
9	245	044	149	345

The following traits were measured:

1) transpiration rate,
2) stomatal conductance,
3) internode length,
4) stomatal density,
5) stomatal length,
6) petiole length,
7) single-leaf abaxial area,
8) single-leaf oven-dry weight,
9) specific leaf weight (SLW), and
10) leaf shape.

a. Transpiration Rates and Stomatal Conductance

Transpiration rates and stomatal conductance were measured on a per unit leaf area basis using the LI-1600 Steady State Porometer, manufactured by LI-COR Inc. (Figure 2). The LI-1600 cuvette was clamped to the leaf, creating a seal, and water loss was determined by maintaining a constant vapor density in the cuvette (LI-COR, Inc., 1986). More precisely, dry air (a relative humidity of two percent) is pumped into the cuvette at a measured rate to obtain a balance, at a predetermined humidity, between the flux of water transpired by the leaf and the flow of moist air from the cuvette. Transpiration was related to the volumetric flow rate F (cm^3/s) by

$$E = (\rho_c - \rho_a)/(F/A)$$

where E ($\mu g/cm^2 s$) is the transpiration rate; ρ_c ($\mu g/cm^3$) is the water vapor density in the cuvette; ρ_a ($\mu g/cm^3$) is the water vapor density of the dry air entering the cuvette, and A (cm^2) is the area of the sample (LI-COR Inc., 1986). Stomatal resistance

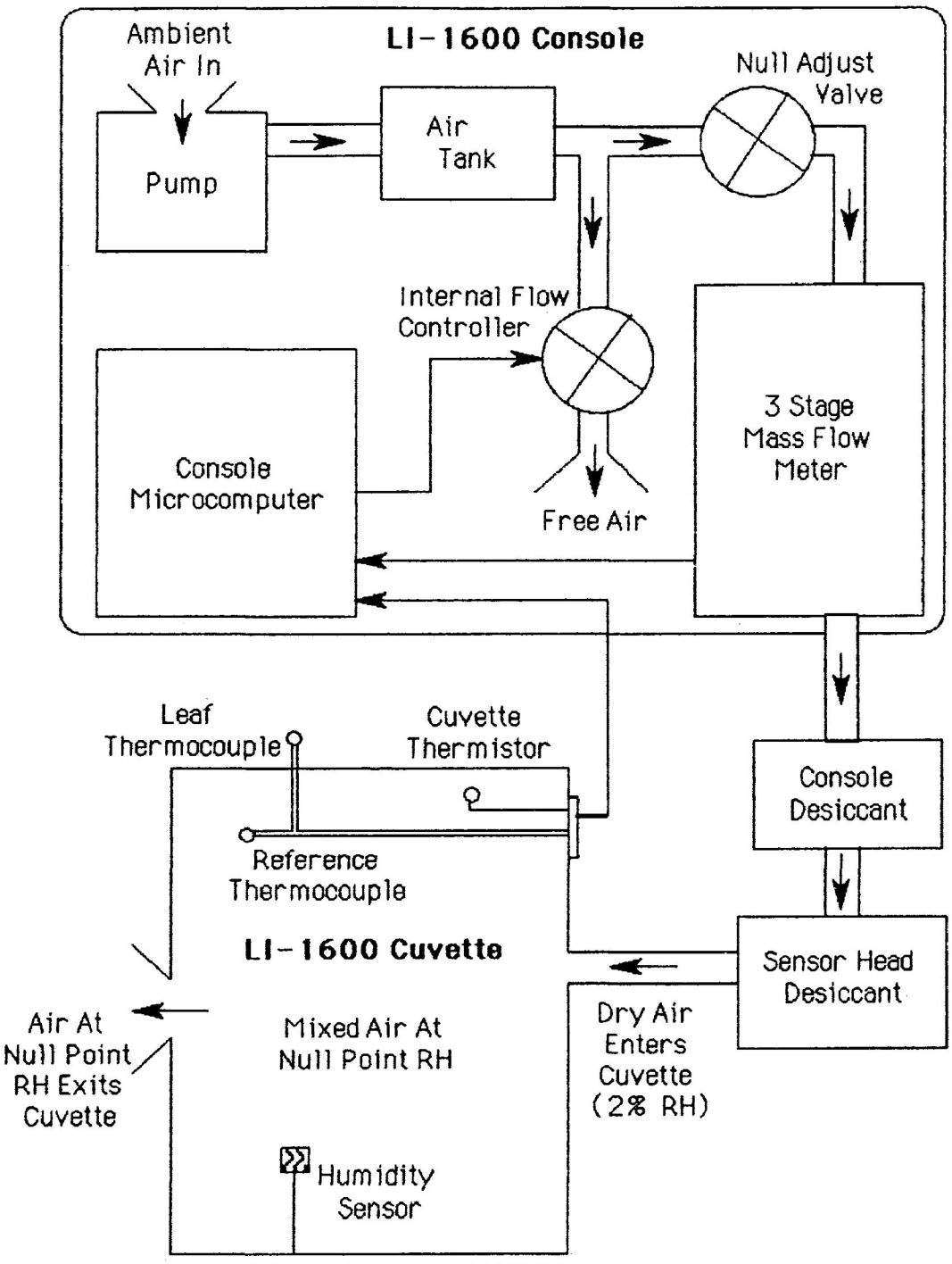


Figure 2. LI-1600 System Diagram (LI-COR Inc., 1986).

R_s (s/cm) was then determined via:

$$R_s = (A/F) * ((\rho_1 - \rho_c)/(\rho_c - \rho_a)) - R_b$$

$$=((\rho_1 - \rho_c)/E) - R_b$$

where ρ_1 ($\mu g/cm^3$) is the water vapor density in the leaf (assumed to be saturated with water) and R_b (s/cm) is the boundary layer resistance of the leaf (assumed to be 15 s/cm). The LI-1600 stores saturation vapor density and temperature information, used in the calculation of ρ_a, ρ_c and ρ_1, in its console microcomputer memory. Stomatal conductance C_s (cm/s) was calculated by taking the inverse of stomatal resistance.

Three fully-expanded sun leaves, produced during indeterminate shoot growth, were sampled for each ramet (Figure 3). The leaves were located, if possible, on a single, lateral long-shoot at mid-crown on the south aspect of each ramet. One reading was taken from the abaxial surface of each leaf at the point of maximum leaf width, between the mid-vein and leaf margin (Figure 3). Results from a preliminary test indicated that transpiration rates from the adaxial leaf surface were negligible when compared to rates of transpiration from the abaxial leaf surface. Complete sets of measurements were taken on four days (July 2, 3, 4 and 7, 1988) from approximately 10:00 am to 12:00 am. Temperature, relative humidity, and light levels were recorded for each series of measurements using the LI-1600. A summary of these values are presented in Table 3.

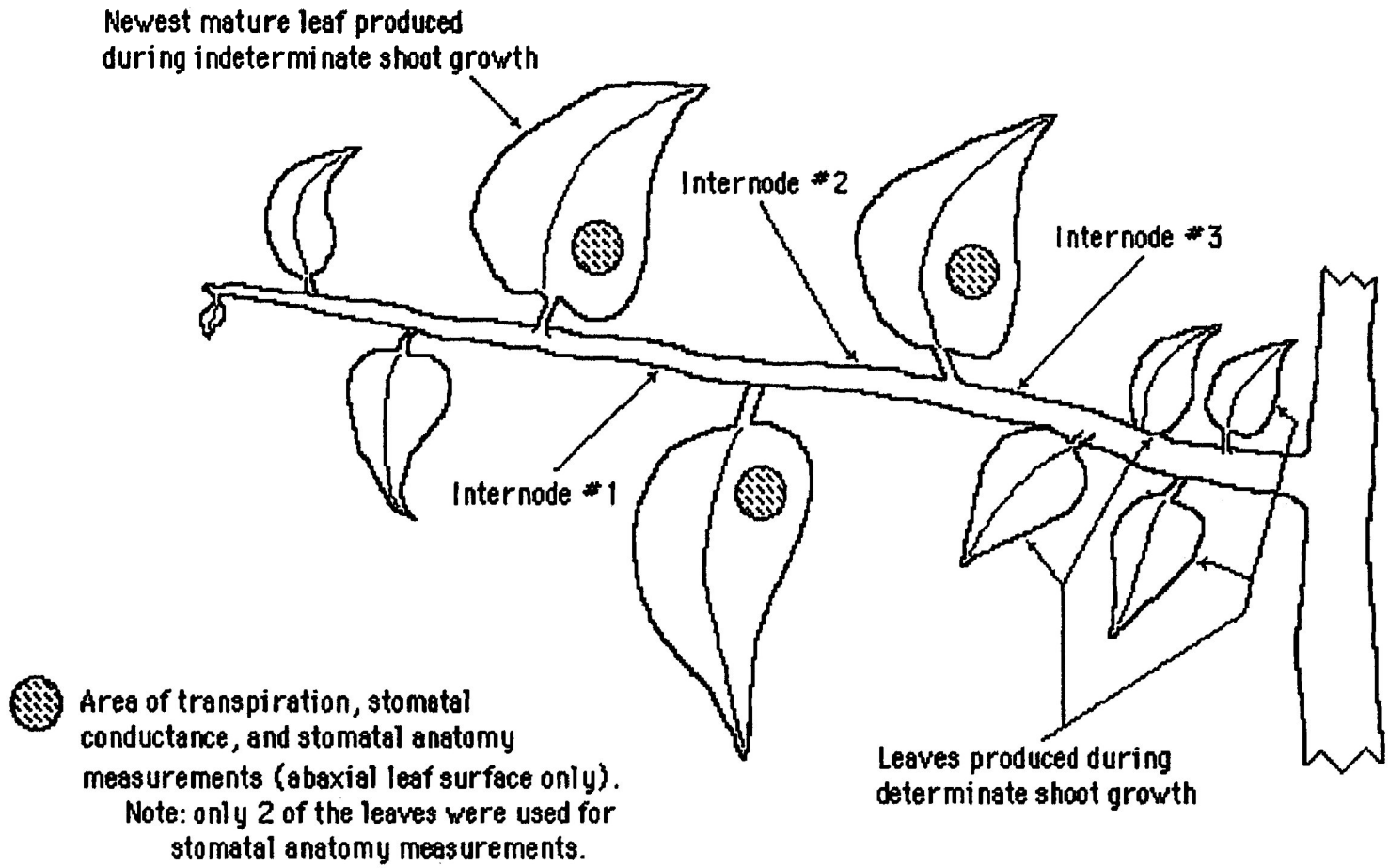


Figure 3. Location of transpiration rate, stomatal conductance, internode length, and stomatal density and length measurements for the field provenance trial.

Table 3. Summary of light levels, relative humidities, and temperatures recorded during the measurement of transpiration rates and stomatal conductance for the field provenance trial.

Day	Block	Light ($\mu E/(m^2 s)$)	Relative Humidity (%)	Temperature (°C)
July 2, 1988	1	1477	31.8	27.7
	2	1149	37.2	25.8
	3	831	55.8	21.0
July 3, 1988	1	1446	47.9	24.7
	2	1156	49.4	25.2
	3	1621	45.6	25.9
July 4, 1988	1	841	59.3	19.8
	2	1504	46.6	25.4
	3	1300	50.0	22.6
July 7, 1988	1	1389	48.7	27.3
	2	1175	56.3	25.6
	3	491	62.6	21.1

b. Internode Length

The same lateral long-shoot used in the measurement of transpiration rates and stomatal conductance was used for the measurement of internode lengths. The first three internodes below the newest, fully-expanded leaf (Figure 3) were measured to the nearest millimeter.

c. Stomatal Density and Length

The two outermost leaves used in the transpiration and stomatal conductance sampling study were used for the stomatal study. Impressions (approximately 2 cm^2) of the abaxial leaf surface were taken with stainless nail polish (Dobrenz *et al*, 1969). All samples were taken from the area of the leaf where

transpiration rates and stomatal conductance were measured. Leaf surface replicas were stored on strips of adhesive tape (Scotch Magic - Transparent Tape). At the time of analysis, the tape and replicas were mounted on microscope slides and analyzed under a light microscope. Stomatal density was determined at 400x magnification by counting the number of stomata in ten fields, each with an area of 0.166 mm^2. Stomatal length, defined as the length of the stomatal complex (Pallardy and Kozlowski, 1979), was measured at 1000x magnification with the aid of an ocular micrometer. Ten stomatal complexes were measured per leaf replica.

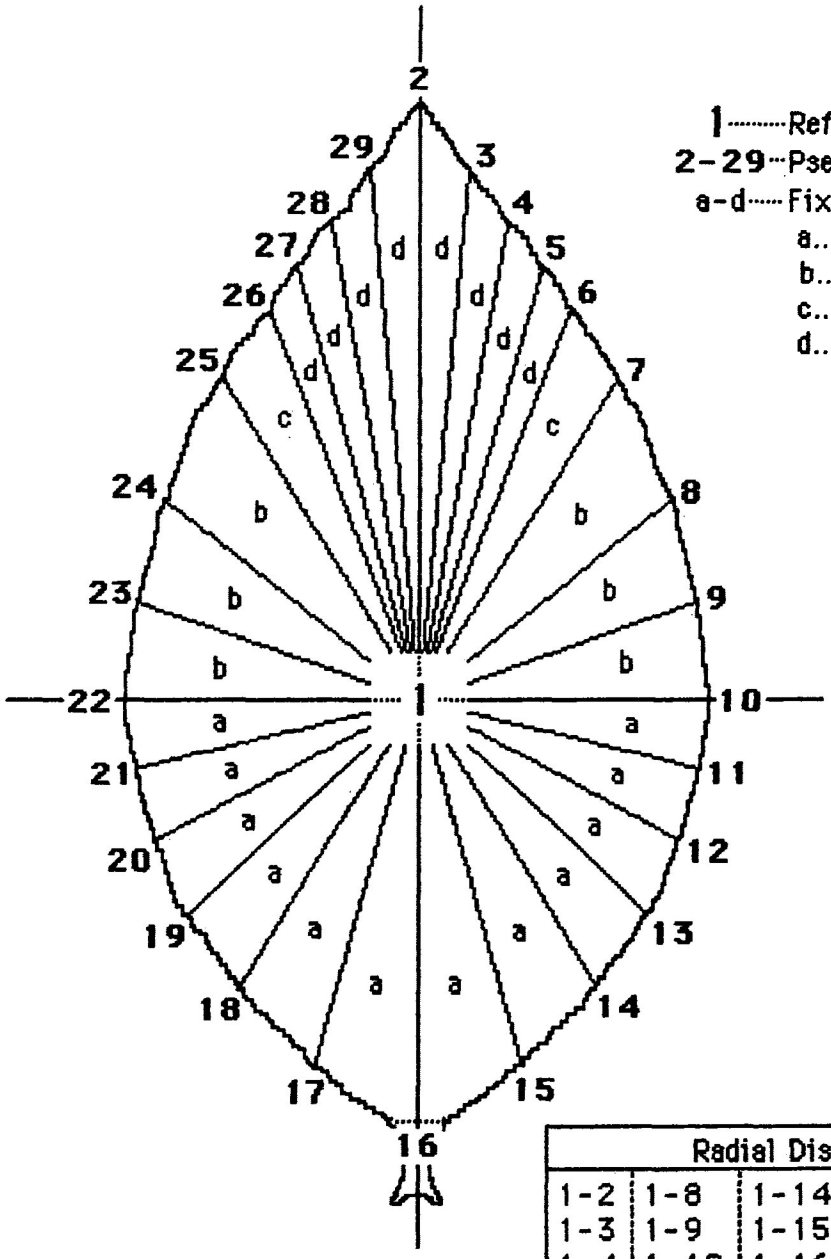
d. Single-Leaf Abaxial Area, Single-Leaf Oven-Dry Weight, Specific Leaf Weight, and Petiole Length

Once stomatal impressions were collected, the two leaves were removed from the ramet, photocopied, and placed in a forced-draft oven at 70°C for forty-eight hours to obtain average single-leaf oven-dry weights. Photocopies of the leaves were used in the determination of petiole length, average single-leaf abaxial area, and leaf shape. Petiole length was measured to the nearest millimeter. Leaf area was measured using a PLANIX 7 Tamaya Digital Planimeter. Each leaf was measured five times and averaged to obtain a single measurement of leaf area. Specific leaf weight (mg/cm^2), an estimator of leaf thickness and/or the amount of leaf tissue for a given leaf area, was calculated by dividing leaf weight by leaf area.

e. Leaf Shape

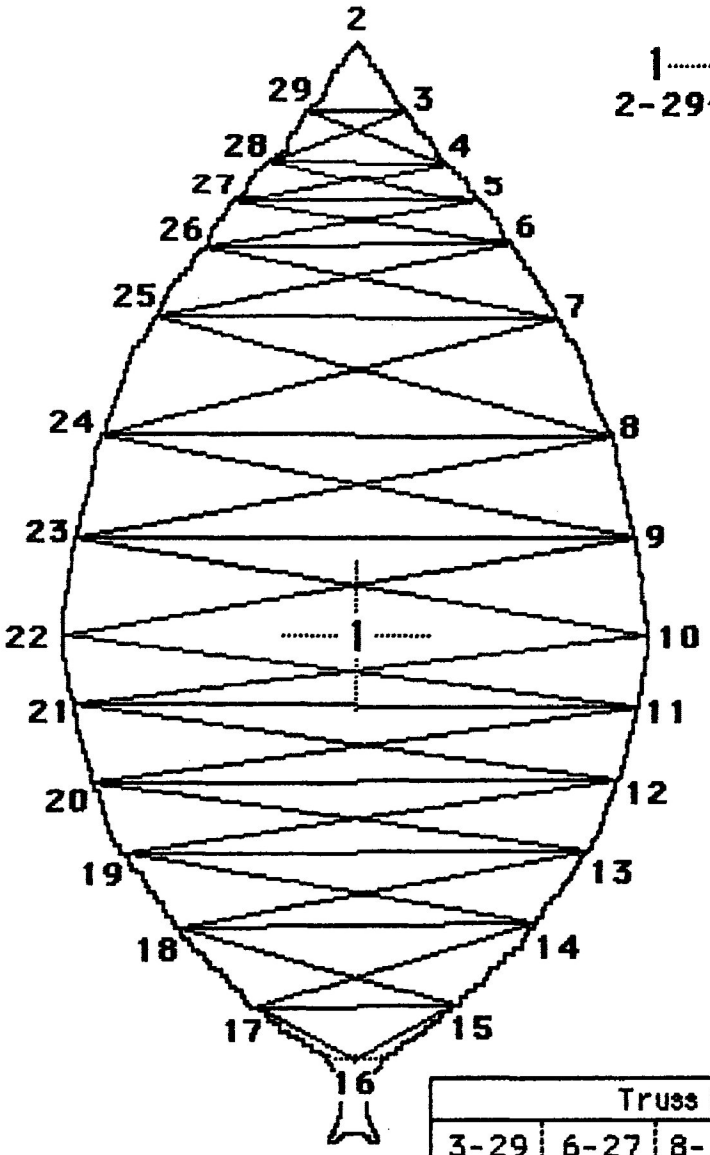
Leaf shape was quantified using the photocopies of the leaves mentioned in the previous section. The outline of the leaves was established by twenty-eight pseudolandmarks (Dickinson *et al*, 1987), using a digitizing tablet attached to an Apple IIe microcomputer. Pseudolandmarks were located along the margin of the leaf at fixed angles from a reference point labelled as 1 in Figure 4. To standardize measurements, the reference point was located on the mid-vein of the leaf at the point of maximum leaf width, so that the line connecting pseudolandmarks 22 and 10 spans the widest point of the leaf while its perpendicular passes through the leaf tip (pseudolandmark 2) and the leaf base (pseudolandmark 16).

From the twenty-eight pseudolandmarks, stored as (x,y) coordinates by the digitizing pad and computer, twenty-eight radial distances (Figure 4) and thirty-eight truss distances (Figure 5) were calculated using a program developed by Dr. W.H. Parker of the School of Forestry at Lakehead University. The program calculates the distances using standard trigonometric functions. Leaf shape is described by the relative magnitude of these distances. The sixty-six distances were calculated so that leaf shape is sampled redundantly. Redundancy of measurement is needed for the statistical analysis of leaf shape, which will be discussed in further detail in Section III.B.1.



Radial Distances				
1-2	1-8	1-14	1-20	1-26
1-3	1-9	1-15	1-21	1-27
1-4	1-10	1-16	1-22	1-28
1-5	1-11	1-17	1-23	1-29
1-6	1-12	1-18	1-24	
1-7	1-13	1-19	1-25	

Figure 4. Leaf of balsam poplar, in outline, showing the reference point (1) located along the mid-vein at the point of maximum leaf width, the pseudolandmarks (2-29) located along the margin of the leaf at fixed angles (a-d) from the reference point, and the 28 radial distances employed in the multivariate analysis.



Truss Distances				
3-29	6-27	8-23	11-20	14-18
3-28	6-26	9-24	12-21	14-17
4-29	6-25	9-23	12-20	15-18
4-28	7-26	9-22	12-19	15-17
4-27	7-25	10-23	13-20	15-16
5-28	7-24	10-21	13-19	16-17
5-27	8-25	11-22	13-18	
5-26	8-24	11-21	14-19	

Figure 5. Leaf of balsam poplar, in outline, showing the network of truss distances employed in the multivariate analysis.

2. Greenhouse Provenance Trial

In March of 1988, leafless long-shoots were collected from the previous seasons growth of clonal material growing in the nursery near Lakehead University. Long-shoots were collected from single ramets of the same clones used in the field provenance trial. To minimize the possible effects of preconditioning, long-shoots were gathered at mid-height from the southern aspect of each ramet's crown.

The long-shoots were stored in a cooler at 3°C and 100% humidity until May 6, 1988. The long-shoots were then cut into 20 cm segments, with each segment having the following characteristics:

1) at least two buds,
2) a diameter between 0.5 and 1.0 cm,
3) no signs of disease, and
4) no physical signs of damage or desiccation.

Cuttings were soaked in a systemic fungicide (Benomyl), rooted in 6 litre plastic pots containing a 60:40 peat:vermiculite potting-soil mixture, and placed in a greenhouse. Up to three cuttings were rooted in each pot, with each clone being represented by three pots. Six litre plastic pots were used to allow for unrestricted root growth during the experiment. After successful rooting was observed, excess ramets were culled, leaving one ramet per pot.

In the greenhouse, ramets were organized into a randomized complete block design. There were three blocks, with four provenances and nine clones per provenance located in each block. Each clone was represented by a single ramet in each block.

Plants were watered daily and fertilized once a week with a 200 ppm, 20:20:20 water-soluble fertilizer, which contained essential micronutrients. Natural photoperiods were used and the temperature varied, from 10-15°C at night to 25-30°C during the day. Plants were periodically treated with Benomyl and Pentac Aquaflow Miticide to irradicate any insect pests and pathogens.

On July 11, after approximately three months of growth, sampling began. The same traits measured in the field provenance trial were measured in the greenhouse provenance trial. Moreover, the same procedures were used for most of the measurements. Transpiration rates and stomatal conductance were measured on July 11, 12, 13 and 14 between 10:00 am and 12:00 am. A summary of temperatures, relative humidities, and light levels, recorded at the time of measurement is presented in Table 4. Two fully-expanded leaves, produced during indeterminate shoot growth, were sampled for each ramet. The mature leaves were located at the top of the shoot immediately below an immature leaf (Figure 6). The same two leaves were used to assay remaining traits, except internode length. The first three internodes below the newest fully-expanded leaf (Figure 6) were used to sample internode length.

Once leaves were photocopied and placed in a forced-draft oven, destructive sampling began. The following traits were measured:

1) shoot length,
2) number of leaves per plant,
3) total abaxial leaf area,
4) total oven-dry leaf weight,

5) oven-dry shoot weight,
6) oven-dry root weight, and
7) root/shoot weight ratio.

Table 4. Summary of light levels, relative humidities, and temperatures recorded during the measurement of transpiration rates and stomatal conductance for the greenhouse provenance trial.

Day	Block	Light (uE/(m^2s))	Relative Humidity (%)	Temperature (°C)
July 11, 1988	1	70	49.2	20.7
	2	78	49.1	21.0
	3	79	49.2	21.0
July 12, 1988	1	142	48.7	23.7
	2	138	51.7	22.9
	3	197	40.4	25.8
July 13, 1988	1	151	55.1	23.0
	2	114	55.0	21.2
	3	87	55.0	21.0
July 14, 1988	1	89	68.2	22.7
	2	95	68.4	21.8
	3	31	69.8	20.6

Shoot length was recorded to the nearest half-a-centimeter. The number of leaves per plant and total abaxial leaf area were measured with a Delta-T Leaf Area Meter. Before use, the area meter was calibrated using templates of known area. Calibration standardizes the frame size. A T.V. then scans the leaf, frame by frame, and since it takes a twenty-fifth of a second to scan one frame (Anon.,n.d.), the time taken to scan the leaf is directly proportional to the area of the leaf. Once total abaxial leaf area and total number of leaves per plant were recorded, oven-dry leaf weight was determined by placing the leaves in a forced-draft oven at 70°C for forty-eight hours. Roots, after being separated

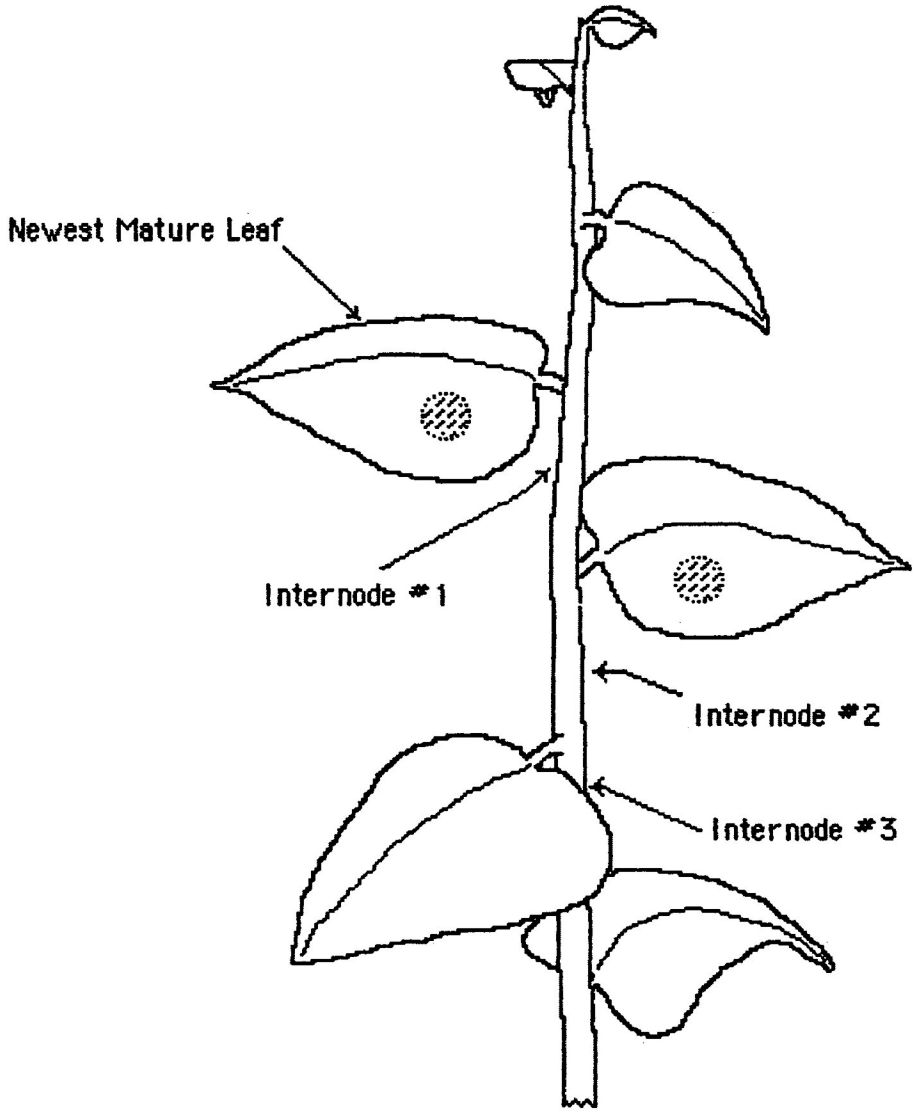


Figure 6. Location of transpiration rate, stomatal conductance, internode length, and stomatal density and length measurements for the greenhouse provenance trial.

from the soil, and shoots were also oven-dried and weighed. The root/shoot weight ratio was calculated by dividing oven-dry root weight by the sum of oven-dry shoot and leaf weights.

B. DATA ANALYSIS

All analysis was completed using the data analysis and graphics package SPSSx running on the Lakehead University Computing Centre Microvax installation.

1. Analysis of Variance

a. Field Provenance Trial

Data from the field provenance trial were analyzed using a nested, split-plot design. Not all clones were represented in each block: clones 303, 314, 319 and 326 were missing from block 1, clone 034 was missing from block 2, and clones 135, 137, 141 and 149 were missing from block 3. So, to facilitate the analysis of the data, missing values were calculated for each trait, excluding leaf shape distances, using a method developed by Anderson (1946):

$$Y = (rW + (a_j b_k) - (a_j))/((r-1)(b-1))$$

where Y is the missing clonal (split-plot) observation; r is the number of blocks; b is the number of clones per provenance (whole-plot); W is the sum of the observed clones in the provenance from which the observation is missing; $(a_j b_k)$ is the sum of the

observed clones, across all blocks, that received the same $a_j b_k$ treatment, and (a_j) is the sum of the observed clones that received the j^{th} level of (a).

Once missing values were calculated and inserted with the original data, computation of the sums-of-squares was completed in the usual fashion, with degrees of freedom being subtracted from the clonal error term and relevant error and interaction terms (Steele and Torrie, 1980). As a consequence, the mean-squares estimates for provenance and block will be biased upward, but because only a few observations are missing, these biases were ignored (Steele and Torrie, 1980).

The linear model and ANOVA Table (Table 5) for measured traits other than transpiration rate, stomatal conductance and leaf shape is as follows:

$$Y_{ijklm} = \mu + B_i + o(i) + P_j + BP_{ij} + w(ij) + C/P(j)_k + BC/P_{i(j)k} + E(ijk)_l + S(ijkl)_m$$

where Y_{ijklm} is the m^{th} observation from the l^{th} ramet within the k^{th} clone within the j^{th} provenance in the i^{th} block; μ is the overall mean; B_i is the effect of the i^{th} block (i=1-3, random); $o(i)$ is the restriction error (Anderson and McLean, 1974) due to blocking; P_j is the effect of the j^{th} provenance (j=1-4, fixed); BP_{ij} is the effect of the interaction of the i^{th} block with the j^{th} provenance; $w(ij)$ is the restriction error due to the provenances; $C/P(j)_k$ is the effect of the k^{th} clone within the j^{th} provenance (k=1-9, fixed); $BC/P_{i(j)k}$ is the effect of the interaction of the i^{th} block

with the k^{th} clone within the j^{th} provenance; $E_{(ijk)l}$ is the experimental error (l=1, fixed), and $S_{(ijkl)m}$ is the subsampling error (fixed). The number of subsamples (m) varies from twenty for stomatal density and length, to three for internode length, and to two for petiole length, single-leaf abaxial area and oven-dry weight, and specific leaf weight.

Table 5. Analysis of variance for shoot, stomatal anatomy, and leaf size and morphology traits for the field provenance trial.

Source	Degrees of Freedom	[1]Expected Mean Squares
Block (B_i)	2	$9m\sigma^2_w + 36m\sigma^2_o + 36m\sigma^2_B$
Restriction Error (o_i)	0	$9m\sigma^2_w + 36m\sigma^2_o$
Provenance (P_i)	3	$9m\sigma^2_w + 9m\sigma^2_{BP} + 27m\phi_P$
BP_{ij}	6	$9m\sigma^2_w + 9m\sigma^2_{BP}$
Restriction Error ($w_{(ij)}$)	0	$9m\sigma^2_w$
Clone ($C/P_{(j)k}$)	32	$m\sigma^2_{BC} + 3m\phi_C$
$BC/P_{i(j)k}$	55	$m\sigma^2_{BC}$
Experimental Error ($E_{(ijk)l}$)	0	$m\phi_E$
Sampling Error ($S_{(ijkl)m}$)	99(m-1)	ϕ_S

[1] m=20 for stomatal density and length; m=3 for internode length; m=2 for petiole length, single-leaf abaxial area and oven-dry weight, and specific leaf weight.

Because transpiration rates and stomatal conductance were measured repeatedly (four times) using the same experimental unit, repeated measures analysis of variance was used to test for treatment effects. The repeated measures design divides the analysis into a between-subjects analysis and a within-subjects analysis, as shown in Table 6 (Hicks, 1982).

The analysis in Table 6 implies that the between-subject

linear model is:

$$Y_{ijklmn} = \mu + B_i + o(i) + P_j + BP_{ij} + w(ij) + C/P(j)k + BC/P_{i(j)k} + A(ijk)lmn$$

where Y_{ijklmn} is the n^{th} observation from the m^{th} ramet on the l^{th} day within the k^{th} clone within the j^{th} provenance in the i^{th} block; μ is the overall mean; B_i is the effect of the i^{th} block (i=1-3, random); $o(i)$ is the restriction error due to blocking; P_j is the effect of the j^{th} provenance (j=1-4, fixed); BP_{ij} is the effect of the interaction of the i^{th} block with the j^{th} provenance; $w(ij)$ is the restriction error due to the provenances; $C/P(j)k$ is the effect of the k^{th} clone within the j^{th} provenance (k=1-9, fixed); $BC/P_{i(j)k}$ is the effect of the interaction of the i^{th} block with the k^{th} clone within the j^{th} provenance, and $A(ijk)lmn$ is the within-subjects effects.

The within-subjects effects can be further partitioned into:

$$A(ijk)lmn = T_l + v(l) + BT_{il} + PT_{jl} + BPT_{ijl} + C/PT(j)kl + BC/PT_{i(j)kl} + E(ijkl)m + S(ijklm)n$$

where T_l is the effect of the l^{th} day (l=1-4, fixed); $v(l)$ is the restriction error due to days; BT_{il} is the effect of the interaction between the i^{th} block and the l^{th} day; PT_{jl} is the effect of the interaction between the j^{th} provenance and the l^{th} day; BPT_{ijl} is the effect of the interaction between the i^{th} block, the j^{th} provenance and the l^{th} day; $C/PT(j)kl$ is the effect of the interaction between the k^{th} clone within the j^{th} provenance and

Table 6. Analysis of variance for transpiration rates and stomatal conductance for the field provenance trial.

Source	Degrees of Freedom	Expected Mean Squares
Between-Subjects	98	
Block (B_i)	2	$3240\sigma^2_V + 1080\sigma^2_W + 4320\sigma^2_O + 4320\sigma^2_B$
Restriction Error (σ_i)	0	$3240\sigma^2_V + 1080\sigma^2_W + 4320\sigma^2_O$
Provenance (P_i)	3	$3240\sigma^2_V + 1080\sigma^2_W + 1080\sigma^2_O + 3240\phi_P$
BP_{ij}	6	$3240\sigma^2_V + 1080\sigma^2_W + 1080\sigma^2_O$
Restriction Error ($W_{(ij)}$)	0	$3240\sigma^2_V + 1080\sigma^2_W$
Clone ($C/P_{(j)k}$)	32	$3240\sigma^2_V + 120\sigma^2_{BC} + 360\phi_C$
$BC/P_{i(j)k}$	55	$3240\sigma^2_V + 120\sigma^2_{BC}$
Within-Subjects	1089	
Day (T_l)	3	$3240\sigma^2_V + 1080\sigma^2_{BT} + 3240\phi_T$
$V_{(l)}$	0	$3240\sigma^2_V$
BT_{il}	6	$1080\sigma^2_{BT}$
PT_{jl}	9	$270\sigma^2_{BPT} + 810\phi_{PT}$
BPT_{ijl}	18	$270\sigma^2_{BPT}$
$C/PT_{(j)kl}$	96	$30\sigma^2_{BCT} + 90\sigma_{CT}$
$BC/PT_{i(j)kl}$	165	$30\sigma^2_{BCT}$
Experimental Error ($E_{(ijkl)m}$)	0	$30\phi_E$
Sampling Error ($S_{(ijklm)n}$)	792	ϕ_S

the l^{th} day; $BC/PT_{i(j)kl}$ is the effect of the interaction between the i^{th} block, the k^{th} clone within the j^{th} provenance and the l^{th} day; $E_{(ijkl)m}$ is the experimental error (m=1, fixed), and $S_{(ijklm)n}$ is the subsampling error (n=3, fixed).

Analysis of variation in leaf shape utilized multivariate statistical procedures. First, the sixty-six distances, calculated from the twenty-eight pseudolandmarks, were transformed using the $\log_{10}$ transformation and analyzed using multi-group Principal

Component Analysis (m-PCA). Log_{10} transformed distances were used in place of the original distances, because logarithms more closely approximate linearity and multivariate normality (Pimental, 1979). Linearity and multivariate normality must be approximated in order to run a meaningful m-PCA.

PCA is a statistical technique used to identify a relatively small number of factors or axes, which represent relationships among sets of intercorrelated variables within a population (Norusis, 1985; Pimental, 1979). The original variables are transformed to factors, which are uncorrelated, linear combinations of the original variables. The transformation of the original variables to factors rotates the original variable axes to new independent axes, while maintaining the original relationships among the data points. Thus, each factor defines an independent component of variation, which in this case, is interpreted as an indicator of variation in size and/or shape (Pimental, 1979).

Initially, PCA was developed as a tool used to analyze patterns of variation within individual populations; however, m-PCA was developed so that variation within a number of populations could be assayed simultaneously. M-PCA is merely PCA based on an eigen-analysis of the pooled within-population covariance or correlation matrix (Pimental, 1979). Differences among populations are maintained in the m-PCA factors, because the PCA rotation of the axes is centered by the grand mean vector rather than the individual population mean vectors (Dickinson *et*

al, 1987).

Identified m-PCA factors, with eigenvalues larger than the average eigenvalue, were used for the remaining leaf shape analysis (Norusis, 1985). Thus, the possible problems associated with the redundancy among the original sixty-six distance variables were avoided.

All remaining m-PCA factors were used simultaneously for Discriminant Functions Analysis (DFA). DFA attempts to find linear composites or axes of the predictor variables (m-PCA factors) which maximize among-provenance to within-provenance variability (Norusis, 1985). Axes are uncorrelated and each successive axis accounts for less variation than the previously computed axis. DFA also identifies which predictor variables contribute most to discriminating among groups.

b. Greenhouse Provenance Trial

Analysis of the data from the greenhouse provenance trial followed a nested, randomized, complete block design. Like the field provenance trial, not all the clones were represented in each block: clone 242 was missing from block 1 and clone 219 was missing from block 2. To facilitate the analysis, missing values for traits other than leaf shape distances were calculated using a method developed by Yates (1933):

$$Y = (rB + tT - G)/((r-1)(t-1))$$

where r is the number of blocks; t is the number of treatments; B is the sum of the observed units in the block containing the missing unit; T is the sum of the observed units in the treatment

containing the missing unit; and G is the grand sum of all the observed units. The estimated values were entered with the observed values and analysis of variance was completed. Degrees of freedom were adjusted for the missing units, and because only two units were missing, any possible mean squares biases were ignored (Steele and Torrie, 1980).

Analysis of traits, other than transpiration rates, stomatal conductance and leaf shape, were completed using the following linear model and ANOVA (Table 7):

$$Y_{ijklm} = \mu + B_i + \sigma(i) + P_j + BP_{ij} + C/P(j)_k + BC/P_{i(j)k} + E(ijk)_l + S(ijkl)_m$$

where Y_{ijklm} is the m^{th} observation from the l^{th} ramet within the k^{th} clone within the j^{th} provenance in the i^{th} block; μ is the overall mean; B_i is the effect of the i^{th} block (i=1-3, random); $\sigma(i)$ is the restriction error due to blocking; P_j is the effect of the j^{th} provenance (j=1-4, fixed); BP_{ij} is the effect of the interaction of the i^{th} block with the j^{th} provenance; $C/P(j)_k$ is the effect of the k^{th} clone within the j^{th} provenance (k=1-9, fixed); $BC/P_{i(j)k}$ is the effect of the interaction of the i^{th} block with the k^{th} clone within the j^{th} provenance; $E(ijk)_l$ is the experimental error (l=1, fixed), and $S(ijkl)_m$ is the subsampling error (fixed). The number of subsamples (m) varies from twenty for stomatal density and length, to three for internode length, to two for petiole length, single-leaf abaxial area and oven-dry weight, and specific leaf weight, and to one for shoot length, number of leaves per plant,

Table 7. Analysis of variance for root and shoot, stomatal anatomy, and leaf size and morphology traits for the greenhouse provenance trial.

Source	Degrees of Freedom	[1]Expected Mean Squares
Block (B_i)	2	$36m\sigma^2_o + 36m\sigma^2_B$
Restriction Error (o_i)	0	$36m\sigma^2_o$
Provenance (P_i)	3	$9m\sigma^2_{BP} + 27m\phi_P$
BP_{ij}	6	$9m\sigma^2_{BP}$
Clone ($C/P_{(j)k}$)	32	$m\sigma^2_{BC} + 3m\phi_C$
$BC/P_{i(j)k}$	62	$m\sigma^2_{BC}$
Experimental Error ($E_{(ijk)l}$)	0	$m\phi_E$
Sampling Error ($S_{(ijkl)m}$)	106(m-1)	ϕ_S

[1] m=20 for stomatal density and length; m=3 for internode length; m=2 for petiole length, single-leaf abaxial area, single-leaf oven-dry weight and specific leaf weight, and m=1 for shoot length, number of leaves per plant, total abaxial leaf area per plant, total oven-dry leaf, shoot and root weights, and the oven-dry root/shoot weight ratio.

total abaxial leaf area, total oven-dry leaf, shoot and root weight, and root/shoot weight ratio.

Transpiration rates and stomatal conductance were analyzed using repeated measures analysis of variance. The linear model and ANOVA are as follows:

$$Y_{ijklmn} = \mu + B_i + o_{(i)} + P_j + BP_{ij} + C/P_{(j)k} + BC/P_{i(j)k} + T_l + \nu_{(l)} + BT_{il} + PT_{jl} + BPT_{ijl} + C/PT_{(j)kl} + BC/PT_{i(j)kl} + E_{(ijkl)m} + S_{(ijklm)n}$$

where Y_{ijklmn} is the n^{th} observation from the m^{th} ramet on the l^{th} day within the k^{th} clone within the j^{th} provenance in the i^{th} block; μ is the overall mean; B_i is the effect of the i^{th} block (i=1-3, random); $o_{(i)}$ is the restriction error due to blocking; P_j is the effect of the j^{th} provenance (j=1-4, fixed); BP_{ij} is the effect of

Table 8. Analysis of variance for transpiration rates and stomatal conductance for the greenhouse provenance trial.

Source	Degrees of Freedom	Expected Mean Squares
Between-Subjects	105	
Block (B_i)	2	$2160\sigma^2_\nu + 2880\sigma^2_o + 2880\sigma^2_B$
Restriction Error (σ_i)	0	$2160\sigma^2_\nu + 2880\sigma^2_o$
Provenance (P_i)	3	$2160\sigma^2_\nu + 720\sigma^2_{BP} + 2160\phi_P$
BP_{ij}	6	$2160\sigma^2_\nu + 720\sigma^2_{BP}$
Clone ($C/P_{(j)k}$)	32	$2160\sigma^2_\nu + 80\sigma^2_{BC} + 240\phi_C$
$BC/P_{i(j)k}$	62	$2160\sigma^2_\nu + 80\sigma^2_{BC}$
Within-Subjects	742	
Day (T_l)	3	$2160\sigma^2_\nu + 720\sigma^2_{BT} + 216\phi_T$
$\nu(l)$	0	$2160\sigma^2_\nu$
BT_{il}	6	$720\sigma^2_{BT}$
PT_{jl}	9	$180\sigma^2_{BPT} + 540\phi_{PT}$
BPT_{ijl}	18	$180\sigma^2_{BPT}$
$C/PT_{(j)kl}$	96	$20\sigma^2_{BCT} + 60\phi_{CT}$
$BC/PT_{i(j)kl}$	186	$20\sigma^2_{BCT}$
Experimental Error ($E_{(ijkl)m}$)	0	$20\phi_E$
Sampling Error ($S_{(ijklm)n}$)	424	ϕ_S

the interaction of the i^{th} block with the j^{th} provenance; $C/P_{(j)k}$ is the effect of the k^{th} clone within the j^{th} provenance (k=1-9, fixed); $BC/P_{i(j)k}$ is the effect of the interaction of the i^{th} block with the k^{th} clone within the j^{th} provenance; T_l is the effect of the l^{th} day (l=1-4, fixed); $\nu(l)$ is the restriction error due to days; BT_{il} is the effect of the interaction between the i^{th} block and the l^{th} day; PT_{jl} is the effect of the interaction between the j^{th} provenance and the l^{th} day; BPT_{ijl} is the effect of the interaction between the i^{th} block, the j^{th} provenance and the l^{th} day; $C/PT_{(j)kl}$ is the effect of

the interaction between the k^{th} clone within the j^{th} provenance and the l^{th} day; $BC/PT_{i(j)kl}$ is the effect of the interaction between the i^{th} block, the k^{th} clone within the j^{th} provenance and the l^{th} day; $E_{(ijkl)m}$ is the experimental error (m=1, fixed), and $S_{(ijklm)n}$ is the subsampling error (n=2, fixed).

Analysis of leaf shape was performed in the same manner as for the field provenance trial.

2. Variance Components

From the analysis of variance, estimates of components of variation were obtained by equating mean-squares to their expectations. An example for the calculation of variance components is presented in Appendix I. The variance components were used to determine the percent of total variation contributed by each component.

3. Phenotypic Correlations

Phenotypic correlations, based on clone means, between measured traits were approximated by Pearson's product-moment coefficient.

IV. RESULTS

A. FIELD PROVENANCE TRIAL

1. Analysis of Variance

The statistical significance and percent of variation attributable to the sources of variation are presented in Table 9. It should be noted that there are no valid tests of significance for blocks and its associated interactions. Detailed analyses of variance, showing sums-of-squares and mean-squares, are presented in Appendix II. Block means for provenances and clones are presented in Appendix III.

a. Variation in Shoot Growth

The only shoot trait that was measured in the field provenance trial was internode length. Internode lengths did not vary significantly from one provenance to another (Table 9). The most northern provenance, Bearskin Lake had the shortest internode length (2.3 cm), while the most southern provenance, Northern Wisconsin, had the longest internode length (2.8 cm) (Table 10). Pickle Lake and Thunder Bay had average internode lengths of 2.5 and 2.4 cm respectively. Approximately 17 percent of the variation was attributable to the significant clone-within-provenance effect, with clonal means ranging from 1.4 to 3.8 cm.

Table 9. Percentages of variation attributable to various sources for shoot, leaf size and morphology, stomatal anatomy, and stomatal control traits measured in the field provenance trial.

Traits	Source of Variation												
	Block (B)	Provenance (P)	B*P	Clone-within-Provenance (C/P)	B*C/P	Day (T)	B*T	P*T	B*P*T	C/P*T	B*C/P*T	Experimental Error (E)	Subsampling Error (S)
Shoot													
Internode Length (cm)	[1]0.5	[2]2.2ns	8.6	[3]16.9**	41.4	[4]NA	NA	NA	NA	NA	NA	[5]NR	30.7
Leaf Size and Morphology													
Petiole Length (mm)	5.0	13.4**	2.2	9.3ns	53.0	NA	NA	NA	NA	NA	NA	NR	16.7
Single-Leaf Abaxial Area (cm^2)	1.9	38.3**	3.4	7.6ns	45.0	NA	NA	NA	NA	NA	NA	NR	3.8
Single-Leaf Oven-Dry Weight (mg)	1.3	28.0**	3.4	8.4ns	53.5	NA	NA	NA	NA	NA	NA	NR	5.5
Specific Leaf Weight (mg/cm^2)	5.1	24.8*	13.8	1.2ns	43.3	NA	NA	NA	NA	NA	NA	NR	11.8
Stomatal Anatomy													
Stomatal Density (#/mm^2)	1.0	4.1ns	4.2	18.4**	43.6	NA	NA	NA	NA	NA	NA	NR	28.9
Stomatal Length (µm)	0.7	2.2ns	4.1	28.8**	36.2	NA	NA	NA	NA	NA	NA	NR	27.9
Stomatal Control													
Transpiration Rate (µg/(cm^2s))	14.7	3.0ns	3.4	3.7**	9.3	±0.0ns	55.9	0.3ns	7.2	1.4**	8.7	NR	7.0
Stomatal Conductance (cm/s)	4.8	3.5ns	6.7	8.4**	18.2	0.9ns	15.1	0.6ns	6.2	1.9ns	16.8	NR	16.8

[1] Percentages of variation not followed by ns, * or ** do not have a valid test of significance. For detailed analyses of variance see Appendix II.

[2] ns indicates non-significance at the 5% level.

[3] * and ** indicate significance at the 5% and 1% level, respectively.

[4] NA indicates that the source of variation is not applicable to the observed trait.

[5] NR indicates that the mean squares value is not retrievable (0 degrees of freedom).

However, the majority of the variation detected in internode lengths was attributable to the block*clone-within-provenance interaction (41.4 percent) and to variation within a single ramet (subsampling error - 30.7 percent).

Table 10. Provenance means for shoot, leaf size and morphology, and stomatal anatomy traits measured in the field provenance trial.

Provenance	Shoot	Leaf Size and Morphology				Stomatal Anatomy	
	Internode Length (cm)	Petiole Length (mm)	Single-Leaf Abaxial Area (cm^2)	Single-Leaf Oven-Dry Leaf Weight (mg)	Specific Leaf Weight (mg/cm^2)	Stomatal Density ($\#/mm^2$)	Stomatal Length (um)
Northern Wisconsin	2.8 [1](1.9-3.8)	18.1 (15.5-21.0)	25.0 (15.9-35.5)	240 (155-353)	9.62 (8.57-10.01)	215 (170-280)	34.6 (29.8-36.9)
Thunder Bay	2.4 (2.0-3.3)	17.6 (14.8-20.5)	18.9 (15.2-23.0)	204 (158-258)	10.92 (9.89-11.76)	243 (198-270)	35.7 (31.8-38.8)
Pickle Lake	2.5 (2.0-2.9)	15.6 (13.0-17.5)	14.4 (10.9-16.9)	159 (126-212)	11.24 (10.39-12.91)	242 (197-273)	33.8 (31.8-37.7)
Bearskin Lake	2.3 (1.4-3.3)	14.9 (10.5-20.3)	11.8 (7.7-23.4)	135 (90-248)	11.66 (10.50-12.50)	237 (213-269)	35.7 (30.4-41.5)

[1] Range of clone means within each provenance.

b. Variation in Leaf Size and Morphology

The provenance effect accounted for 13.4 to 38.3 percent of the variation in leaf size and morphology traits (Table 9). Differences among provenances were significant and there was a north-south trend apparent. Leaves from the most northern provenance (Bearskin Lake) had the shortest petiole lengths (14.9 mm), smallest single-leaf abaxial areas (11.8 cm^2) and oven-dry weights (135 mg), and the highest average specific leaf weights (11.66 mg/cm^2) (Table 10). The most southern provenance (Northern Wisconsin) had the longest petiole lengths (18.1 mm), largest single-leaf abaxial areas (25.0 cm^2) and oven-dry weights (240 mg), and the lowest average specific leaf weights (9.62

mg/cm2). Significant differences were not detected among clones within-provenances for the aforementioned traits, but approximately half of the observed variation in each of the traits was attributable to the block*clone-within-provenance interaction (Table 9).

Provenance mean leaf outlines are presented in Figure 7. In general, the southern provenances have wider and longer leaves than the more northern provenances. Leaf shape is similar, however, the ratio of leaf width to leaf length decreases slightly with latitude.

Multi-group principal components analysis of the sixty-six leaf shape distances extracted three factors which accounted for 97.9 percent of the observed variation in leaf shape (Table 11). The first axis (PCAF1) accounted for 88.4 percent of the observed variation. All sixty-six radial and truss distances made large positive contributions, indicating that this axis is mainly a descriptor of variation in size (Pimental, 1979). The second axis (PCAF2) accounted for 6.1 percent of the variation and was bipolar in nature, indicating variation in leaf shape (Pimental, 1979). Distances incorporating pseudolandmarks near the base of the leaf made the largest positive loadings, while near the middle of the leaf, loadings were very small and were either positive or negative. At the leaf tip, loadings were negative, but larger in magnitude than those near the middle of the leaf. Since the largest positive loadings occurred at the base of the leaf, PCAF2 can be interpreted as being a descriptor of variation in the shape

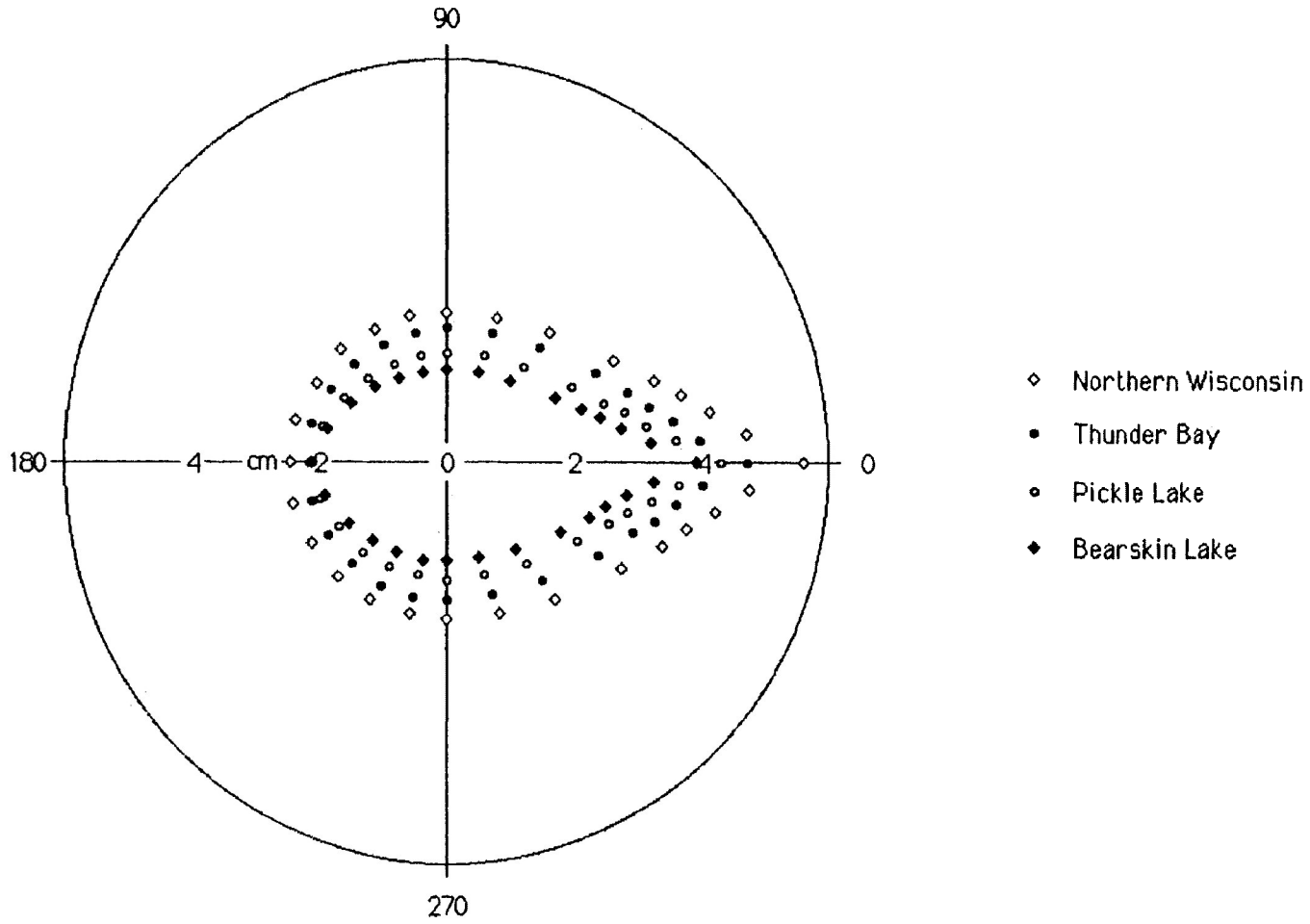


Figure 7. Average leaf outlines for the four provenances of balsam poplar in the field provenance trial.

Table 11. Multi-group principal components analysis of variance of the sixty-six radial and truss distances for the four provenances of balsam poplar in the field provenance trial.

	Principal Components		
	PCAF1	PCAF2	PCAF3
Cummulative Variance (%)	88.4	94.5	97.9
Radial and Truss Distances	Eigenvectors		
R1,2	0.896	-0.146	0.378
R1,3	0.937	-0.153	0.297
R1,4	0.955	-0.154	0.221
R1,5	0.964	-0.155	0.159
R1,6	0.969	-0.150	0.104
R1,7	0.972	-0.140	0.008
R1,8	0.959	-0.105	-0.137
R1,9	0.952	-0.088	-0.188
R1,10	0.954	-0.073	-0.201
R1,11	0.958	-0.041	-0.203
R1,12	0.963	0.046	-0.191
R1,13	0.953	0.183	-0.155
R1,14	0.918	0.354	-0.062
R1,15	0.818	0.555	0.086
R1,16	0.649	0.688	0.251
R1,17	0.831	0.536	0.078
R1,18	0.924	0.338	-0.057
R1,19	0.961	0.145	-0.144
R1,20	0.963	0.003	-0.186
R1,21	0.956	-0.071	-0.193
R1,22	0.950	-0.106	-0.192
R1,23	0.954	-0.125	-0.162
R1,24	0.965	-0.143	-0.094
R1,25	0.971	-0.171	0.032
R1,26	0.965	-0.184	0.128
R1,27	0.960	-0.184	0.177
R1,28	0.952	-0.171	0.236
R1,29	0.938	-0.151	0.301
T3,29	0.926	-0.151	0.302
T3,28	0.908	-0.138	0.337
T4,29	0.880	-0.144	0.379
T4,28	0.952	-0.172	0.239
T4,27	0.957	-0.160	0.218
T5,28	0.944	-0.175	0.251
T5,27	0.966	-0.177	0.172
T5,26	0.972	-0.164	0.143
T6,27	0.965	-0.181	0.164
T6,26	0.976	-0.171	0.113
T6,25	0.977	-0.172	0.092
T7,26	0.981	-0.157	0.072
T7,25	0.964	-0.157	0.016
T7,24	0.986	-0.141	-0.041
T8,25	0.985	-0.146	-0.033
T8,24	0.982	-0.125	-0.120
T8,23	0.978	-0.118	-0.154
T9,24	0.980	-0.121	-0.144
T9,23	0.975	-0.112	-0.181
T9,22	0.973	-0.102	-0.197
T10,23	0.974	-0.104	-0.189
T10,21	0.974	-0.077	-0.204
T11,22	0.974	-0.079	-0.203
T11,21	0.976	-0.060	-0.203
T11,20	0.978	-0.023	-0.199
T12,21	0.979	-0.017	-0.196
T12,20	0.980	0.019	-0.191
T12,19	0.979	0.092	-0.169
T13,20	0.978	0.086	-0.172
T13,19	0.971	0.159	-0.149
T13,18	0.953	0.266	-0.103
T14,19	0.959	0.242	-0.104
T14,18	0.931	0.342	-0.066
T14,17	0.879	0.468	0.030
T15,18	0.882	0.460	0.022
T15,17	0.834	0.534	0.089
T15,16	0.665	0.642	0.264
T16,17	0.651	0.663	0.237

[1] R, T, 1 and 2-29 indicate radial distances, truss distances, reference point and pseudolandmarks respectively.

of the leaf base. The third axis (PCAF3), also bipolar, accounted for 3.4 percent of the detected variation in radial and truss distances. Distances incorporating pseudolandmarks near the leaf

tip made the largest, positive contributions, while distances near the middle of the leaf made the largest, negative contributions. Radial and truss distances incorporating pseudolandmarks at the extreme base of the leaf (pseudolandmarks 15, 16 and 17) also had large, positive loadings. Thus, PCAF3 is a descriptor of variation in the shape of the leaf tip and to a lesser extent the leaf base.

Further results of the m-PCA analysis are presented in Figures 8 through 10 as two dimensional ordinations of the four provenances of balsam poplar. Axis score population means have been plotted, with one standard deviation above and below the provenance mean being indicated by horizontal and vertical lines. This plotting procedure summarizes the scatter diagrams that result when individual leaves of clones within provenances are plotted (Parker and Maze, 1984). On the first axis (PCAF1), an indicator of variation in leaf size, the provenances form a continuously overlapping cluster, arranged according to their respective latitudes, with Bearskin Lake and Northern Wisconsin appearing distinct from each other (Figure 8 and 9). On the second (PCAF2) and third (PCAF3) axes, indicators of variation in leaf shape, provenances form a continuously overlapping cluster, with the arrangement of provenances not reflecting any latitudinal trend (Figure 10).

Discriminant functions analysis using the three m-PCA axes as predictor variables formed three DFA axes, which accounted for 99.9 percent of the observed variation in the m-PCA axes (Table 12). PCAF1 made a large positive contribution to the first axis (DFAS1), which accounted for 86.3 percent of the total variation

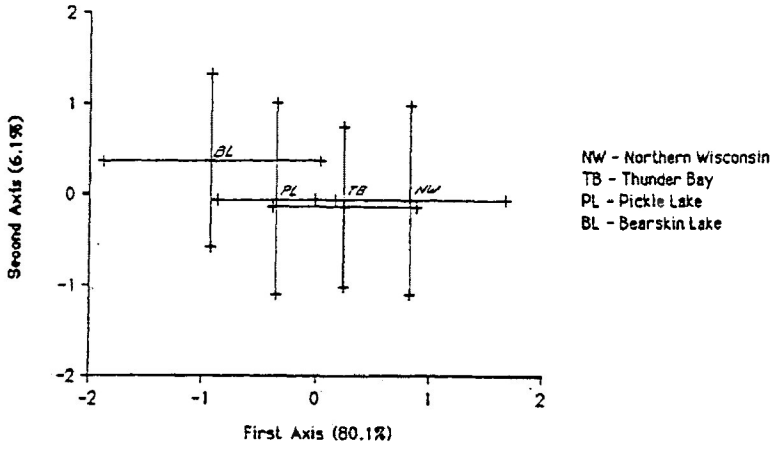


Figure 8. Two-dimensional ordination of four provenances of balsam poplar based on the first (PCAF1) and second (PCAF2) principal components axes for the field provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

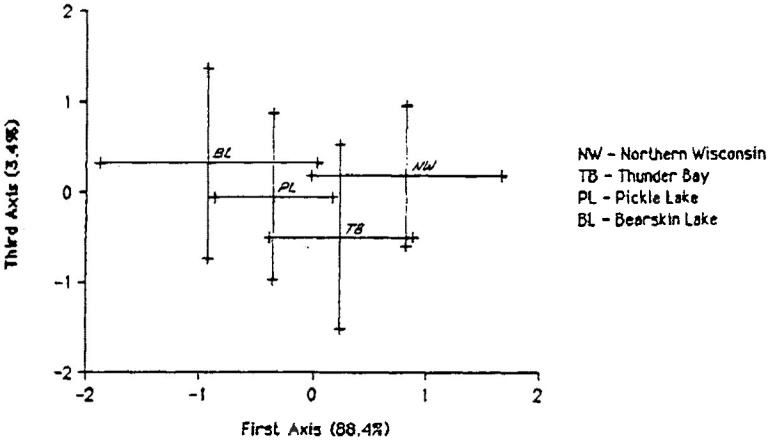


Figure 9. Two-dimensional ordination of four provenances of balsam poplar based on the first (PCAF1) and third (PCAF3) principal components axes for the field provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

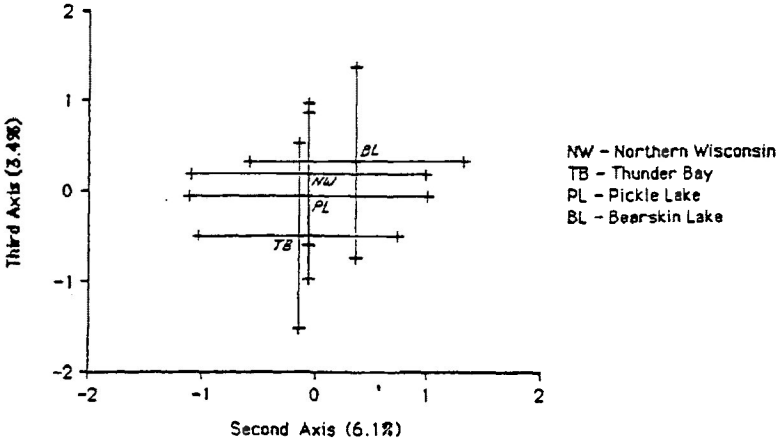


Figure 10. Two-dimensional ordination of four provenances of balsam poplar based on the second (PCAF2) and third (PCAF3) principal components axes for the field provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

in the m-PCA axes. PCAF2 and PCAF3 made smaller negative contributions. The second DFA axis (DFAS2) accounted for 13.0 percent of the variation exhibited by the m-PCA axes. PCAF3 made the largest positive contribution, while PCAF1 and PCAF2 made similar, but much smaller contributions. The third axis (DFAS3), which accounted for only 0.6 percent of the variation in

Table 12. Discriminant functions analysis of the three multi-group principal component functions for the four balsam poplar provenances in the field provenance trial.

	Discriminant Functions		
	DFAS1	DFAS2	DFAS3
Cummulative Variance (%)	86.3	99.3	99.9
PCA Factor	Discriminant Functions Coefficients		
PCAF1	1.263	0.308	0.122
PCAF2	-0.279	0.302	0.930
PCAF3	-0.318	0.958	-0.333

m-PCA axes, loaded most heavily with PCAF2. PCAF1 made a much smaller positive contribution, while PCAF3 made a small negative contribution.

Two dimensional ordinations of the four provenances based on discriminant functions analysis are presented in Figures 11 through 13, using the same format as for the principal components analysis. The results are very similar to that of the m-PCA analysis. On the first axis, which loaded most heavily with PCAF1, the provenances are arranged according to their respective latitudes. The provenances form a continuously overlapping cluster, with Bearskin Lake and Northern Wisconsin being distinct

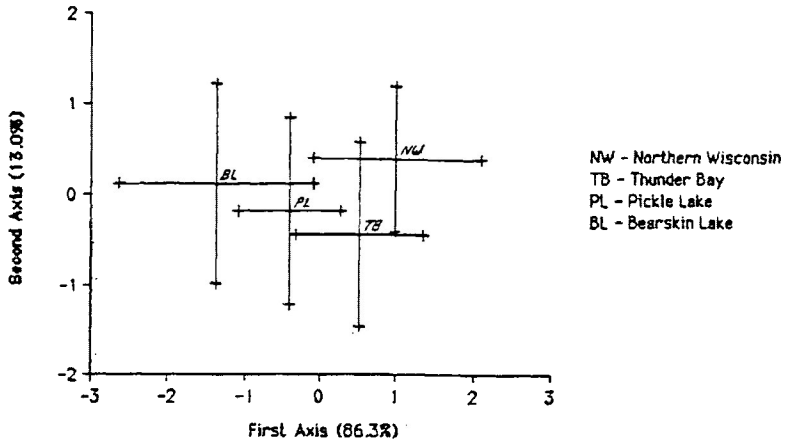


Figure 11. Two-dimensional ordination of four provenances of balsam poplar based on the first (DFAS1) and second (DFAS2) discriminant functions axes for the field provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

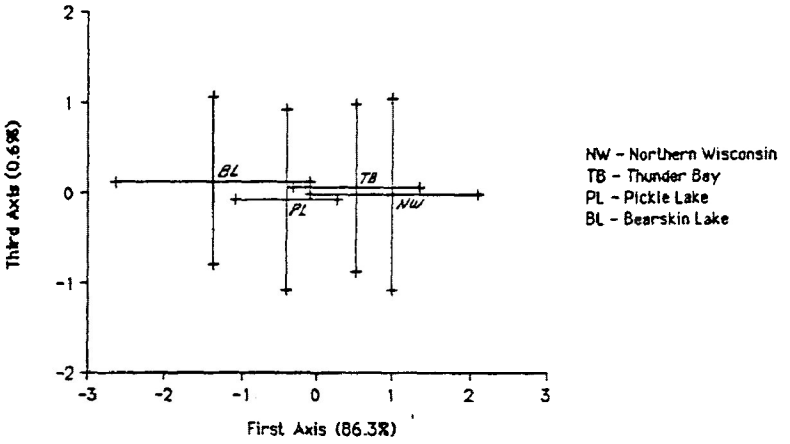


Figure 12. Two-dimensional ordination of four provenances of balsam poplar based on the first (DFAS1) and third (DFAS3) discriminant functions axes for the field provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

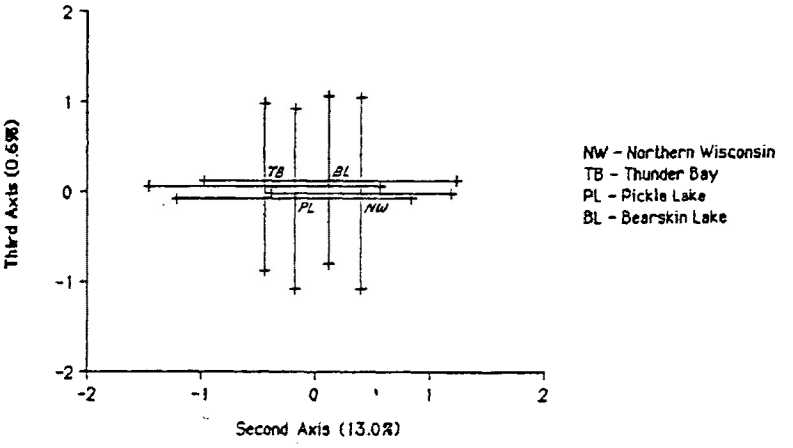


Figure 13. Two-dimensional ordination of four provenances of balsam poplar based on the second (DFAS2) and third (DFAS3) discriminant functions axes for the field provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

from one another (Figures 11 and 12). On the second and third axes, the provenances form a continuously overlapping cluster, with no apparent north-south trend (Figure 13).

c. Variation in Stomatal Anatomy

Stomatal density and stomatal length did not differ significantly among provenances (Table 9). Stomatal densities (stomata/mm^2) ranged from 215 for Northern Wisconsin to 243 for Thunder Bay. Stomatal length (µm) ranged from 33.8 for Pickle Lake to 35.7 for both Thunder Bay and Bearskin Lake (Table 10). The clone-within-provenance effect had a significant influence on stomatal traits. Over 40 percent of the variation in stomatal densities was attributable to the clone-within-provenance effect, with clone means ranging from 170 to 280 stomata/mm^2. The clone-within-provenance effect accounted for 36.2 percent of the variation in stomatal lengths. Clonal average stomatal lengths ranged from 29.8 to 41.5 µm. Variation attributable to the block*clone-within-provenance interaction accounted for much of the remaining variation in both stomatal anatomy traits (28.9 percent for stomatal density and 27.9 percent for stomatal length).

d. Variation in Stomatal Control

Much of the observed variation in transpiration rates was not attributable to genetic sources such as provenances or clones-within-provenances, but was attributable to environmental

sources such as blocks (14.7 percent) and the interaction between blocks and days (55.4 percent) (Table 9). There were no significant differences in daily average transpiration rates, which ranged from 8.507 µg/(cm^{2}s) on July 2 to 6.794 µg/(cm^{2}s) on July 7 (Table 13). Moreover, transpiration rates did not differ significantly among provenances (Table 9). However, on three of the four days (July 2, 3 and 4, 1988), Bearskin Lake had the highest average transpiration rates and was followed by Pickle Lake, Northern Wisconsin and Thunder Bay, respectively (Table 13). On July 7, Bearskin Lake still had the highest average transpiration rate, but Thunder Bay had the second highest rate of transpiration. There were significant differences among clones-within-provenances. For example, clones-within-provenance means ranged from 5.234 to 10.429 µg/(cm^{2}s) on July 2. But, only 3.4 percent of the observed variation was attributable to this effect (Table 9).

The results for stomatal conductance were very similar to that of transpiration rates, as expected. Although the amount of variation in stomatal conductance was large, much of it (67.8 percent) was attributable to blocks and its associated interactions (Table 9). There were no significant differences among daily average stomatal conductance, which ranged from 0.674 cm/s for July 2 to 0.831 cm/s on July 4 (Table 13). Stomatal conductance did not differ significantly among provenances and trends in provenance means were similar to that for transpiration rates. Significant differences among clones

-within-provenances were detected, and accounted for 8.4 percent of the observed variation. The range of clonal means depended upon the day of measurement, but on July 3, for example, clone -within-provenance means ranged from 0.573 to 0.803 cm/s.

Table 13. Average transpiration rates and stomatal conductance for days and provenances in the field provenance trial.

Date	Provenance	Mean Provenance Transpiration Rate ($\mu g/cm^2 s$)	Mean Provenance Stomatal Conductance (cm/s)
July 2, 1988.	Northern Wisconsin	8.569 *(6.942-9.887)	0.670 *(0.480-0.795)
	Thunder Bay	7.134 (6.021-8.444)	0.615 (0.531-0.736)
	Pickle Lake	8.838 (8.110-11.722)	0.696 (0.617-0.793)
	Bearskin Lake	9.487 (7.301-10.954)	0.715 (0.631-0.790)
	Mean	8.507	0.674
July 3, 1988.	Northern Wisconsin	7.788 (5.881-8.751)	0.704 (0.513-0.794)
	Thunder Bay	7.073 (5.266-9.243)	0.639 (0.454-0.868)
	Pickle Lake	8.396 (5.234-10.369)	0.753 (0.461-0.952)
	Bearskin Lake	8.413 (6.312-10.429)	0.803 (0.678-0.930)
	Mean	7.918	0.725
July 4, 1988.	Northern Wisconsin	6.928 (5.801-7.540)	0.757 (0.596-0.905)
	Thunder Bay	6.105 (5.038-7.236)	0.732 (0.605-0.894)
	Pickle Lake	8.234 (5.706-10.928)	0.923 (0.584-1.300)
	Bearskin Lake	8.376 (7.195-9.868)	0.913 (0.767-1.030)
	Mean	7.411	0.831
July 7, 1988.	Northern Wisconsin	6.054 (5.261-6.973)	0.647 (0.552-0.715)
	Thunder Bay	7.030 (5.383-8.430)	0.718 (0.539-0.907)
	Pickle Lake	6.205 (4.961-8.517)	0.715 (0.565-0.997)
	Bearskin Lake	7.886 (6.267-8.598)	0.854 (0.640-0.958)
	Mean	6.794	0.733

* Range of clone means within each provenance.

2. Phenotypic Correlations

Pearson's product-moment correlations among measured traits and latitude are presented in Table 14. Internode length was significantly correlated with most leaf size and morphology traits, having moderately high correlation coefficients. Internode lengths were positively correlated with traits indicative of leaf size (petiole length, average single-leaf abaxial area and oven-dry weight, and PCAF1) and negatively correlated with PCAF2, and indicator of variation in the shape of the leaf base. Internode lengths were not significantly correlated with stomatal traits and were only weakly correlated with transpiration rates and stomatal conductance. The correlation between internode length and latitude was moderately weak, negative, but significant at the 1 percent level.

Traits indicative of leaf size (petiole length, average single-leaf abaxial area and oven-dry weight, and PCAF1) were significantly correlated, with high positive correlation coefficients. Specific leaf weight, an indicator of leaf thickness, was negatively correlated with the leaf size traits, having moderately high, negative correlation coefficients. Traits indicative of variation in leaf shape (PCAF2 and PCAF3) were not correlated to leaf size traits. Of the stomatal traits measured, stomatal density was significantly correlated with leaf size variables, but not with leaf shape variables. Stomatal length was not significantly correlated with leaf traits. For the most part, stomatal conductance and transpiration rates were not significantly correlated with measured leaf traits. However,

transpiration rates on July 4 and stomatal conductances on July 2, 3, 4 and 7 were significantly, but weakly, correlated to the leaf shape variable PCAF3, and indicator of variation in the shape of the leaf tip. Latitude was significantly correlated to leaf size traits, having high, negative correlation coefficients. The correlation coefficient between specific leaf weight and latitude was also significant, but negative. Leaf shape traits showed no signs of significant correlations with latitude.

Measured stomatal traits (stomatal density and length) were negatively correlated (r=-0.582), but were not correlated with transpiration rates and stomatal conductance. A weak, but significant correlation was found between latitude and stomatal density; however, there was no significant correlation between stomatal length and latitude.

Transpiration rates and stomatal conductance for each day were, on average, significantly correlated with high positive correlation coefficients. Exceptions to this trend involve correlations across days. Transpiration rates on July 7 were not significantly correlated with transpiration rates and stomatal conductance on July 3 and 4. Excluding stomatal conductance for July 2 and transpiration rates for July 2 and 3, stomatal control traits showed significant, but moderately-low positive correlations with latitude.

Table 14. Pearson's product-moment correlation coefficients and their one-tailed significance for clone-mean traits measured in the field provenance trial.

	Shoot	Leaf Size and Morphology							Stomatal Anatomy	
	Internode Length (cm)	Petiole Length (mm)	Single-Leaf Abaxial Area (cm^2)	Single-Leaf Oven-Dry Weight (mg)	Specific Leaf Weight ($mg/(cm^2 s)$)	PCAF1	PCAF2	PCAF3	Stomatal Density ($\#/mm^2$)	Stomatal Length (μm)
Shoot										
Internode Length (cm)	1.000									
Leaf Size and Morphology										
Petiole Length (mm)	[1]0.377**	1.000								
Single-Leaf Abaxial Area (cm^2)	0.410**	0.600**	1.000							
Single-Leaf Oven-Dry Weight (mg/cm^2)	0.458**	0.618**	0.961**	1.000						
Specific Leaf Weight (mg/cm^2)	-0.061	-0.265**	-0.522**	-0.291**	1.000					
PCAF1	0.438**	0.638**	0.967**	0.933**	-0.555**	1.000				
PCAF2	-0.325**	-0.004	0.004	-0.029	-0.122	-0.027	1.000			
PCAF3	-0.033	-0.022	0.034	-0.013	-0.153	-0.002	0.138	1.000		
Stomatal Anatomy										
Stomatal Density ($\#/mm^2$)	-0.023	-0.219*	-0.313**	-0.273**	0.135	-0.278**	-0.052	-0.135	1.000	
Stomatal Length (μm)	0.043	0.085	0.101	0.145	0.133	0.106	-0.068	-0.186*	-0.582**	1.000
Stomatal Control										
Transpiration Rate ($\mu g/(cm^2 s)$) July 2, 1988.	0.073	-0.087	-0.100	-0.109	0.038	-0.107	-0.067	0.089	-0.073	0.081
Stomatal Conductance (cm/s) July 2, 1988.	0.165*	0.022	-0.049	-0.087	-0.140	-0.038	0.052	0.171*	-0.028	-0.018
Transpiration Rate ($\mu g/(cm^2 s)$) July 3, 1988.	0.116	-0.017	0.017	-0.013	-0.099	0.004	0.001	0.092	0.079	-0.097
Stomatal Conductance (cm/s) July 3, 1988.	0.118	-0.067	-0.017	-0.054	-0.091	-0.039	0.033	0.225**	0.086	-0.126
Transpiration Rate ($\mu g/(cm^2 s)$) July 4, 1988.	0.135	0.049	-0.022	-0.057	-0.097	-0.024	0.149	0.281**	-0.054	-0.103
Stomatal Conductance (cm/s) July 4, 1988.	0.163*	0.006	-0.076	-0.116	-0.099	-0.073	0.105	0.239**	0.064	-0.152
Transpiration Rate ($\mu g/(cm^2 s)$) July 7, 1988.	0.044	-0.100	-0.095	-0.070	0.139	-0.099	-0.133	0.057	0.053	0.051
Stomatal Conductance (cm/s) July 7, 1988.	0.104	-0.037	-0.089	-0.083	0.051	-0.080	-0.035	0.207*	0.075	-0.024
Latitude	-0.272**	-0.361**	-0.609**	-0.524**	0.550**	-0.641**	0.161	0.120	0.207*	0.069

[1] * and ** indicate significance at the 5% and 1% level, respectively.

Table 14 continued.

	Stomatal Control								Latitude
	Transpiration Rate (μg/(cm²s)) July 2, 1988.	Stomatal Conductance (cm/s) July 2, 1988.	Transpiration Rate (μg/(cm²s)) July 3, 1988.	Stomatal Conductance (cm/s) July 3, 1988.	Transpiration Rate (μg/(cm²s)) July 4, 1988.	Stomatal Conductance (cm/s) July 4, 1988.	Transpiration Rate (μg/(cm²s)) July 7, 1988.	Stomatal Conductance (cm/s) July 7, 1988.	Latitude
Shoot									
Internode Length (cm)									
Leaf Size and Morphology									
Petiole Length (mm)									
Single-Leaf Abaxial Area (cm^2)									
Single-Leaf Oven-Dry Weight (mg/cm^2)									
Specific Leaf Weight (mg/cm^2)									
PCAF1									
PCAF2									
PCAF3									
Stomatal Anatomy									
Stomatal Density (#/mm^2)									
Stomatal Length (μm)									
Stomatal Control									
Transpiration Rate (μg/(cm²s)) July 2, 1988.	1.000								
Stomatal Conductance (cm/s) July 2, 1988.	0.663**	1.000							
Transpiration Rate (μg/(cm²s)) July 3, 1988.	-0.104	0.305**	1.000						
Stomatal Conductance (cm/s) July 3, 1988.	0.168*	0.478**	0.911**	1.000					
Transpiration Rate (μg/(cm²s)) July 4, 1988.	0.086	0.501**	0.334**	0.403**	1.000				
Stomatal Conductance (cm/s) July 4, 1988.	0.046	0.509**	0.578**	0.642**	0.844**	1.000			
Transpiration Rate (μg/(cm²s)) July 7, 1988.	0.745**	0.285**	-0.137	0.117	-0.115	-0.028	1.000		
Stomatal Conductance (cm/s) July 7, 1988.	0.539**	0.420**	0.174*	0.371**	0.346**	0.406**	0.809**	1.000	
Latitude	0.099	0.130	0.162	0.258**	0.259**	0.306**	0.166*	0.328**	1.000

B. GREENHOUSE PROVENANCE TRIAL

1. Analysis of Variance

The percent of variation attributable to the various sources of variation and their statistical significance are presented in Table 15. The analyses of variance upon which it is based is presented in Appendix IV.

For traits measured in the greenhouse provenance trial, block means for provenances and clones-within-provenances are presented in Appendix V.

a. Variation in Root and Shoot Growth

Provenances means for internode length ranged from a low of 3.2 cm for Bearskin Lake to a high of 3.7 cm for Thunder Bay (Table 16). Pickle Lake and Northern Wisconsin had average internode lengths of 3.6 and 3.4 cm, respectively. Differences among provenances were significant, and accounted for 8.5 percent of the observed variation (Table 15). The majority of the observed variation was attributable to the clone-within-provenance effect (27.6 percent), its interaction with blocks (36.1 percent) and to variation within ramets of a clone (25.5 percent). Clonal means ranged from 2.6 cm, found in both Bearskin Lake and Northern Wisconsin, to 4.6 cm, found in both Thunder Bay and Pickle Lake.

The only other root or shoot trait that had a significant provenance effect was the number of leaves per plant (Table 15). The provenance effect accounted for 6.9 percent of the observed

Table 15. Percentages of variation attributable to various sources for the root and shoot, leaf size and morphology, stomatal anatomy, and stomatal control traits measured in the greenhouse provenance trial.

Traits	Source of Variation												
	Block (B)	Provenance (P)	B*P	Clone-within-Provenance (C/P)	B*C/P	Day (T)	B*T	P*T	B*P*T	C/P*T	B*C/P*T	Experimental Error (E)	Subsampling Error (S)
Root and Shoot													
Internode Length (cm)	[1]0.2[2]	[1]8.5**	2.1	27.6**	36.1	[3][4]NA	NA	NA	NA	NA	NA	[5]NR	25.5
Shoot Length (cm)	6.0	[1]0.2ns	6.3	2.5ns	85.0	NA	NA	NA	NA	NA	NA	NR	NR
Number of Leaves per Plant	5.4	6.9**	3.7	11.0ns	73.1	NA	NA	NA	NA	NA	NA	NR	NR
Total Abaxial Leaf Area per Plant (cm^2)	3.3	4.9ns	4.9	±0.0ns	86.9	NA	NA	NA	NA	NA	NA	NR	NR
Total Oven-Dry Leaf Weight per Plant (g)	4.8	2.3ns	5.4	±0.0ns	87.4	NA	NA	NA	NA	NA	NA	NR	NR
Oven-Dry Shoot Weight (g)	5.1	±0.0ns	7.2	±0.0ns	87.8	NA	NA	NA	NA	NA	NA	NR	NR
Oven-Dry Root Weight (g)	3.5	1.7ns	8.6	±0.0ns	86.2	NA	NA	NA	NA	NA	NA	NR	NR
Root/Shoot Oven-Dry Weight Ratio	4.0	2.7ns	6.7	20.0*	66.7	NA	NA	NA	NA	NA	NA	NR	NR
Leaf Size and Shape													
Petiole Length (mm)	4.7	5.9*	4.7	36.7**	37.4	NA	NA	NA	NA	NA	NA	NR	10.6
Single-Leaf Abaxial Area (cm^2)	5.1	18.0**	3.2	±0.0ns	70.1	NA	NA	NA	NA	NA	NA	NR	3.7
Single-Leaf Oven-Dry Weight (mg)	7.4	7.4*	4.4	±0.0ns	73.5	NA	NA	NA	NA	NA	NA	NR	7.4
Specific Leaf Weight (mg/cm^2)	17.1	2.7ns	4.6	27.8**	47.5	NA	NA	NA	NA	NA	NA	NR	0.4
Stomatal Anatomy													
Stomatal Density ($\#/mm^2$)	1.0	6.5**	1.3	38.6**	20.2	NA	NA	NA	NA	NA	NA	NR	32.5
Stomatal Length (µm)	0.5	2.8ns	3.6	42.4**	22.5	NA	NA	NA	NA	NA	NA	NR	28.3
Stomatal Control													
Transpiration Rate ($\mu g/(cm^2 s)$)	3.7	0.6**	0.2	4.3**	6.1	47.4*	28.9	0.1ns	0.3	0.4ns	5.6	NR	2.4
Stomatal Conductance (cm/s)	3.6	2.4*	1.2	15.4**	24.9	10.7ns	9.5	0.2ns	1.2	2.4ns	16.6	NR	11.9

[1] Percentages of variation not followed by ns, * or ** do not have a valid test of significance. For detailed analyses of variance see Appendix IV.

[2] * and ** indicate significance at the 5% and 1% level, respectively.

[3] ns indicates non-significance at the 5% level.

[4] NA indicates that the source of variation is not applicable to the observed trait.

[5] NR indicates that the mean squares value is not retrievable (0 degrees of freedom).

Table 16. Provenance means for root and shoot traits measured in the greenhouse provenance trial.

Provenance	Internode Length (cm)	Shoot Length (mm)	Number of Leaves per Plant	Total Abaxial Leaf Area per Plant (cm^2)	Total Oven-Dry Leaf Weight per Plant (g)	Total Oven-Dry Shoot Weight (g)	Total Oven-Dry Root Weight (g)	Root/Shoot Weight Ratio
Northern Wisconsin	3.4 [1](2.6-3.8)	63.1 (51.0-78.5)	20 (15-24)	1189 (649-1585)	4.445 (2.170-5.757)	2.492 (1.057-3.693)	1.730 (1.000-2.277)	0.294 (0.188-0.358)
Thunder Bay	3.7 (3.0-4.6)	59.0 (41.0-74.8)	17 (11-22)	1035 (581-1654)	4.080 (2.170-7.607)	2.123 (0.970-3.983)	1.690 (1.003-3.020)	0.317 (0.220-0.454)
Pickle Lake	3.6 (2.8-4.6)	54.6 (32.5-85.3)	17 (11-23)	760 (303-1323)	3.072 (1.253-5.757)	1.814 (0.493-3.947)	1.329 (0.850-2.537)	0.348 (0.179-0.532)
Bearskin Lake	3.2 (2.6-4.0)	56.8 (48.2-75.7)	21 (16-25)	999 (521-1424)	4.038 (2.063-6.167)	2.334 (1.293-4.777)	1.882 (1.217-3.187)	0.348 (0.221-0.443)

[1] Range of clone means within each provenance.

variation, with Thunder Bay and Pickle Lake having the lowest average number of leaves per plant (17) and Bearskin Lake having the highest (21) (Table 16). Northern Wisconsin had an average of 20 leaves per plant. The clone-within-provenance effect accounted for 11.0 percent of the variation, while the block*clone-within-provenance interaction accounted for the majority of the variation (73.1 percent). Clone-within-provenance means ranged from 11 to 25 leaves per plant.

The provenance effect was not significant for the remaining root and shoot traits (shoot length, total abaxial leaf area per plant, total oven-dry leaf, shoot and root weights and root/shoot oven-dry weight ratio) (Table 15). On average, the provenance effect accounted for less than 3 percent of the observed variation. Shoot lengths, total abaxial leaf area, and total oven-dry leaf and shoot weights ranged from a high of 63.1 cm, 1189 cm^2, 4.445 g and 2.492 g for Northern Wisconsin to a low of 54.6 cm, 760 cm^2, 3.072 g and 1.814 g for Pickle Lake, respectively (Table 16). Pickle Lake also had the lowest oven-dry root weight (1.814 g) and the highest root/shoot weight ratio (0.348). Bearskin Lake had the highest oven-dry root weight (1.882 g) and a root/shoot ratio (0.348) similar to that of Pickle Lake. Northern Wisconsin had the lowest root/shoot ratio (0.294). Of the aforementioned traits, the clone-within-provenance effect was only significant for the root/shoot ratio, and accounted for 20.0 percent of the variation. Clone mean root/shoot ratios ranged from 0.179 to 0.532. However, large ranges in clone means were also observed for

shoot lengths, total abaxial leaf areas, and total oven-dry leaf, shoot and root weights, but this was attributable to a large block*clone-within-provenance interaction, which accounted for over 85 percent of the variation in these traits.

b. Variation in Leaf Size and Morphology

The provenance effect accounted for only 5.9 percent of the variation observed in petiole lengths, but was significant at the 5 percent level (Table 15). There was a noted decrease in petiole length from southern to northern provenances (Table 17). Northern Wisconsin, the most southern provenance, had a petiole length of 23.5 mm, while Bearskin Lake, the most northern provenance, had a petiole length of 19.3 mm. The clone-within-provenance effect had a significant influence on petiole lengths, accounting for 36.7 percent of the variation. Clone-within-provenance means ranged from 11.7 to 33.5 mm. The interaction between blocks and clones-within-provenances accounted for 37.4 percent of the detected variation.

A significant provenance effect accounted for 18.0 and 7.4 percent of the variation in single-leaf abaxial leaf area and oven-dry leaf weight, respectively (Table 15). The Northern Wisconsin provenance had larger, heavier leaves than those from Thunder Bay, Bearskin Lake and Pickle Lake, which are listed in decreasing order of magnitude (Table 17). Although clone means ranged from 35.6 to 101.9 cm^2 for single-leaf abaxial area and from 123 to 423 g for single-leaf oven-dry weights, the clone-within-

Table 17. Provenance means for leaf size and morphology and stomatal anatomy traits measured in the greenhouse provenance trial.

Provenance	Leaf Size and Morphology				Stomatal Anatomy	
	Petiole Length (mm)	Single-Leaf Abaxial Area (cm^2)	Single-Leaf Oven-Dry Leaf Weight (mg)	Specific Leaf Weight (mg/cm^2)	Stomatal Density ($\#/mm^2$)	Stomatal Length (um)
Northern Wisconsin	23.5 [1](19.8-33.5)	85.6 (63.1-100.6)	293 (186-398)	3.36 (2.86-4.11)	189 (147-236)	30.2 (27.3-32.4)
Thunder Bay	21.9 (17.0-28.3)	79.7 (62.9-101.9)	286 (210-423)	3.53 (3.00-4.12)	227 (197-273)	30.6 (27.2-33.4)
Pickle Lake	21.1 (14.3-26.8)	58.6 (35.6-78.6)	216 (123-318)	3.62 (3.17-4.04)	214 (185-285)	29.4 (27.1-32.4)
Bearskin Lake	19.3 (11.7-25.7)	63.7 (41.1-86.7)	236 (142-327)	3.65 (3.35-4.16)	204 (142-259)	31.2 (27.5-39.5)

[1] Range of clone means within each provenance.

provenance effect was not significant. This was due to the large error term (block*clone-within-provenance interaction), which accounted for over 70 percent of the observed variation in these traits.

There were no significant differences among provenance specific leaf weights (Table 15), but a north-south trend was noted (Table 17). There was a gradual increase in specific leaf weights from 3.36 g/cm^2 for Northern Wisconsin, the most southern provenance, to 3.65 g/cm^2 for Bearskin Lake, the most northern provenance. The clone-within-provenance effect accounted for 27.8 percent of the observed variation and was significant at the 1 percent level. Clone-within-provenance means ranged from 2.86 to 4.16 g/cm^2. The block*clone-within-provenance interaction accounted for 47.5 percent of the observed variation.

Provenance mean leaf outlines are presented in Figure 14. Generally, leaf width and length decrease with latitude, while the

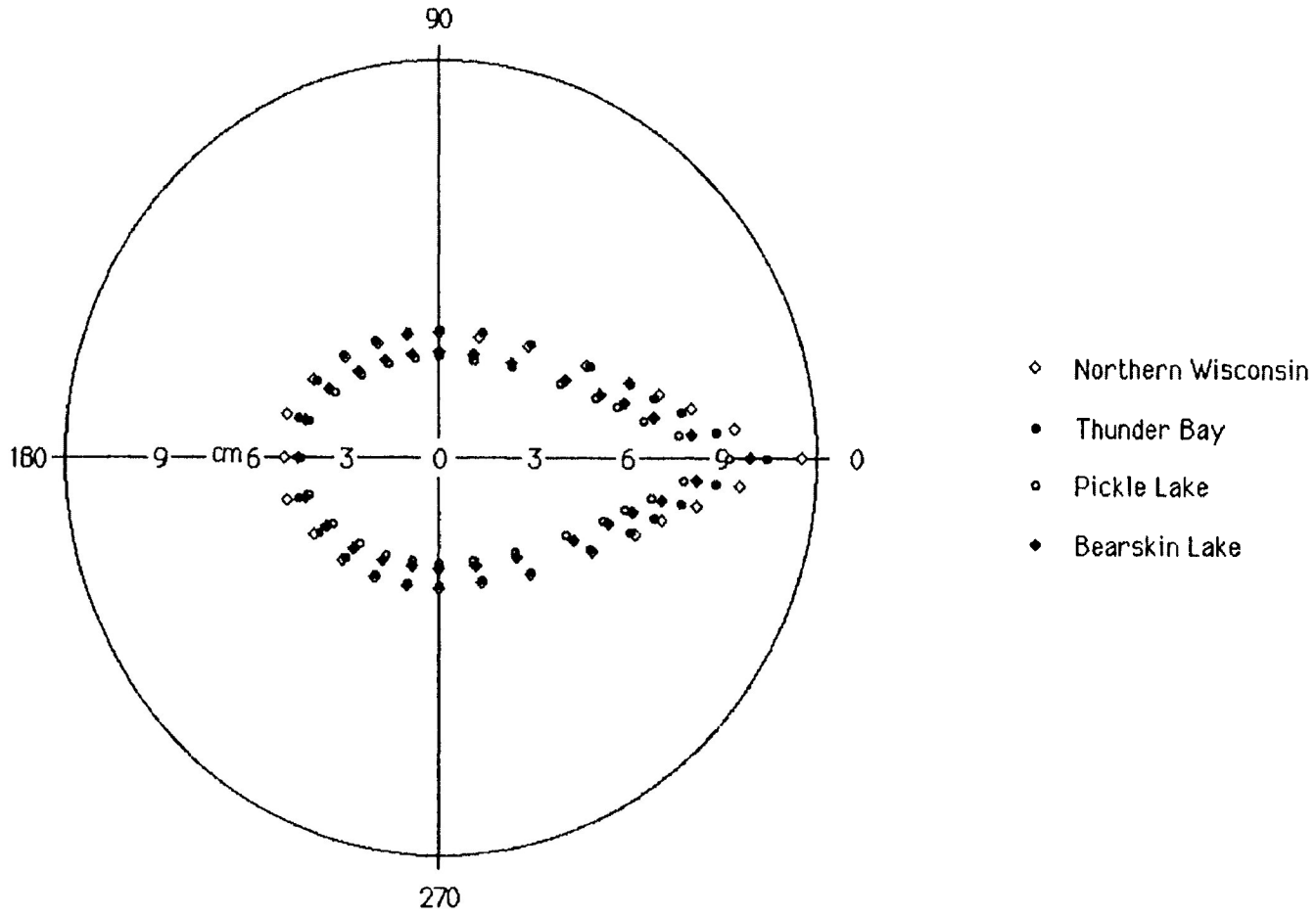


Figure 14. Average leaf outlines for the four provenances of balsam poplar in the greenhouse provenance trial.

ratio of leaf length to leaf width increases. The lone exception to this trend is the Pickle Lake provenance. The average leaf of the Pickle Lake provenance is slightly shorter and narrower than the average leaf of the Bearskin Lake provenance, which has a higher latitude (Figure 14).

Table 18 and Figures 15 through 20 present the results of the m-PCA analysis of leaf shape data. M-PCA analysis of the sixty-six radial and truss distances resulted in the extraction of four principal component axes, accounting for 98.3 percent of the detected variation (Table 18).

The first axis (PCAF1) accounted for 85.6 percent of the variation exhibited by the sixty-six distances. On the first axis, all radial and truss distances made large positive contributions, indicating that this axis is mainly a descriptor of variation in leaf size (Pimental, 1979).

Radial and truss distances near the base of the leaf made large positive contributions to the second axis (PCAF2), which accounted for 7.1 percent of the variation in leaf distances. Loadings decreased in magnitude towards the middle of the leaf and became negative. Contributions remained negative and generally increased in magnitude as distances incorporated pseudolandmarks closer to the base of the leaf. Thus, having both positive and negative loadings, PCAF2 can be interpreted as describing variation in leaf shape (Pimental, 1979). Moreover, since leaf shape distances incorporating pseudolandmarks near the base of the leaf made the largest positive loadings, PCAF2 can be classified as being a descriptor of variation in the shape of the

leaf base.

Table 18. Multi-group principal components analysis of variance of the sixty-six radial and truss distances for the four provenances of balsam poplar in the greenhouse provenance trial.

	Principal Components			
	PCAF1	PCAF2	PCAF3	PCAF4
Cummulative Variance (%)	85.6	92.7	96.2	98.3
Radial and Truss Distances	Eigenvectors			
R1,2	0.914	-0.097	0.330	0.091
R1,3	0.936	-0.135	0.255	0.139
R1,4	0.948	-0.160	0.151	0.184
R1,5	0.953	-0.177	0.093	0.200
R1,6	0.948	-0.186	0.030	0.226
R1,7	0.940	-0.187	-0.062	0.247
R1,8	0.924	-0.207	-0.186	0.234
R1,9	0.919	-0.192	-0.249	0.211
R1,10	0.917	-0.177	-0.276	0.195
R1,11	0.923	-0.150	-0.177	0.188
R1,12	0.935	-0.075	-0.266	0.176
R1,13	0.944	0.080	-0.229	0.152
R1,14	0.910	0.324	-0.132	0.144
R1,15	0.790	0.589	0.015	0.116
R1,16	0.572	0.773	0.178	0.085
R1,17	0.778	0.616	0.054	-0.025
R1,18	0.894	0.403	-0.031	-0.128
R1,19	0.941	0.202	-0.089	-0.209
R1,20	0.949	0.048	-0.108	-0.264
R1,21	0.939	-0.042	-0.096	-0.302
R1,22	0.932	-0.064	-0.089	-0.324
R1,23	0.930	-0.075	-0.061	-0.332
R1,24	0.934	-0.098	0.010	-0.317
R1,25	0.945	-0.115	0.125	-0.245
R1,26	0.950	-0.128	0.203	-0.168
R1,27	0.949	-0.130	0.242	-0.119
R1,28	0.943	-0.126	0.261	-0.058
R1,29	0.933	-0.119	0.317	0.029
T3,29	0.908	-0.088	0.332	0.043
T3,28	0.867	-0.127	0.231	0.310
T4,29	0.806	-0.061	0.476	-0.145
T4,28	0.942	-0.135	0.261	0.029
T4,27	0.945	-0.159	0.180	0.180
T5,28	0.920	-0.113	0.332	-0.093
T5,27	0.964	-0.152	0.204	0.021
T5,26	0.966	-0.167	0.144	0.108
T6,27	0.958	-0.113	0.222	-0.065
T6,26	0.973	-0.161	0.141	0.013
T6,25	0.971	-0.147	0.139	-0.064
T7,26	0.974	-0.172	0.068	0.091
T7,25	0.981	-0.157	0.034	-0.001
T7,24	0.979	-0.163	-0.035	0.045
T8,25	0.981	-0.153	0.010	-0.066
T8,24	0.978	-0.161	-0.093	-0.033
T8,23	0.975	-0.156	-0.135	-0.015
T9,24	0.977	-0.149	-0.118	-0.065
T9,23	0.973	-0.142	-0.166	-0.049
T9,22	0.970	-0.137	-0.181	-0.042
T10,23	0.971	-0.132	-0.179	61.000
T10,21	0.970	-0.115	-0.198	-0.044
T11,22	0.970	-0.111	-0.195	-0.060
T11,21	0.972	-0.100	-0.198	-0.049
T11,20	0.975	-0.053	-0.202	-0.033
T12,21	0.976	-0.059	-0.193	-0.054
T12,20	0.977	-0.013	-0.196	-0.039
T12,19	0.977	0.069	-0.183	-0.017
T13,20	0.978	0.070	-0.174	-0.044
T13,19	0.971	0.147	-0.160	-0.022
T13,18	0.950	0.269	-0.123	0.006
T14,19	0.949	0.275	-0.113	-0.017
T14,18	0.917	0.375	-0.083	0.007
T14,17	0.844	0.530	-0.004	0.037
T15,18	0.844	0.530	-0.005	0.021
T15,17	0.790	0.607	0.038	0.040
T15,16	0.644	0.677	0.139	0.132
T16,17	0.661	0.690	0.149	-0.009

[1] R, T, 1 and 2-29 indicate radial distances, truss distances, reference point and pseudolandmarks respectively.

The third axis (PCAF3) was also bipolar, indicating variation in leaf shape. Accounting for 3.5 percent of the total variation in radial and truss distances, the third axis loaded most heavily with leaf distances incorporating pseudolandmarks near the tip of the leaf. Towards the middle of the leaf, contributions decreased in magnitude and became negative. At the leaf base, distances incorporating pseudolandmarks 15, 16 and 17 (see Figures 4 and 5) made positive contributions, but were smaller in magnitude than the contributions from distances at the leaf tip. Thus, the third axis (PCAF3) is a descriptor of variation in the shape of the leaf tip and to a lesser extent the extreme base of the leaf.

The fourth axis (PCAF4), a bipolar component, accounted for 2.1 percent of the total variation detected in the radial and truss distances. On average truss distances did not make a large contribution to the fourth axis. In contrast, radial distances made the largest contributions to the axis. Furthermore, the contributions were positive on the right side of the leaf and negative on the left side. Thus, the fourth axis, unlike the previous axes, is a descriptor of variation in the size and shape of each side of the leaf.

Figures 15 through 20 show that provenances form a continuously overlapping cluster, with the arrangement of provenances in the ordinations not reflecting their geographic affinity (latitude). The only suggestion of any distinctions among provenances occur in the first and third axes. The first axis (Figures 15, 16 and 17) appears to group Northern Wisconsin, Thunder Bay and Bearskin Lake together, leaving Pickle Lake

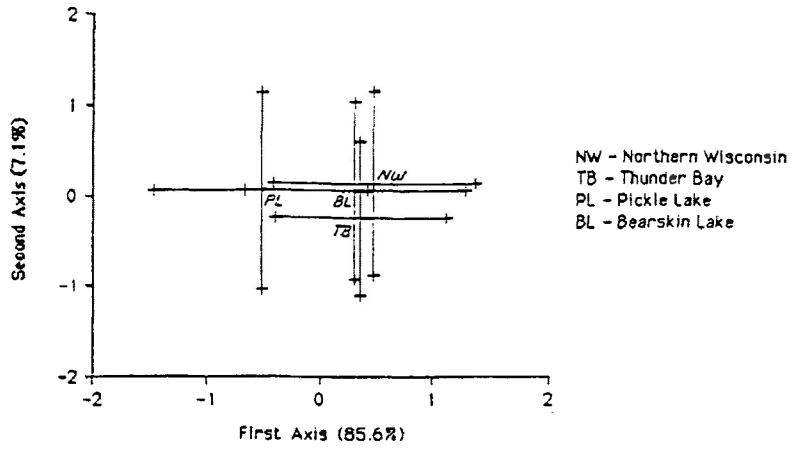


Figure 15. Two-dimensional ordination of four provenances of balsam poplar based on the first (PCAF1) and second (PCAF2) principal components axes for the greenhouse provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

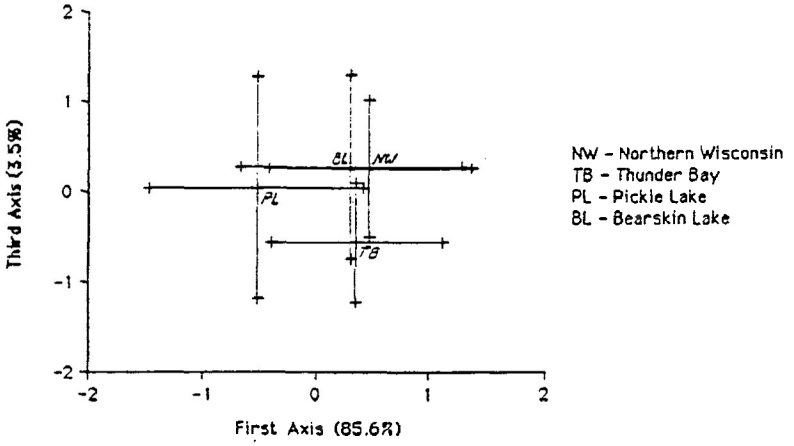


Figure 16. Two-dimensional ordination of four provenances of balsam poplar based on the first (PCAF1) and third (PCAF3) principal components axes for the greenhouse provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

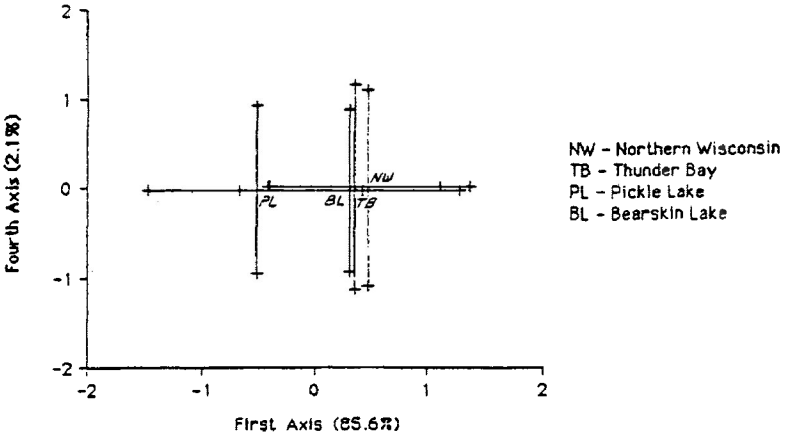


Figure 17. Two-dimensional ordination of four provenances of balsam poplar based on the first (PCAF1) and fourth (PCAF4) principal components axes for the greenhouse provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

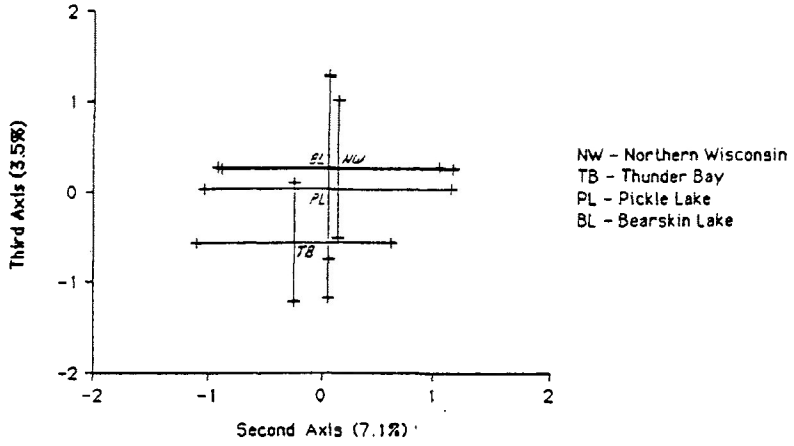


Figure 18. Two-dimensional ordination of four provenances of balsam poplar based on the second (PCAF2) and third (PCAF3) principal components axes for the greenhouse provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

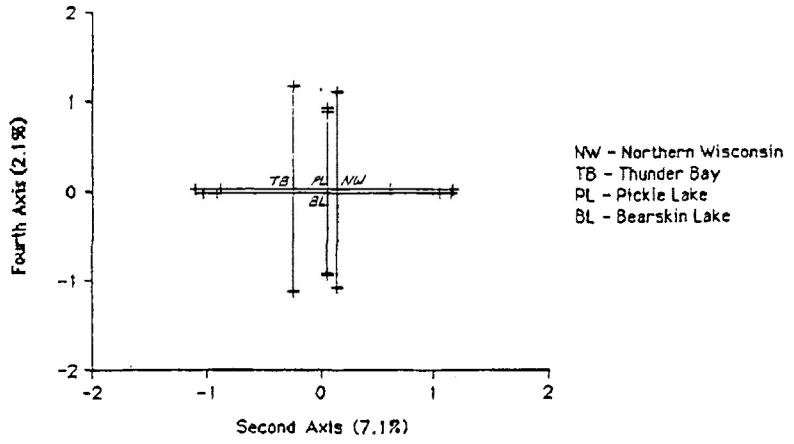


Figure 19. Two-dimensional ordination of four provenances of balsam poplar based on the second (PCAF2) and fourth (PCAF4) principal components axes for the greenhouse provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

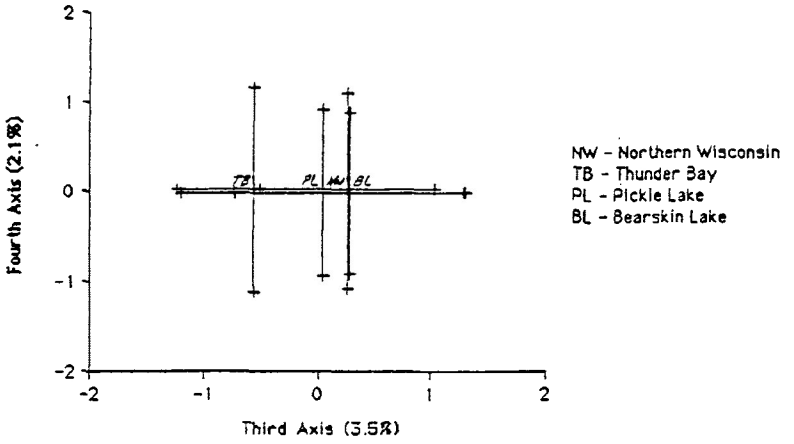


Figure 20. Two-dimensional ordination of four provenances of balsam poplar based on the third (PCAF3) and fourth (PCAF4) principal components axes for the greenhouse provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

somewhat distinct. The third axis separates Thunder Bay from the other three provenances.

Discriminant functions analysis using the four m-PCA factors or axes as predictor variables formed three DFA axes, which accounted for 100 percent of the observed variation in the m-PCA axes (Table 19). PCAF1 made a large positive contribution to the first axis (DFAS1), which accounted for 71.4 percent of the variation. PCAF3 and PCAF2 made smaller negative contributions, while PCAF4 made the smallest contribution. The second DFA axis (DFAS2) accounted for 28.3 percent of the observed variation exhibited by the m-PCA axes. PCAF3 made the largest positive contribution and was followed by PCAF1 and PCAF2, respectively. PCAF4 made a very small negative contribution to the second axis. The third axis (DFAS3) accounted for only 0.3 percent of the total variation in m-PCA axes. PCAF2 made a large negative contribution to DFAS3. PCAF3 made a smaller negative contribution, while PCAF1 made a much smaller negative

Table 19. Discriminant functions analysis of the four multi-group principal component functions for the four balsam poplar provenances in the greenhouse provenance trial.

	Discriminant Functions		
	DFAS1	DFAS2	DFAS3
Cummulative Variance (%)	71.4	99.7	100.0
PCA Factor	Discriminant Functions Coefficients		
PCAF1	0.940	0.574	-0.010
PCAF2	-0.234	0.346	-0.910
PCAF3	-0.570	0.804	-0.384
PCAF4	0.040	-0.005	0.101

contribution. PCAF4 made a small contribution of the opposite polarity.

Two dimensional ordinations of the four provenances based on discriminant functions analysis are presented in Figures 21, 22 and 23. Although populations form a continuously overlapping cluster, the first and second axes (DFAS1 and DFAS2) groups the two most northern provenances (Bearskin Lake and Pickle Lake) together (Figures 21 and 22). Northern Wisconsin and Thunder Bay are somewhat distinct from each other and the more northern provenances. The third axis does not separate the provenances and does not reflect any geographic trends.

c. Variation in Stomatal Anatomy

The provenance effect had a significant influence on stomatal densities, with 6.5 percent of the variation being attributable to this effect (Table 15). All provenances except Northern Wisconsin (189 stomata/mm^2) had stomatal densities greater than 200 per mm^2 (Table 17). Thunder Bay (227 stomata/mm^2) had the greatest number of stomata per square millimeter. The clone-within-provenance effect was also highly significant, accounting for 38.6 percent of the variation. Clonal means for stomatal density ranged from 142 to 285 stomata/mm^2. The block*clone-within-provenance interaction and sampling error (ie. variation within ramets of a single clone) accounted for 20.2 and 32.5 percent of the variation in stomatal densities, respectively.

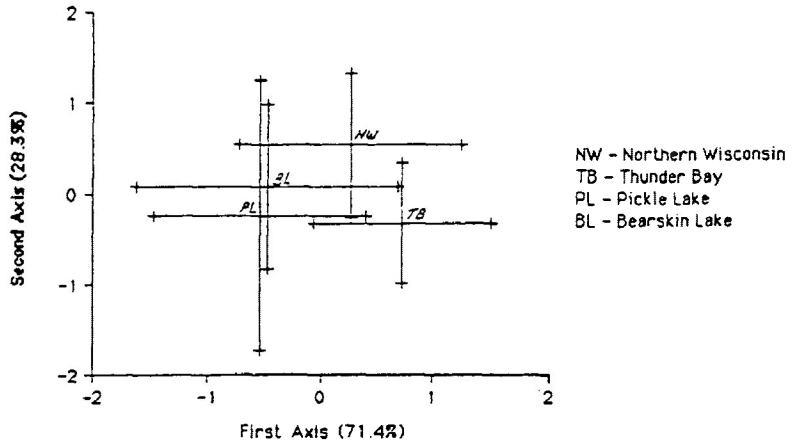


Figure 21. Two-dimensional ordination of four provenances of balsam poplar based on the first (DFAS1) and second (DFAS2) discriminant functions axes for the greenhouse provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

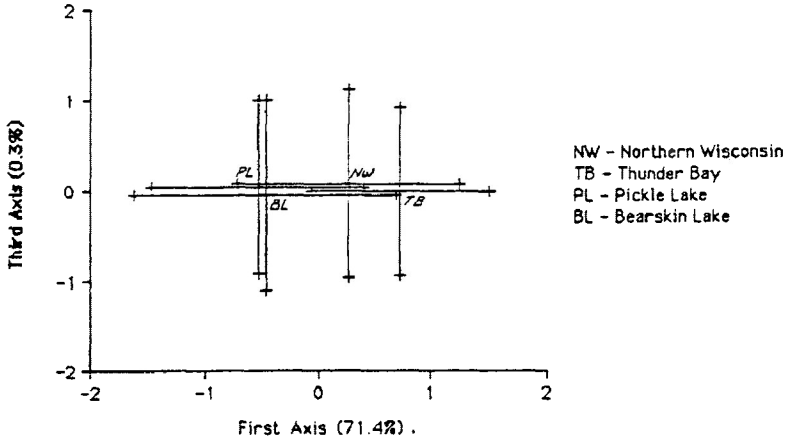


Figure 22. Two-dimensional ordination of four provenances of balsam poplar based on the first (DFAS1) and third (DFAS3) discriminant functions axes for the greenhouse provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

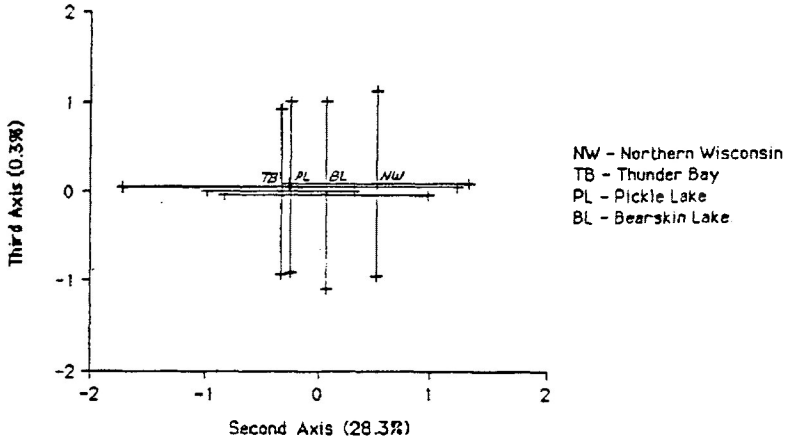


Figure 23. Two-dimensional ordination of four provenances of balsam poplar based on the second (DFAS2) and third (DFAS3) discriminant functions axes for the greenhouse provenance trial. The horizontal and vertical lines represent one standard deviation to each side of the provenance means.

The provenance effect did not have a significant influence on stomatal lengths (Table 15). Provenance means ranged from 29.4 µm for Pickle Lake to 31.2 µm for Bearskin Lake (Table 17). Only 2.8 percent of the variation in stomatal lengths was attributable to the provenance effect. The clone-within-provenance effect, accounting for 40 percent of the variation, had a significant influence, with values ranging from 27.1 to 39.5 µm. The majority of the remaining variation was attributable to the block*clone-within-provenance interaction and subsampling error.

d. Variation in Stomatal Control

The day, provenance and clone-within-provenance effects all had a significant effect on transpiration rates (Table 15). The day effect accounted for 47.4 percent of the variation observed in transpiration rates. The lowest rate was recorded for July 14 (4.264 µg/(cm^2s)), while July 12 had the highest rate (10.283 µg/(cm^2s)) (Table 20). The average rates of transpiration for July 11 and 13 were 7.345 and 7.416 µg/(cm^2s) respectively. The interaction between blocks and days accounted for 28.9 percent of the variation. Only 0.6 percent of the variation was attributable to the provenance effect. There was no apparent pattern in variation, but generally, Thunder Bay and Bearskin Lake have higher average transpiration rates than Pickle Lake and Northern Wisconsin. Lowest average transpiration rates, which ranged from 3.919 µg/(cm^2s) for Pickle Lake to 4.454 µg/(cm^2s) for Thunder Bay, occurred on July 14. Highest provenance mean

transpiration rates were recorded on July 12, and ranged from 9.883 µg/(cm2s) for Northern Wisconsin to 10.665 µg/(cm2s) for Thunder Bay. The clone-within-provenance effect accounted for 4.3 percent of the variation.

Table 20. Average transpiration rates and stomatal conductance for days and provenances in the greenhouse provenance trial.

Date	Provenance	Mean Provenance Transpiration Rate (µg/ cm2s)	Mean Provenance Stomatal Conductance (cm/s)
July 11, 1988.	Northern Wisconsin	7.177	0.940
		*(6.305-7.708)	(0.829-1.048)
	Thunder Bay	7.531	0.986
		(5.285-8.456)	(0.650-1.121)
	Pickle Lake	7.194	0.938
		(6.230-8.309)	(0.789-1.136)
	Bearskin Lake	7.478	0.987
		(6.243-8.459)	(0.804-1.146)
	Mean	7.345	0.963
July 12, 1988.	Northern Wisconsin	9.883	1.073
		(8.379-11.279)	(0.821-1.291)
	Thunder Bay	10.660	1.156
		(7.780-12.136)	(0.765-1.332)
	Pickle Lake	9.951	1.106
		(8.967-11.506)	(0.898-1.272)
	Bearskin Lake	10.635	1.189
		(8.951-11.931)	(0.995-1.357)
	Mean	10.283	1.131
July 13, 1988.	Northern Wisconsin	7.229	1.015
		(5.416-8.335)	(0.736-1.152)
	Thunder Bay	7.631	1.094
		(5.649-9.002)	(0.751-1.348)
	Pickle Lake	7.121	1.014
		(4.953-8.346)	(0.650-1.220)
	Bearskin Lake	7.680	1.092
		(6.267-8.664)	(0.822-1.268)
	Mean	7.416	1.054
July 14, 1988.	Northern Wisconsin	4.276	0.877
		(3.191-5.176)	(0.639-1.090)
	Thunder Bay	4.454	0.943
		(2.467-5.798)	(0.475-1.324)
	Pickle Lake	3.919	0.796
		(2.603-4.874)	(0.493-1.017)
	Bearskin Lake	4.408	0.911
		(3.070-5.070)	(0.611-1.105)
	Mean	4.264	0.882

* Range of clone means within each provenance.

Unlike transpiration rates, days did not have a significant influence on stomatal conductances, but the pattern of variation was similar to that of transpiration rates (Table 15). Daily values ranged from a low of 0.882 cm/s on July 14 to a high of 1.113 cm/s on July 12 (Table 20). In total, the day effect and its interactions with blocks, provenances and clones-within-provenances accounted for 40.6 percent of the observed variation. The provenance effect accounted for 2.4 percent of the variation and was significant at the 5 percent level. The lowest provenance means were recorded on July 14, and ranged from 0.796 cm/s for Pickle Lake to 0.943 cm/s for Thunder Bay. The highest provenance means, which ranged from 1.073 cm/s for Northern Wisconsin to 1.189 cm/s for Pickle Lake, occurred on July 12. Differences among clones-within-provenances were significant at the 1 percent level of significance and 15.4 percent of the variation in stomatal conductances was attributable to this effect.

2. Phenotypic Correlations

Pearson's product-moment correlations among measured traits and latitude are presented in Table 21. Root and shoot traits, excluding internode lengths, were significantly correlated. Correlations among shoot length, number of leaves per plant, total abaxial leaf area, and total oven-dry leaf, shoot and root weights were all high and positive. Correlations between root/shoot weight ratios and the aforementioned traits were also significant, but negative. The only root and shoot trait having a

Table 21. Pearson's product-moment correlation coefficients and their one-tailed significance for clone-mean traits measured in the greenhouse provenance trial.

	Root and Shoot								Leaf Size and Morphology							
	Internode Length (cm)	Shoot Length (cm)	Number of Leaves per Plant	Total Abaxial Leaf Area per Plant (cm^2)	Total Oven-Dry Leaf Weight per Plant (g)	Total Oven-Dry Shoot Weight (g)	Total Oven-Dry Root Weight (g)	Root/Shoot Oven-Dry Weight Ratio	Petiole Length (mm)	Single-Leaf Abaxial Area (cm^2)	Single-Leaf Oven-Dry Weight (mg)	Specific Leaf Weight ($mg/(cm^2 s)$)	PCAF1	PCAF2	PCAF3	PCAF4
Root and Shoot																
Internode Length (cm)	1.000															
Shoot Length (cm)	*0.250**	1.000														
Number of Leaves per Plant	-0.054	0.875**	1.000													
Total Abaxial Leaf Area per Plant (cm^2)	0.087	0.917**	0.872**	1.000												
Total Oven-Dry Leaf Weight per Plant (g)	0.100	0.900**	0.854**	0.986**	1.000											
Total Oven-Dry Shoot Weight (g)	0.119	0.926**	0.873**	0.952**	0.968**	1.000										
Total Oven-Dry Root Weight (g)	0.066	0.758**	0.737**	0.838**	0.883**	0.877**	1.000									
Root/Shoot Oven-Dry Weight Ratio	-0.108	-0.713**	-0.669**	-0.661**	-0.608**	-0.588**	-0.286**	1.000								
Leaf Size and Morphology																
Petiole Length (mm)	0.252**	0.254**	0.122	0.306**	0.317**	0.297**	0.318**	-0.137	1.000							
Single-Leaf Abaxial Area (cm^2)	0.231**	0.790**	0.644**	0.878**	0.853**	0.771**	0.706**	-0.628**	0.434**	1.000						
Single-Leaf Oven-Dry Weight (mg/cm^2)	0.229**	0.794**	0.654**	0.882**	0.901**	0.830**	0.797**	-0.562**	0.450**	0.956**	1.000					
Specific Leaf Weight (mg/cm^2)	0.111	0.326**	0.308**	0.365**	0.479**	0.476**	0.545**	-0.059	-0.292**	-0.286**	-0.536**	1.000				
PCAF1	0.240**	0.797**	0.657**	0.855**	0.826**	0.750**	0.683**	-0.667**	0.413**	0.983**	0.934**	0.277**	1.000			
PCAF2	-0.092	-0.161*	-0.066	-0.104	-0.117	-0.150	-0.101	-0.001	-0.076	-0.032	-0.059	-0.113	-0.050	1.000		
PCAF3	-0.041	0.107	0.194*	0.100	0.094	0.126	0.132	-0.194*	0.133	0.001	0.008	0.035	-0.013	0.183*	1.000	
PCAF4	-0.078	0.050	0.126	0.056	0.035	0.032	-0.004	-0.070	0.117	0.025	0.006	-0.003	0.020	-0.004	0.199*	1.000
Stomatal Anatomy																
Stomatal Density (#/mm^2)	0.020	0.005	-0.003	-0.081	-0.064	-0.040	-0.060	-0.018	-0.176*	-0.147	-0.110	0.054	-0.099	-0.253**	-0.222**	-0.151
Stomatal Length (µm)	0.118	0.149	0.042	0.266**	0.300**	0.230**	0.297**	-0.021	0.243**	0.323**	0.380**	0.280**	0.275**	-0.021	-0.092	0.000
Stomatal Control																
Transpiration Rate ($\mu g/(cm^2 s)$) July 11, 1988.	-0.021	-0.057	-0.074	-0.018	-0.013	-0.076	-0.019	0.007	-0.134	-0.026	-0.010	0.013	-0.038	0.045	0.015	0.021
Stomatal Conductance (cm/s) July 11, 1988.	-0.013	-0.072	-0.079	-0.030	-0.025	-0.090	-0.036	0.008	-0.137	-0.025	-0.015	-0.006	-0.040	0.078	0.011	0.010
Transpiration Rate ($\mu g/(cm^2 s)$) July 12, 1988.	-0.044	0.128	0.132	0.139	0.173*	0.156	0.181	-0.067	0.051	0.157*	0.226**	0.282**	0.149	-0.058	-0.027	-0.062
Stomatal Conductance (cm/s) July 12, 1988.	0.045	0.155	0.151	0.169*	0.205*	0.162*	0.199*	-0.075	-0.018	0.153	0.232**	0.330**	0.137	-0.004	-0.019	-0.082
Transpiration Rate ($\mu g/(cm^2 s)$) July 13, 1988.	0.124	0.179*	0.137	0.217*	0.215*	0.186*	0.198*	-0.153	-0.141	-0.146	0.148	-0.006	0.144	0.048	0.021	-0.088
Stomatal Conductance (cm/s) July 13, 1988.	0.139	0.253**	0.192*	0.280**	0.292**	0.245**	0.253**	-0.218*	-0.092	0.217*	0.246**	0.125	0.216*	0.007	0.018	-0.087
Transpiration Rate ($\mu g/(cm^2 s)$) July 14, 1988.	0.130	0.162*	0.118	0.190*	0.180*	0.131	0.142	-0.105	-0.034	0.124	0.120	-0.003	0.117	0.000	0.099	0.043
Stomatal Conductance (cm/s) July 14, 1988.	0.124	0.211*	0.154	0.247**	0.249**	0.198*	0.222*	-0.110	-0.005	0.180*	0.196*	0.079	0.170*	-0.058	0.064	0.034
Latitude																
Latitude	-0.108	-0.123	0.083	-0.146	-0.089	-0.049	0.020	-0.169*	-0.267**	-0.357**	-0.239**	0.218*	-0.351**	0.008	0.078	-0.019

[1] * and ** indicate significance at the 5% and 1% level, respectively.

Table 21 continued.

	Stomatal Anatomy		Stomatal Control								Latitude
	Stomatal Density (#/mm²)	Stomatal Length (µm)	Transpiration Rate (µg/(cm²s)) July 11, 1988.	Stomatal Conductance (cm/s) July 11, 1988.	Transpiration Rate (µg/(cm²s)) July 12, 1988.	Stomatal Conductance (cm/s) July 12, 1988.	Transpiration Rate (µg/(cm²s)) July 13, 1988.	Stomatal Conductance (cm/s) July 13, 1988.	Transpiration Rate (µg/(cm²s)) July 14, 1988.	Stomatal Conductance (cm/s) July 14, 1988.	Latitude
Root and Shoot											
Internode Length (cm)											
Shoot Length (cm)											
Number of Leaves per Plant											
Total Abaxial Leaf Area per Plant (cm²)											
Total Oven-Dry Leaf Weight per Plant (g)											
Total Oven-Dry Shoot Weight (g)											
Total Oven-Dry Root Weight (g)											
Root/Shoot Oven-Dry Weight Ratio											
Leaf Size and Morphology											
Petiole Length (mm)											
Single-Leaf Abaxial Area (cm²)											
Single-Leaf Oven-Dry Weight (mg/cm²)											
Specific Leaf Weight (mg/cm²)											
PCAF1											
PCAF2											
PCAF3											
PCAF4											
Stomatal Anatomy											
Stomatal Density (#/mm²)	1.000										
Stomatal Length (µm)	-0.440**	1.000									
Stomatal Control											
Transpiration Rate (µg/(cm²s)) July 11, 1988.	-0.029	0.395**	1.000								
Stomatal Conductance (cm/s) July 11, 1988.	-0.027	0.369**	0.979**	1.000							
Transpiration Rate (µg/(cm²s)) July 12, 1988.	-0.073	0.242**	0.267**	0.322**	1.000						
Stomatal Conductance (cm/s) July 12, 1988.	-0.018	0.345**	0.536**	0.600**	0.785**	1.000					
Transpiration Rate (µg/(cm²s)) July 13, 1988.	0.143	0.330**	0.624**	0.640**	0.123	0.482**	1.000				
Stomatal Conductance (cm/s) July 13, 1988.	0.118	0.426**	0.683**	0.697**	0.273**	0.631**	0.938**	1.000			
Transpiration Rate (µg/(cm²s)) July 14, 1988.	0.082	0.354**	0.571**	0.545**	-0.081	0.295**	0.665**	0.694**	1.000		
Stomatal Conductance (cm/s) July 14, 1988.	0.074	0.449**	0.613**	0.587**	0.111	0.420**	0.688**	0.743**	0.961**	1.000	
Latitude											
Latitude	0.095	0.060	0.068	0.067	0.051	0.145	0.086	0.095	0.008	0.001	1.000

significant correlation with internode length was shoot length. The correlation coefficient was positive, but low (r=0.250).

Internode length was significantly correlated with the leaf size traits: petiole length, single-leaf abaxial area, single leaf oven-dry weight and PCAF1. The correlation coefficients were low and positive. The root/shoot weight ratio was significantly correlated with single-leaf abaxial area, single-leaf oven-dry weight and PCAF1, having moderately high negative correlation coefficients. Excluding the correlation between the number of leaves per plant and petiole length, which was not significant, correlations of shoot lengths, number of leaves per plant, total abaxial leaf areas, and total oven-dry leaf, shoot and root weights with petiole lengths, single-leaf abaxial areas, single leaf oven-dry weights, specific leaf weights and PCAF1 were high, positive and significant at the 1 percent level. Moderately high, positive correlations were detected among stomatal lengths and total abaxial leaf areas and total oven-dry leaf, shoot and root weights. Dependent upon the day of measurement, significant correlations, although weak, were detected among stomatal control traits and root and shoot traits. For example, shoot length was significantly correlated with stomatal conductance and transpiration rates on July 13 and 14, but not on July 11 and 12.

Among leaf size and morphology traits, petiole lengths, single-leaf abaxial areas, single-leaf oven-dry weights and PCAF1 were, on average, positively correlated, with moderately high, significant correlation coefficients. Specific leaf weight was negatively correlated to the aforementioned traits. These traits

also showed a positive relationship with stomatal lengths, although the correlation coefficients were quite low. Once again sporadic significant correlations were noted among leaf shape traits and stomatal conductances and transpiration rates.

Stomatal density and stomatal length were negatively correlated, having a moderately high correlation coefficient that was significant at the 1 percent level. Stomatal density was not correlated with transpiration rates or stomatal conductance. However, stomatal length showed a significant positive relationship with both transpiration rates and stomatal conductance.

As expected, correlations among transpiration rates and stomatal conductance for individual days were high, positive and significant at the 1 percent level. The only exceptions involve correlations across days. Correlation coefficients were close to zero for correlations between transpiration rates on July 12 and stomatal conductance measurements on July 14 and transpiration rates on July 13 and 14.

Correlations between latitude and the measured traits indicate that there is no significant relationship between latitude and stomatal control traits. In fact, the only traits having significant correlations with latitude were the root/shoot oven-dry weight ratio, petiole length, single-leaf abaxial area and oven-dry weight, specific leaf weight and PCAF1. For all except the specific leaf weight, the correlation coefficients were negative and moderately low. The correlation coefficient for specific leaf weight was also moderately low, but positive.

V. DISCUSSION

There were two main objectives for this study. The first objective was to determine the extent and pattern of genetic variation in balsam poplar, especially for traits potentially affecting the control of transpiration, and hence, the photosynthesis-transpiration compromise. The second objective was to determine how the observed variation in traits were correlated to each other and to measured transpiration rates.

Contrary to what was expected, few significant differences among provenances in traits potentially affecting the water relations of balsam poplar were detected. In the both the field and greenhouse provenance trial, significant differences were noted for traits indicative of leaf size and morphology: petiole length, single-leaf abaxial area and oven-dry leaf weight, and specific leaf weight. Moreover a clinal trend with latitude was observed. Leaves of plants of northern origin were smaller in area, lighter in weight, had shorter petiole lengths, and were thicker than those of more southern origin. Although climatic information for each seed source was not gathered, it would appear that the leaves of seedlings from more northern sources are best suited for drier climates. Drew and Bazzaz (1978) studied populations of eastern cottonwood ranging over the north -south distribution of the species along the Mississippi River, and

found that leaves from the Wisconsin area (most northern source) had similar characteristics of those of balsam poplar from northern Wisconsin. Drew and Bazzaz (1978) postulated that the thinner leaves and higher specific leaf area (lower specific leaf weight) could be associated with the shorter growing season and/or higher moisture availability. Although the species differ, results from this study indicate that it is highly likely that the adaptations are a response to increased moisture availability. If thinner leaves were a response to shorter growing seasons, one would expect thinner and larger leaves for seedlings of the more northern sources. The opposite occurred.

In the greenhouse provenance trial, the provenance effect was significant for traits other the leaf size and morphology traits. The pattern of variation , however, was not similar. There was no north-south clinal trend in internode lengths, number of leaves per plant, and stomatal density. Significant differences among provenances were also noted for stomatal conductance and transpiration rates. However, no pattern of variation could be ascertained and less than 2.5 percent of the observed variation was attributable to provenances.

For both provenance tests, there was considerable within-provenance variation. Variation associated with the clone-within-provenance effect accounted for as much as 85 percent of the observed variation. Similar results (large within-provenance variability) for balsam poplar have been reported for dormancy relations (Farmer and Reinholt, 1985), early growth (Farmer *et al*, 1986) and rooting (Farmer *et al*, 1989).

The evolutionary and ecological significance of the relatively low provenance variance and the high within-provenance is not clear given the large climatic differences throughout the range of balsam poplar. For example, average July temperatures range from 53°F to 75°F and annual precipitation varies from a low of 7 inches in Alaska to a high of 55 inches in the Maritime Provinces (Fowells, 1965). Moreover, the edaphic requirements of balsam poplar appear to restrict growth to specific sites. Growth is usually limited to moist, nutrient-rich alluvial soils, with a good supply of calcium, magnesium and nitrates (Krajina *et al*, 1982). Thus, variability associated with geographic origin would be expected to be greater than that associated with variability within a population. One possible explanation is that the observed variation may be an artifact of adaptive characteristics which had more fitness value prior to the post-glacial expansion of balsam poplar's range. This hypothesis has also been postulated by Farmer and Reinholt (1985) concerning variation in the dormancy relations of balsam poplar.

The second purpose of this study was to examine how the observed variations in traits are related to each other and to measured transpiration rates. As expected, stomatal conductance was positively correlated with transpiration rates for both provenance tests. This is no surprise, in that if the resistance to the flow of water from the leaf to the air decreases, as indicated by increasing stomatal conductance, then the water loss from the leaf will also increase. The only other trait having a significant correlation with transpiration rates was stomatal length. Larger

stomata were associated with higher transpiration rates, indicating that stomata size, rather than number, may be more important in the control of transpiration rates. However, this relation was found only in the greenhouse provenance trial. These results seem to typify previous attempts in relating stomatal characters to transpiration rates or gas exchange potential in genus *Populus*. Some researchers report that transpiration rates are proportional to both stomatal frequency and size (Siwecki and Kozlowski, 1973; Ceulemens *et al*, 1978; Blake, 1980), while others do not (Blake *et al*, 1984). Relations between transpiration rates and stomatal characteristics depend upon the environment in which the measurement are taken, the time of measurement, and the opening or closing pattern or rate of each genotype (Blake *et al*, 1984), or for that matter any factor that affects the stomatal resistance or the moisture concentration gradient from the leaf to the air. Therefore, any change in one or more of these factors may alter the results. In this study, the time of measurement for each day was similar and the genotypes were the same, but the day and the environment (field vs. greenhouse) differed. Thus, it is highly likely that the differing environment and day of measurement is responsible for the contrasting results.

In both provenance trials, most leaf size and morphology traits were significantly correlated as alluded to earlier. Leaves that had larger areas, generally, were heavier, had longer petiole lengths, but had lower specific leaf weights. It appears that the more southern sources have evolved a "shade-leaf" morphology in

contrast to the more "sun-leaf" morphology of the northern sources. Generally, plants with larger individual leaf areas and weights, also were taller, had more leaves per stem, and larger root, shoot and leaf weights. However, the root/shoot weight ratio was smaller. Thus, more photosynthate appears to have been channelled into stem and leaf production rather than root production. Correlations with latitude were weak, but trends found in Table 16 further indicate that the northern populations may be best suited for drier climates.

These results represent the first effort to examine the water relations of balsam poplar within the context of a provenance trial. However, Hansen *et al.* (1988) examined several clones of balsam poplar from the Lakehead University nursery, measuring traits such as stomatal conductance and stomatal density. Hansen *et al.* (1988) reported stomatal conductances ranging from 0.75 to 1.1 cm/s, which are similar to those reported in this study. Stomatal densities ranged from 115.3 to 175.4 stomata/mm^2, which are lower than the values obtained in this study. Differences, however, are most likely attributable to differing experimental conditions. Although reports on the water relations of balsam poplar are few, black cottonwood (thought to be a subspecies of balsam polar) has received more attention. In a report central to the work on black cottonwood, Schulte *et al.* (1987) studied the water relations under both cut-leaf and whole plant conditions. Using cut leaves, stomata remained open in spite of the lack of turgor pressure in the bulk leaf and guard

cells. These results are somewhat anomalous in that the opening or closing movements of stomata are thought to be dependent upon changes in turgor or pressure potential inside the guard cells. The observed responses may be a result of the nature of the method used in desiccating the leaves. The transition from full saturation to complete loss of turgor was less than one hour - an occurrence that is non-existent in natural range of the species. However, even under whole-plant conditions, stomata of well-watered plants remained open in spite of decreasing leaf water potentials. A period of water stress modified the stomatal behavior and produced a degree of stomatal sensitivity to leaf water potential, although less than that of eastern cottonwood and hybrids of the two species. Ceulemans *et al* (1978) also found that low soil water potential decreased the leaf conductance of black cottonwood foliage, but to a lesser degree than other observed poplar hybrids. In the Schulte *et al* (1987) study, it was also apparent that older wilted leaves did not survive unless rewatered immediately, while younger, expanding leaves did. It is apparent that younger, expanding leaves had acquired some response to leaf water potential. Moreover, trees grown under non-irrigated field conditions had lower maximum conductance than greenhouse plants and were more sensitive to changes in leaf water potential. Plant processes such as stomatal function and leaf abscission appear to have been affected by low soil water availability in such a manner that plants on drier sites were able to maintain leaf water potentials similar to those of plants growing on wetter sites. Lower maximum stomatal

conductances were also noted for non-irrigated field grown plants than greenhouse grown plants in this study.

Although differences between clones from the different locations were not analyzed, the study by Schulte *et al.* (1987) offers insight and direction to future genetic research in balsam poplar, assuming black cottonwood and balsam poplar are similar both genetically and physiologically. Firstly, do the stomata of balsam poplar leaves exhibit a response to decreasing bulk leaf and guard cell water potentials under well-watered conditions? If not, what is the cause or mechanism responsible for the control of stomata and what is its significance for plant growth and survival? Furthermore, what is the extent of genetic variation or lack thereof in this mechanism or response? Secondly, is stomatal behavior modified, and to what extent, by preconditioning treatments (water stress for example) and is there variation in the response?

This study indicated that there is ample variation present in traits potentially affecting the water relations of balsam poplar. Significant provenance effects were noted for most leaf size and morphology traits and a north-south trend was apparent. However, for traits such as specific leaf weight in the field study and the root/shoot weight ratio in the greenhouse study a clear provenance trend was apparent, but the provenance effect was not significant. It is possible that the lack of the provenance effect could be due the wide clonal variance within each provenance. This could, in turn, be due to experimental design limitations rather than a clear lack of provenance variation. Firstly, the

design limitations involved in measuring stomatal conductance and transpiration rates will be addressed. Then, design limitations involving the remaining traits will be discussed.

It is well known that stomata open or close in response to many factors in the aerial environment, such as light (amount, duration and quality), humidity, CO_2 concentration, and atmospheric pollutants (Salisbury and Ross, 1978). However, changes in stomatal aperture are not instantaneous, usually occurring within a few minutes, which is rapid enough to adjust to commonplace changes in the environment (Mansfield and Davies, 1985). Thus, to minimize the effects of a varying environment so that genetic sources of variation could be examined, the experiment was designed utilizing blocks to minimize environmental changes. Moreover, to minimize changes within blocks, the number of clones and ramets representing each clone had to be minimized. Thus, operationally, ten or less clones per provenance could be analyzed, and only one ramet could represent each clone within each provenance in each block. As a consequence, clonal representation and replication was sacrificed, in order to maximize genetic sources of variation and minimize environmental sources of variation. The end result was that a large portion of the observed variation was consumed by variation among and within clones (within-clone variability represented by the block*clone interaction). Possibly, this could be due to variations in the experimental environment or to an inherently large within-provenance variability in balsam poplar.

In hindsight, the problem of a varying environment could have been minimized in one of two ways. Firstly, the experiment could have been completed in a controlled environment, such as a walk-in growth chamber. Thus, environmental conditions could be controlled for an extended period of time, allowing more ramets per clone and more clones per provenance to be examined. However, the one draw-back to this process is that the experimental material could not be measured under natural conditions and the size and age of the plant material would be limited. A second possible procedure involves the analysis of the data. If environmental data was collected accurately with the stomatal conductance or transpiration rates, and a relationship (regression) established among each, then, an analysis of covariance could be performed. This would result in the removal of the effects of the concomitant (environmental) variables and would allow for the analysis of the genetic effects on the desired trait. The advantages of this procedure are that the experimental material could be measured under natural conditions. There are, however, several drawbacks. Firstly, all environmental variables thought to affect the measured trait must be measured and incorporated into the analysis. Secondly, it must be assumed that a significant relationship among variables exists and that the regression is linear (Hicks, 1982).

For traits other than transpiration rates and stomatal conductance, there were no restrictions on the number of clones representing each provenance other than the clones had to be represented in the majority of the blocks in the field test and had

to be free of pests and disease. To keep the design and analysis relatively simple, the same material was used as for the measurement of transpiration rates and stomatal conductance. It was thought that nine clones per provenance, represented by one ramet per block would be an adequate sample. However, in hindsight, more clones and replication of clonal material in each block may have been advantageous in the investigation of the pattern of genetic variation.

Also concerning experimental design and data analysis, the objective of using the same clones in both the field and greenhouse experiment was to make a comparison of the results and determine if age and/or environment made a difference in the pattern of variation expressed. At the provenance level, patterns of variation suggest that performance is parallel in the two tests. For example, leaf size and morphology traits showed similar patterns of variation (north-south trends) although values for leaf areas and weights were lower in the field provenance trial. At the clonal level, the parallel trend in performance is also true. However, there are deviations, probably the result of the lack of replication of clonal material in each block.

This study was meant to be a preliminary step in the study of genetic variation in traits potentially affecting the water relations, and ultimately, the photosynthesis-transpiration compromise of balsam poplar. As such, the information gained in this study is, by itself, too general to have much significance in a breeding or selection program. For example, a north-south trend in leaf size and morphology traits was discovered. However, the

implications of this trend in plant growth and survival cannot be ascertained from this study. Further investigation is needed. In summary, the results from this test indicate that, at least in the northwestern Ontario portion of its range, balsam poplar is highly variable, but most of the variation is related to differences among and within clones. Although differences among provenances were sometimes significant, the proportion of variance attributable to this was usually smaller than that for clones.

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APPENDICES

APPENDIX I

EXAMPLE OF THE CALCULATION OF VARIANCE COMPONENTS FOR STOMATAL CONDUCTANCE (cm/s) IN THE GREENHOUSE PROVENANCE TRIAL

In the following calculations, variables on the left side of the equations are the expected mean-squares taken from the appropriate table in Section III.B.1.b of the thesis (Table 8 in this case), while the values on the right are the actual mean-squares values obtained from the analyses of variance presented in either Appendix II (field provenance trial) or Appendix IV (greenhouse provenance trial).

Calculation of Components:

Step 1. Calculation of the sampling error ($\emptyset_S$) component:

$$\emptyset_S = 0.010$$

Step 2. Calculation of the block*clone-within-provenance*day interaction (δ^2_{BCT}) component:

$$2\delta^2_{BCT} = 0.027$$
$$\delta^2_{BCT} = 0.027/2 = 0.014$$

Step 3. Calculation of the clone-within-provenance*day interaction ($\emptyset_{CT}$) component:

$$2\delta^2_{BCT} + 6\emptyset_{CT} = 0.037$$
$$\emptyset_{CT} = (0.037 - 0.027)/6 = 0.002$$

Step 4. Calculation of the block*provenance*day interaction (δ^2_{BPT}) component:

$$18\delta^2_{BPT} = 0.024$$
$$\delta^2_{BPT} = 0.024/18 = 0.001$$

Step 5. Calculation of the provenance*day interaction (ϕ_{PT}) component:

$$18\hat{\sigma}^2_{BPT} + 54\phi_{PT} = 0.034$$
$$\phi_{PT} = (0.034 - 0.024)/54 = 0.0002$$

Step 6. Calculation of the block*day interaction ($\hat{\sigma}^2_{BT}$) component:

$$72\hat{\sigma}^2_{BT} = 0.600$$
$$\hat{\sigma}^2_{BT} = 0.600/72 = 0.008$$

Step 7. Calculation of the day (ϕ_T) component:

$$72\hat{\sigma}^2_{BT} + 216\phi_T = 2.440$$
$$\phi_T = (2.440 - 0.600)/216 = 0.009$$

Step 8. Calculation of the block*clone-within-provenance interaction ($\hat{\sigma}^2_{BC}$) component:

$$8\hat{\sigma}^2_{BC} = 0.168$$
$$\hat{\sigma}^2_{BC} = 0.168/8 = 0.021$$

Step 9. Calculation of the clone-within-provenance (ϕ_C) component:

$$8\hat{\sigma}^2_{BC} + 24\phi_C = 0.467$$
$$\phi_C = (0.467 - 0.168)/24 = 0.013$$

Step 10. Calculation of the block*provenance interaction ($\hat{\sigma}^2_{BP}$) component:

$$72\hat{\sigma}^2_{BP} = 0.045$$
$$\hat{\sigma}^2_{BP} = 0.045/72 = 0.001$$

Step 11. Calculation of the provenance (ϕ_P) component:

$$72\hat{\sigma}^2_{BP} + 216\phi_P = 0.380$$
$$\phi_P = (0.380 - 0.045)/216 = 0.002$$

Step 12. Calculation of the block ($\hat{\sigma}^2_B$) component:

$$288\hat{\sigma}^2_B = 0.745$$
$$\hat{\sigma}^2_B = 0.745/288 = 0.003$$

Calculation of the percentage of total variance attributable to each source:

Step 13. Calculation of total variance:
-sum of all components calculated in steps 1-12

$$\Sigma = 0.084$$

Step 14. Claculation of the percent of total variance attributable to each component:

$\emptyset_S$ .....(0.010/0.084)*100 = 11.9%

σ^2_{BCT} .....(0.014/0.084)*100 = 16.6%

$\emptyset_{CT}$ .....(0.002/0.084)*100 = 2.4%

σ^2_{BPT} .....(0.001/0.084)*100 = 1.2%

$\emptyset_{PT}$ .....(0.0002/0.084)*100= 0.2%

σ^2_{BT} .....(0.008/0.084)*100 = 9.5%

$\emptyset_T$ .....(0.009/0.084)*100 = 10.7%

σ^2_{BC} .....(0.021/0.084)*100 = 24.9%

$\emptyset_C$ .....(0.013/0.084)*100 = 15.4%

σ^2_{BP} .....(0.001/0.084)*100 = 1.2%

$\emptyset_P$ .....(0.002/0.084)*100 = 2.4%

σ^2_B .....(0.003/0.084)*100 = 3.6%

100.0%

APPENDIX II

ANALYSES OF VARIANCE FOR TRAITS MEASURED IN THE FIELD PROVENANCE TRIAL

Table 2.1. Analyses of variance for traits measured in the field provenance trial.

Source	Root-Shoot Growth			Leaf Size and Shape								
		Internode Length (cm)			Petiole Length (mm)		Single-Leaf Abaxial Area (cm^2)		Single-Leaf Oven-Dry Weight (mg)		Specific Leaf Weight (mg/cm^2)	
	d.f.	SS	MS	df	SS	MS	SS	MS	SS	MS	SS	MS
Block (B)	2	0.6	'0.3	2	129	65	215	108	12812	6406	18.1	9.1
Restriction Error	0	"NR	NR	0	NR	NR	NR	NR	NR	NR	NR	NR
Provenance (P)	3	7.9	"'2.6ns	3	419	140**	5046	1682**	328634	109545**	121.6	40.5*
B*P	6	8.9	1.5	6	39	7	290	48	25708	4285	37.7	6.3
Restriction Error	0	NR	NR	0	NR	NR	NR	NR	NR	NR	NR	NR
Clone-within-Provenance (C/P)	32	57.1	1.8**	32	929	29ns	3434	107ns	350420	10951ns	77.2	2.4ns
B*C/P	55	42.9	0.8	55	1059	19	3898	71	410224	7459	121.5	2.2
Day (T)	"""NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Restriction Error	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
B*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
B*P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
C/P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
B*C/P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Experimental Error (E)	0	NR	NR	0	NR	NR	NR	NR	NR	NR	NR	NR
Sampling Error (S)	198	36.8	0.2	99	264	3	260	3	38000	384	26.9	0.3
Total	296	154.2		197	2839		13143		1165798		403.0	

' Mean squares values not followed by ns, * or ** do not have a valid test of significance.

" NR indicates that the sumsof squares and the mean squares values are not retrievable (0 degrees of freedom).

"' ns, * and ** indicate non-significance at the 5% level, significance at the 5% level and significance at the 1% level, respectively.

"" NA indicates that the source of variation is not applicable to the measured trait.

Table 2.1. continued.

Source	Stomatal Anatomy					Stomatal Control				
		Stomatal Density (#/mm^2)		Stomatal Length (µm)			Transpiration Rate (µg/(cm^{2}s))		Stomatal Conductance (cm/s)	
	df	SS	MS	SS	MS	df	SS	MS	SS	MS
Block (B)	2	27648	13824	190	95	2	1332	666	2.46	1.23
Restriction Error	0	NR	NR	NR	NR	0	NR	NR	NR	NR
Provenance (P)	3	178006	59335ns	1053	351ns	3	424	141ns	3.31	1.10ns
B*P	6	90399	15067	802	134	6	231	38	2.57	0.43
Restriction Error	0	NR	NR	NR	NR	0	NR	NR	NR	NR
Clone-within-Provenance (C/P)	32	1268992	39656**	9919	310**	32	816	26**	10.04	0.31**
B*C/P	55	963826	17524	7151	130	55	639	12	7.09	0.13
Day (T)	NA	NA	NA	NA	NA	3	413	138ns	3.42	1.14ns
Restriction Error	NA	NA	NA	NA	NA	0	NR	NR	NR	NR
B*T	NA	NA	NA	NA	NA	6	3793	632	5.84	0.97
P*T	NA	NA	NA	NA	NA	9	209	23ns	1.26	0.14ns
B*P*T	NA	NA	NA	NA	NA	18	365	20	1.80	0.10
C/P*T	NA	NA	NA	NA	NA	96	389	4**	3.75	0.04ns
B*C/P*T	NA	NA	NA	NA	NA	165	452	3	4.07	0.03
Experimental Error (E)	NR	NR	NR	NR	NR	0	NR	NR	NR	NR
Sampling Error (S)	1881	1092280	581	10042	5	792	575	1	6.48	0.01
Total	1979	3621151		29157		1187	9637		52.09	

' Mean squares values not followed by ns, * or ** do not have a valid test of significance.

" NR indicates that the sumsof squares and the mean squares values are not retrievable (0 degrees of freedom).

"' ns, * and ** indicate non-significance at the 5% level, significance at the 5% level and significance at the 1% level, respectively.

"'' NA indicates that the source of variation is not applicable to the measured trait.

APPENDIX III

AVERAGE PROVENANCE AND CLONE-WITHIN-PROVENANCE MEANS FOR TRAITS MEASURED IN THE FIELD PROVENANCE TRIAL

Table 3.1. Average internode length (cm) for provenances and clones-within-provenances in the field provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	1.7	1.6	2.4	1.9
	219	2.8	2.6	3.3	2.9
	222	2.8	3.4	3.2	3.1
	229	2.1	2.4	3.0	2.5
	233	2.8	1.5	3.6	2.6
	238	2.4	3.1	3.1	2.9
	240	2.5	3.2	2.3	2.7
	242	3.3	4.5	3.6	3.8
	245	2.0	2.2	3.1	2.4
	Mean	2.5	2.7	3.1	2.8
Thunder Bay	1	2.9	2.4	2.1	2.5
	6	2.0	1.6	2.3	2.0
	8	2.5	2.2	2.4	2.4
	15	3.5	2.6	1.8	2.6
	24	2.7	3.4	1.9	2.7
	34	2.4		1.8	2.1
	37	2.2	1.5	2.2	2.0
	43	3.4	3.2	3.3	3.3
	44	2.0	3.1	2.2	2.4
	Mean	2.6	2.5	2.2	2.4
Pickle Lake	102	2.1	3.0	1.8	2.3
	112	3.3	3.0	2.5	2.9
	119	2.1	1.8	2.8	2.2
	122	2.4	2.6	3.4	2.8
	135	2.4	1.5		2.0
	137	2.6	2.6		2.6
	141	2.7	2.7		2.7
	142	2.1	3.1	2.6	2.6
	149	1.2	3.2		2.2
	Mean	2.3	2.6	2.6	2.5
Bearskin Lake	303		2.4	1.7	2.1
	308	3.6	2.7	3.3	3.2
	314		1.8	0.9	1.4
	319		3.1	3.4	3.3
	322	2.2	1.6	1.8	1.9
	326		2.3	2.5	2.4
	330	1.8	2.9	1.3	2.0
	337	2.9	1.9	2.6	2.5
	345	1.6	2.2	1.4	1.7
	Mean	2.4	2.3	2.1	2.3

Table 3.2. Average petiole length (mm) for provenances and clones-within-provenances in the field provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	14.0	22.0	18.5	18.2
	219	18.0	14.0	14.5	15.5
	222	19.5	24.0	13.5	19.0
	229	20.0	19.5	23.5	21.0
	233	15.0	11.0	21.5	15.8
	238	15.5	21.5	24.5	20.5
	240	14.5	19.0	15.5	16.3
	242	18.0	19.5	21.0	19.5
	245	15.5	17.5	18.5	17.2
	Mean	16.7	18.7	19.0	18.1
Thunder Bay	1	18.0	19.0	18.5	18.5
	6	13.5	15.5	17.0	15.3
	8	16.5	19.0	18.5	18.0
	15	22.0	17.5	22.0	20.5
	24	20.5	24.5	15.0	20.0
	34	14.5		19.0	16.8
	37	15.0	15.5	15.5	15.3
	43	18.5	11.5	14.5	14.8
	44	17.0	18.5	20.5	18.7
	Mean	17.3	17.6	17.8	17.6
Pickle Lake	102	10.0	17.0	12.5	13.2
	112	17.0	17.5	18.0	17.5
	119	13.5	13.5	15.5	14.2
	122	15.0	15.5	17.5	16.0
	135	16.5	16.5		16.5
	137	14.0	16.0		15.0
	141	13.5	21.5		17.5
	142	11.0	14.0	14.0	13.0
	149	14.0	21.0		17.5
	Mean	13.8	16.9	15.5	15.6
Bearskin Lake	303		12.0	9.0	10.5
	308	19.5	19.0	22.5	20.3
	314		11.0	17.0	14.0
	319		10.0	11.0	10.5
	322	12.0	18.5	9.0	13.2
	326		19.0	20.5	19.8
	330	17.0	15.5	16.0	16.2
	337	17.0	16.5	15.0	16.2
	345	8.5	13.5	15.0	12.3
	Mean	14.8	15.0	15.0	14.9

Table 3.3. Average single-leaf abaxial area (cm^2) for provenances and clones-within-provenances in the field provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	24.3	37.7	34.4	32.1
	219	27.3	19.9	17.1	21.4
	222	39.6	36.7	30.2	35.5
	229	15.7	26.0	17.5	19.7
	233	26.3	12.0	47.1	28.5
	238	19.6	30.9	28.2	26.2
	240	18.4	33.1	18.8	23.4
	242	21.3	20.0	26.5	22.6
	245	11.9	19.1	16.6	15.9
	Mean	22.7	26.2	26.3	25.0
Thunder Bay	1	21.7	11.9	24.4	19.3
	6	13.9	17.0	17.3	16.1
	8	18.6	21.1	16.8	18.8
	15	27.5	16.2	17.5	20.4
	24	24.2	28.0	14.6	22.3
	34	14.1		16.3	15.2
	37	14.0	18.1	15.9	16.0
	43	29.7	11.6	27.8	23.0
	44	12.5	18.1	26.3	19.0
	Mean	19.6	17.8	19.7	18.9
Pickle Lake	102	9.7	15.1	16.7	13.8
	112	15.5	18.7	22.6	18.9
	119	16.9	10.3	18.2	15.1
	122	13.5	14.3	13.6	13.8
	135	13.6	16.5		15.1
	137	14.3	14.9		14.6
	141	8.2	15.9		12.1
	142	9.9	11.6	11.2	10.9
	149	8.9	12.9		10.9
	Mean	12.3	14.5	16.5	14.4
Bearskin Lake	303		20.1	8.0	14.1
	308	14.9	15.9	20.1	17.0
	314		5.8	9.6	7.7
	319		7.0	11.6	9.3
	322	6.7	12.4	7.9	9.0
	326		29.6	17.1	23.4
	330	9.3	9.0	6.6	8.3
	337	11.0	10.3	14.3	11.9
	345	4.8	18.5	11.1	11.5
	Mean	9.3	14.3	11.8	11.8

Table 3.4. Average single-leaf oven-dry weight (mg) for provenances and clones-within-provenances in the field provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	205	320	300	275
	219	300	190	155	215
	222	355	395	310	353
	229	150	235	155	180
	233	255	115	480	283
	238	170	290	275	245
	240	185	315	215	238
	242	225	170	260	218
	245	120	180	165	155
	Mean	218	245	257	240
Thunder Bay	1	225	135	250	203
	6	145	160	170	158
	8	225	205	175	202
	15	250	175	205	210
	24	255	320	165	247
	34	180		170	175
	37	165	225	175	188
	43	345	135	275	252
	44	140	200	270	203
	Mean	214	194	206	204
Pickle Lake	102	120	195	135	150
	112	190	220	225	212
	119	175	125	175	158
	122	155	150	125	143
	135	150	175		163
	137	195	180		188
	141	105	205		155
	142	120	150	135	135
	149	100	155		128
	Mean	146	173	159	159
Bearskin Lake	303		210	100	155
	308	180	165	250	198
	314		75	105	90
	319		80	130	105
	322	80	150	90	107
	326		320	175	248
	330	95	130	80	102
	337	145	115	185	148
	345	60	150	120	110
	Mean	112	155	137	135

Table 3.5. Average specific leaf weight (mg/cm^2) for provenances and clones-within-provenances in the field provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	8.46	8.52	8.72	8.57
	219	11.02	9.53	9.10	9.88
	222	8.98	10.80	10.26	10.01
	229	9.58	9.04	8.85	9.16
	233	9.70	9.64	10.19	9.84
	238	8.70	9.40	9.69	9.26
	240	10.07	9.53	11.45	10.35
	242	10.60	8.53	9.83	9.65
	245	10.09	9.44	9.92	9.82
	Mean	9.69	9.38	9.77	9.62
Thunder Bay	1	10.37	11.37	10.24	10.66
	6	10.40	9.40	9.86	9.89
	8	12.10	9.72	10.42	10.75
	15	9.11	10.80	11.75	10.55
	24	10.55	11.42	11.32	11.10
	34	12.86		10.48	11.67
	37	11.81	12.42	11.06	11.76
	43	11.66	11.66	9.87	11.06
	44	11.20	11.09	10.27	10.85
	Mean	11.12	10.99	10.59	10.92
Pickle Lake	102	12.44	12.93	8.08	11.15
	112	12.30	11.74	9.90	11.31
	119	10.37	12.17	9.62	10.72
	122	11.50	10.51	9.17	10.39
	135	11.03	10.61		10.82
	137	13.72	12.10		12.91
	141	12.76	12.96		12.86
	142	12.15	12.93	12.02	12.37
	149	11.33	12.02		11.68
	Mean	11.96	12.00	9.76	11.24
Bearskin Lake	303		10.50	12.57	11.54
	308	12.08	10.40	12.44	11.64
	314		13.08	10.88	11.98
	319		11.44	11.25	11.35
	322	11.91	12.09	11.47	11.82
	326		10.82	10.27	10.55
	330	10.21	14.50	12.10	12.27
	337	13.26	11.21	13.02	12.50
	345	12.51	8.11	10.88	10.50
	Mean	11.99	11.35	11.65	11.66

Table 3.6. Average stomatal density (#/mm^2) for provenances and clones-within-provenances in the field provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	183	154	174	170
	219	184	180	184	183
	222	180	199	239	206
	229	171	150	201	174
	233	224	236	230	230
	238	180	194	200	191
	240	273	218	261	251
	242	293	272	275	280
	245	284	211	268	254
	Mean	219	202	226	215
Thunder Bay	1	230	255	249	245
	6	286	257	267	270
	8	256	243	236	245
	15	216	221	170	202
	24	200	198	196	198
	34	210		275	243
	37	253	253	249	252
	43	285	285	235	268
	44	290	264	228	261
	Mean	247	247	234	243
Pickle Lake	102	219	243	247	236
	112	273	228	246	249
	119	284	198	228	237
	122	255	277	288	273
	135	299	245		272
	137	237	178		208
	141	262	245		254
	142	237	258	214	236
	149	209	185		197
	Mean	253	229	245	242
Bearskin Lake	303		229	286	258
	308	209	223	207	213
	314		225	313	269
	319		296	195	246
	322	275	253	213	247
	326		229	237	233
	330	282	178	286	249
	337	250	177	248	225
	345	169	234	246	216
	Mean	237	227	248	237

Table 3.7. Average stomatal length (µm) for provenances and clones-within-provenances in the field provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	35.7	38.4	35.0	36.4
	219	36.2	38.1	36.2	36.8
	222	37.5	36.2	36.9	36.9
	229	37.8	36.8	33.2	35.9
	233	33.4	33.3	32.1	32.9
	238	37.3	36.0	36.3	36.5
	240	33.1	34.1	35.0	34.1
	242	31.6	32.7	31.1	31.8
	245	28.8	31.1	29.4	29.8
	Mean	34.6	35.2	33.9	34.6
Thunder Bay	1	32.6	33.8	32.8	33.1
	6	33.6	33.8	33.2	33.5
	8	31.7	32.6	31.0	31.8
	15	35.3	39.2	41.8	38.8
	24	37.0	36.4	36.3	36.6
	34	40.6		33.9	37.3
	37	39.9	36.7	39.8	38.8
	43	35.9	32.1	38.9	35.6
	44	35.3	35.5	35.8	35.5
	Mean	35.8	35.0	35.9	35.7
Pickle Lake	102	37.5	35.9	29.9	34.4
	112	31.3	32.6	34.4	32.8
	119	34.5	41.7	36.9	37.7
	122	33.0	31.9	33.6	32.8
	135	30.3	33.2		31.8
	137	33.7	36.7		35.2
	141	34.2	30.5		32.4
	142	33.6	31.5	31.2	32.1
	149	37.3	35.3		36.3
	Mean	33.9	34.4	33.2	33.8
Bearskin Lake	303		36.6	32.1	34.4
	308	43.0	41.3	40.2	41.5
	314		33.2	27.6	30.4
	319		32.2	37.7	35.0
	322	34.2	33.0	37.4	34.9
	326		36.4	38.5	37.5
	330	32.7	38.4	33.0	34.7
	337	35.4	40.1	35.6	37.0
	345	37.3	31.4	32.2	33.6
	Mean	36.5	35.8	34.9	35.7

Table 3.8. Average transpiration rates ($\mu g/(cm^2 s)$) for provenances and clones-within-provenances in the field provenance trial on July 2, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	8.944	8.770	4.213	7.309
	219	9.921	9.054	6.955	8.643
	222	10.477	10.226	4.303	8.335
	229	10.245	10.041	5.162	8.483
	233	10.803	13.227	4.541	9.524
	238	12.528	12.280	4.853	9.887
	240	9.092	8.803	2.930	6.942
	242	11.003	12.693	4.711	9.469
	245	8.950	11.167	5.470	8.529
	Mean	10.218	10.696	4.793	8.569
Thunder Bay	1	9.056	6.012	3.193	6.087
	6	7.857	7.488	2.717	6.021
	8	12.047	9.475	2.897	8.140
	15	12.800	6.074	2.951	7.275
	24	8.967	7.821	2.816	6.535
	34	12.573		4.315	8.444
	37	11.503	7.761	3.017	7.427
	43	12.430	7.328	2.361	7.373
	44	11.633	7.191	2.929	7.251
	Mean	10.985	7.394	3.022	7.134
Pickle Lake	102	9.108	8.935	8.170	8.738
	112	10.112	9.318	6.107	8.512
	119	8.596	8.478	7.256	8.110
	122	9.414	8.069	9.244	8.909
	135	8.794	10.903		9.849
	137	7.379	11.807		9.593
	141	12.680	10.763		11.722
	142	9.847	8.639	6.335	8.274
	149	11.017	7.979		9.498
	Mean	9.661	9.432	7.422	8.838
Bearskin Lake	303		13.697	3.998	8.848
	308	13.993	14.520	4.350	10.954
	314		11.977	3.389	7.683
	319		11.793	3.560	7.677
	322	13.150	11.310	5.739	10.066
	326		10.950	3.651	7.301
	330	14.453	11.463	3.491	9.802
	337	8.896	15.787	4.969	9.884
	345	7.974	12.090	4.168	8.077
	Mean	11.693	12.621	4.146	9.487

Table 3.9. Average transpiration rates ($\mu g/(cm^2 s)$) for provenances and clones-within-provenances in the field provenance trial on July 3, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	9.672	7.298	9.282	8.751
	219	7.048	5.788	10.037	7.624
	222	7.556	7.667	8.815	8.013
	229	5.962	5.861	9.868	7.230
	233	7.451	9.426	8.834	8.570
	238	7.416	7.916	8.152	7.828
	240	5.472	5.795	6.376	5.881
	242	8.658	8.154	8.736	8.516
	245	7.692	7.536	7.861	7.696
	Mean	7.432	7.271	8.662	7.788
Thunder Bay	1	7.841	7.027	9.513	8.127
	6	4.559	5.996	5.242	5.266
	8	8.788	10.471	8.471	9.243
	15	9.487	4.694	6.480	6.887
	24	5.502	6.348	5.983	5.944
	34	5.635		8.432	7.034
	37	6.984	9.071	7.978	8.011
	43	7.280	5.055	7.748	6.694
	44	5.485	6.646	7.331	6.487
	Mean	6.840	6.914	7.464	7.073
Pickle Lake	102	7.075	7.957	11.777	8.936
	112	5.647	8.310	10.793	8.250
	119	6.271	5.741	8.915	6.976
	122	8.912	9.852	12.343	10.369
	135	6.433	7.201		6.817
	137	7.518	9.110		8.314
	141	8.751	8.778		8.765
	142	6.692	7.610	8.596	7.633
	149	5.889	4.579		5.234
	Mean	7.021	7.682	10.485	8.396
Bearskin Lake	303		10.498	10.360	10.429
	308	8.356	9.399	10.271	9.342
	314		8.580	8.042	8.311
	319		7.983	10.765	9.374
	322	8.218	3.018	7.701	6.312
	326		7.626	9.589	8.608
	330	9.181	6.819	10.138	8.713
	337	8.755	8.534	9.624	8.971
	345	7.405	3.246	9.514	6.722
	Mean	8.383	7.300	9.556	8.413

Table 3.10. Average transpiration rates ($\mu g/(cm^2 s)$) for provenances and clones-within-provenances in the field provenance trial on July 4, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	5.245	9.067	8.222	7.511
	219	3.438	9.739	9.442	7.540
	222	2.537	9.523	7.819	6.626
	229	2.702	8.871	8.553	6.709
	233	1.987	10.740	8.453	7.060
	238	3.480	9.485	7.819	6.928
	240	1.742	9.505	6.157	5.801
	242	3.091	11.577	7.580	7.416
	245	1.962	10.409	7.905	6.759
	Mean	2.909	9.880	7.994	6.928
Thunder Bay	1	3.835	8.975	6.416	6.409
	6	3.438	6.644	5.175	5.086
	8	4.374	11.243	6.090	7.236
	15	4.618	9.141	5.649	6.469
	24	3.048	8.510	3.877	5.145
	34	3.647		6.429	5.038
	37	3.502	9.897	6.026	6.475
	43	3.925	8.127	5.611	5.888
	44	3.394	8.645	5.668	5.902
	Mean	3.757	8.898	5.660	6.105
Pickle Lake	102	4.357	9.350	10.903	8.203
	112	4.870	9.482	9.640	7.997
	119	4.089	6.816	9.511	6.805
	122	5.877	12.927	13.980	10.928
	135	5.481	8.594		7.038
	137	3.465	12.047		7.756
	141	4.912	10.171		7.542
	142	4.248	9.351	8.675	7.425
	149	3.188	8.223		5.706
	Mean	4.498	9.662	10.542	8.234
Bearskin Lake	303		10.860	8.341	9.601
	308	6.341	11.043	7.822	8.402
	314		12.067	6.624	9.346
	319		10.736	9.000	9.868
	322	5.821	9.954	5.811	7.195
	326		11.143	5.892	8.518
	330	7.138	8.206	7.944	7.763
	337	7.368	12.043	8.435	9.282
	345	5.767	13.430	8.424	9.207
	Mean	6.487	11.054	7.588	8.376

Table 3.11. Average transpiration rates ($\mu g/(cm^2 s)$) for provenances and clones-within-provenances in the field provenance trial on July 7, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	10.713	6.460	2.758	6.644
	219	8.120	6.146	3.430	5.899
	222	11.087	7.274	2.557	6.973
	229	7.847	5.477	2.790	5.371
	233	9.746	7.106	2.511	6.454
	238	9.261	6.246	2.219	5.909
	240	8.107	6.445	2.058	5.537
	242	8.893	7.671	2.747	6.437
	245	7.519	6.258	2.006	5.261
	Mean	9.032	6.565	2.564	6.054
Thunder Bay	1	10.988	6.923	5.477	7.796
	6	7.095	6.398	2.655	5.383
	8	10.903	10.943	3.444	8.430
	15	11.853	9.512	3.702	8.356
	24	5.477	7.956	2.848	5.427
	34	8.360		3.482	5.921
	37	8.946	8.282	3.307	6.845
	43	10.215	8.592	3.550	7.452
	44	8.689	8.560	3.437	6.895
	Mean	9.170	8.376	3.545	7.030
Pickle Lake	102	8.022	6.274	3.146	5.814
	112	8.656	7.736	2.603	6.332
	119	7.192	4.710	3.042	4.981
	122	10.720	10.005	3.908	8.211
	135	9.051	6.412		7.732
	137	7.170	9.174		8.172
	141	8.179	8.855		8.517
	142	8.748	7.538	1.888	6.058
	149	7.439	5.401		6.420
	Mean	8.353	7.345	2.917	6.205
Bearskin Lake	303		9.896	3.794	6.845
	308	11.520	9.387	4.887	8.598
	314		8.384	4.149	6.267
	319		8.971	5.291	7.131
	322	9.112	6.970	3.012	6.365
	326		9.079	5.148	7.114
	330	11.843	6.779	4.326	7.649
	337	10.538	7.760	4.678	7.659
	345	9.566	10.867	4.896	8.443
	Mean	10.516	8.677	4.465	7.886

Table 3.12. Average stomatal conductance (cm/s) for provenances and clones-within-provenances in the field provenance trial on July 2, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	0.576	0.572	0.606	0.585
	219	0.648	0.609	0.765	0.674
	222	0.663	0.717	0.576	0.652
	229	0.645	0.667	0.718	0.677
	233	0.664	0.876	0.649	0.730
	238	0.828	0.871	0.687	0.795
	240	0.534	0.559	0.347	0.480
	242	0.700	0.851	0.692	0.748
	245	0.549	0.771	0.848	0.723
	Mean	0.645	0.721	0.645	0.670
Thunder Bay	1	0.587	0.568	0.445	0.533
	6	0.456	0.747	0.389	0.531
	8	0.757	0.997	0.438	0.731
	15	0.770	0.582	0.421	0.591
	24	0.558	0.734	0.390	0.561
	34	0.820		0.652	0.736
	37	0.699	0.766	0.452	0.639
	43	0.797	0.721	0.338	0.619
	44	0.690	0.697	0.424	0.604
	Mean	0.681	0.726	0.439	0.615
Pickle Lake	102	0.535	0.665	0.913	0.704
	112	0.575	0.720	0.674	0.656
	119	0.533	0.613	0.790	0.645
	122	0.572	0.576	1.053	0.734
	135	0.503	0.819		0.661
	137	0.411	0.865		0.638
	141	0.756	0.830		0.793
	142	0.577	0.628	0.677	0.627
	149	0.661	0.572		0.617
	Mean	0.569	0.699	0.821	0.696
Bearskin Lake	303		0.908	0.627	0.768
	308	0.830	0.928	0.611	0.790
	314		0.800	0.488	0.644
	319		0.809	0.559	0.684
	322	0.760	0.725	0.836	0.774
	326		0.745	0.517	0.631
	330	0.890	0.740	0.529	0.720
	337	0.506	1.067	0.735	0.769
	345	0.436	0.855	0.647	0.646
	Mean	0.685	0.842	0.617	0.715

Table 3.13. Average stomatal conductance (cm/s) for provenances and clones-within-provenances in the field provenance trial on July 3, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	0.927	0.646	0.809	0.794
	219	0.670	0.538	0.883	0.697
	222	0.740	0.738	0.745	0.741
	229	0.543	0.512	0.846	0.634
	233	0.698	0.864	0.771	0.778
	238	0.664	0.767	0.716	0.716
	240	0.512	0.492	0.534	0.513
	242	0.808	0.738	0.737	0.761
	245	0.732	0.697	0.690	0.706
	Mean	0.699	0.666	0.748	0.704
Thunder Bay	1	0.767	0.655	0.792	0.738
	6	0.410	0.520	0.431	0.454
	8	0.864	1.004	0.735	0.868
	15	0.927	0.412	0.528	0.622
	24	0.516	0.576	0.473	0.522
	34	0.529		0.714	0.622
	37	0.670	0.879	0.676	0.742
	43	0.711	0.451	0.632	0.598
	44	0.519	0.608	0.607	0.578
	Mean	0.657	0.639	0.621	0.639
Pickle Lake	102	0.684	0.699	1.044	0.809
	112	0.525	0.716	0.939	0.727
	119	0.589	0.491	0.787	0.622
	122	0.876	0.874	1.107	0.952
	135	0.602	0.628		0.615
	137	0.717	0.810		0.764
	141	0.828	0.775		0.802
	142	0.631	0.658	0.748	0.679
	149	0.538	0.383		0.461
	Mean	0.665	0.670	0.925	0.753
Bearskin Lake	303		1.003	0.856	0.930
	308	0.817	0.895	0.875	0.862
	314		0.870	0.669	0.770
	319		0.876	0.922	0.899
	322	0.808	0.570	0.655	0.678
	326		0.729	0.813	0.771
	330	0.878	0.730	0.809	0.806
	337	0.847	0.849	0.800	0.832
	345	0.696	0.661	0.812	0.723
	Mean	0.809	0.798	0.801	0.803

Table 3.14. Average stomatal conductance (cm/s) for provenances and clones-within-provenances in thefield provenance trial on July 4, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	1.038	0.761	0.915	0.905
	219	0.647	0.835	0.991	0.824
	222	0.466	0.830	0.864	0.720
	229	0.493	0.729	0.966	0.729
	233	0.377	0.900	0.912	0.730
	238	0.644	0.819	0.873	0.779
	240	0.317	0.818	0.653	0.596
	242	0.567	0.984	0.847	0.799
	245	0.365	0.880	0.944	0.730
	Mean	0.546	0.839	0.885	0.757
Thunder Bay	1	0.681	0.892	0.732	0.768
	6	0.573	0.666	0.576	0.605
	8	0.766	1.221	0.695	0.894
	15	0.791	0.923	0.637	0.784
	24	0.535	0.882	0.441	0.619
	34	0.644		0.708	0.676
	37	0.574	1.021	0.688	0.761
	43	0.687	0.800	0.644	0.710
	44	0.535	0.864	0.662	0.687
	Mean	0.643	0.909	0.643	0.732
Pickle Lake	102	0.646	0.922	1.223	0.930
	112	0.685	0.871	1.078	0.878
	119	0.611	0.668	1.036	0.772
	122	0.959	1.243	1.698	1.300
	135	0.742	0.853		0.798
	137	0.525	1.116		0.821
	141	0.706	1.015		0.861
	142	0.644	0.827	0.626	0.699
	149	0.458	0.709		0.584
	Mean	0.664	0.914	1.192	0.923
Bearskin Lake	303		0.917	0.973	0.945
	308	0.890	0.899	0.916	0.902
	314		1.007	0.768	0.888
	319		0.950	1.110	1.030
	322	0.803	0.847	0.650	0.767
	326		0.919	0.656	0.788
	330	1.003	0.691	0.956	0.883
	337	1.059	1.018	0.994	1.024
	345	0.792	1.171	1.019	0.994
	Mean	0.909	0.935	0.894	0.913

Table 3.15. Average stomatal conductance (cm/s) for provenances and clones-within-provenances in the field provenance trial on July 7, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	0.937	0.734	0.473	0.715
	219	0.706	0.684	0.575	0.655
	222	0.902	0.847	0.432	0.727
	229	0.669	0.631	0.474	0.591
	233	0.769	0.836	0.425	0.677
	238	0.772	0.724	0.381	0.626
	240	0.638	0.769	0.333	0.580
	242	0.724	0.883	0.487	0.698
	245	0.586	0.714	0.357	0.552
	Mean	0.745	0.758	0.437	0.647
Thunder Bay	1	0.979	0.772	0.729	0.827
	6	0.526	0.716	0.375	0.539
	8	0.859	1.359	0.502	0.907
	15	0.973	0.893	0.458	0.775
	24	0.435	0.847	0.414	0.565
	34	0.707		0.531	0.619
	37	0.729	0.787	0.484	0.667
	43	0.877	0.937	0.482	0.765
	44	0.686	0.916	0.510	0.704
	Mean	0.752	0.903	0.498	0.718
Pickle Lake	102	0.643	0.722	0.605	0.657
	112	0.751	0.949	0.490	0.730
	119	0.606	0.520	0.570	0.565
	122	0.947	1.273	0.770	0.997
	135	0.782	0.721		0.752
	137	0.583	1.113		0.848
	141	0.652	1.069		0.861
	142	0.753	0.906	0.337	0.665
	149	0.614	0.616		0.615
	Mean	0.703	0.876	0.554	0.711
Bearskin Lake	303		1.042	0.675	0.859
	308	1.009	1.060	0.759	0.943
	314		0.837	0.630	0.734
	319		0.909	0.928	0.919
	322	0.777	0.687	0.456	0.640
	326		0.908	0.871	0.890
	330	1.060	0.650	0.770	0.827
	337	0.969	0.736	0.757	0.821
	345	0.808	1.255	0.812	0.958
	Mean	0.925	0.898	0.740	0.854

APPENDIX IV

ANALYSES OF VARIANCE FOR TRAITS MEASURED IN THE GREENHOUSE PROVENANCE TRIAL

Table 4.1. Analyses of variance for root and shoot traits measured in the greenhouse provenance trial.

Source	Root-Shoot Growth																	
	Internode Length (cm)			Shoot Length (cm)			Number of Leaves per Shoot		Total Abaxial Leaf Area per Shoot (cm^2)		Total Oven-Dry Leaf Weight per Shoot (g)		Total Oven-Dry Shoot Weight (g)		Total Oven-Dry Root Weight (g)		Root/Shoot Oven-Dry Weight Ratio	
	df	SS	MS	df	SS	MS	SS	MS	SS	MS	SS	MS	SS	MS	SS	MS	SS	MS
Block (B)	2	0.2	[1]0.08	2	2205	1102	155	77	1062251	531126	28.4	14.2	13.4	6.7	2.8	1.4	0.04	0.02
Restriction Error	0	[2]NR	NR	0	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR
Provenance (P)	3	10.3	[1]13.4**	3	957	319ns	270	90*	2401023	800341ns	27.2	9.1ns	6.6	2.2ns	4.4	1.5as	0.05	0.02ns
B*P	6	1.9	0.3	6	1728	288	81	14	1199718	199953	24.1	4.0	14.2	2.4	5.1	0.9	0.05	0.01
Clone-within-Provenance (C/P)	32	54.8	1.7	32	15109	472ns	1392	44ns	10459366	326855ns	202.2	6.3ns	94.6	3.0ns	29.7	0.9ns	0.69	0.02*
B*C/P	62	31.0	0.5**	62	26897	434	1851	30	24393534	393444	441.8	7.1	203.8	3.3	59.0	1.0	0.90	0.01
Day (T)	[1]NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Restriction Error	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
B*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
B*P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
C/P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
B*C/P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Experimental Error (E)	0	NR	NR	0	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR
Sampling Error (S)	212	26.2	0.1	0	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR
Total	317	124.3		105	46896		3749		39515892		723.7		332.6		101.0		1.73	

[1] Mean squares values not followed by ns, * or ** do not have a valid test of significance.

[2] NR indicates that the sums of squares and the mean squares values are not retrievable (0 degrees of freedom).

[3] ns, * and ** indicate non-significance at the 5% level, significance at the 5% level and significance at the 1% level, respectively.

[4] NA indicates that the source of variation is not applicable to the measured trait.

Table 4.2. Analyses of variance for leaf size and shape traits, stomatal anatomy traits and stomatal control traits in the greenhouse provenance trial.

Source	Leaf Size and Shape									Stomatal Anatomy					Stomatal Control				
		Petiole Length (mm)		Single-Leaf Abaxial Area (cm^2)		Single-Leaf Oven-Dry Weight (mg)		Specific Leaf Weight (mg/cm^2)			Stomatal Density ($\#/mm^2$)		Stomatal Length (µm)			Transpiration Rate ($\mu g/(cm^2 s)$)		Stomatal Conductance (cm/s)	
	df	SS	MS	SS	MS	SS	MS	SS	MS	df	SS	MS	SS	MS	df	SS	MS	SS	MS
Block (B)	2	268	134	6199	3100	0.18	0.09	6.42	3.21	2	27167	13584	93	47	2	221.5	110.8	1.49	0.75
Restriction Error	0	NR	NR	NR	NR	NR	NR	NR	NR	0	NR	NR	NR	NR	0	NR	NR	NR	NR
Provenance (P)	3	482	161*	26106	8702**	0.24	0.08*	1.76	0.59ns	3	217787	72596**	863	288ns	3	45.7	15.2**	1.14	0.38*
B*P	6	202	34	2926	488	0.06	0.01	1.30	0.22	6	27750	4625	533	89	6	6.6	1.1	0.27	0.05
Clone-within-Provenance (C/P)	32	3836	120**	37002	1156ns	0.75	0.02ns	22.14	0.69**	32	1688744	52773**	12868	402**	32	502.5	15.7**	14.93	0.47**
B*C/P	62	1887	30	73422	1184	1.29	0.02	15.43	0.25	62	486219	7842	3746	60	62	323.3	5.2	10.43	0.17
Day (T)	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3	3804.9	1268.3*	7.32	2.44ns
Restriction Error	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0	NR	NR	NR	NR
B*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	6	1282.4	213.7	3.60	0.60
P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	9	8.9	01.0ns	0.31	0.03ns
B*P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	18	10.9	0.6	0.44	0.02
C/P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	96	137.0	1.4ns	3.58	0.04ns
B*C/P*T	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	186	215.3	1.2	5.07	0.03
Experimental Error (E)	0	NR	NR	NR	NR	NR	NR	NR	NR	0	NR	NR	NR	NR	0	NR	NR	NR	NR
Sampling Error (S)	106	457	4	3329	31	0.06	0.01	2.65	0.01	2014	1270363	631.0	7720	4	424	107.3	0.3	4.41	0.01
Total	211	7132		148984		2.58		49.70		2119	3718030		25823		847	6666.3		52.99	

* Mean squares values not followed by ns, * or ** do not have a valid test of significance.

** NR indicates that the sums of squares and the mean squares values are not retrievable (0 degrees of freedom).

*** ns, * and ** indicate non-significance at the 5% level, significance at the 5% level and significance at the 1% level, respectively.

**** NA indicates that the source of variation is not applicable to the measured trait.

APPENDIX V

AVERAGE PROVENANCE AND CLONE-WITHIN-PROVENANCE MEANS FOR TRAITS MEASURED IN THE GREENHOUSE PROVENANCE TRIAL

Table 5.1. Average internode lengths (cm) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	2.9	2.6	2.3	2.6
	219	4.0		3.3	3.7
	222	3.1	3.5	3.6	3.4
	229	4.2	3.3	3.3	3.6
	233	3.0	3.7	3.5	3.4
	238	3.2	3.3	3.2	3.2
	240	2.9	3.3	3.3	3.2
	242		3.7	3.8	3.8
	245	4.0	4.2	3.3	3.8
	Mean	3.4	3.5	3.3	3.4
Thunder Bay	1	4.1	3.8	3.0	3.6
	6	4.3	4.8	4.6	4.6
	8	3.7	3.5	3.0	3.4
	15	4.6	3.9	3.7	4.1
	24	3.4	3.9	4.1	3.8
	34	3.7	3.4	3.7	3.6
	37	3.5	3.0	3.7	3.4
	43	3.8	3.7	3.8	3.8
	44	3.1	3.0	2.8	3.0
	Mean	3.8	3.7	3.6	3.7
Pickle Lake	102	2.9	2.4	3.0	2.8
	112	3.4	4.9	3.6	4.0
	119	3.2	3.0	3.0	3.1
	122	3.1	3.3	4.8	3.7
	135	4.9	4.3	4.6	4.6
	137	3.7	3.7	4.2	3.9
	141	3.3	3.7	3.8	3.6
	142	3.2	4.1	3.1	3.5
	149	3.8	3.2	3.7	3.6
	Mean	3.5	3.6	3.7	3.6
Bearskin Lake	303	3.6	3.1	3.1	3.3
	308	2.8	4.3	3.7	3.6
	314	3.3	3.1	3.4	3.3
	319	3.9	3.9	4.1	4.0
	322	3.0	2.6	2.2	2.6
	326	3.1	3.6	3.3	3.3
	330	2.9	3.1	3.0	3.0
	337	3.5	2.8		3.2
	345	3.0	2.8	2.6	2.8
	Mean	3.2	3.3	3.2	3.2

Table 5.2. Average shoot length (cm) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	38.0	69.0	83.0	63.3
	219	64.5		43.5	54.0
	222	35.0	82.5	61.0	59.5
	229	72.5	49.5	86.5	69.5
	233	48.0	59.0	71.0	59.3
	238	51.5	92.0	92.0	78.5
	240	60.0	66.5	82.5	69.7
	242		45.0	80.5	62.8
	245	65.0	41.5	46.5	51.0
	Mean	54.3	63.1	71.8	63.1
Thunder Bay	1	98.0	71.0	45.0	71.3
	6	55.0	70.0	71.0	65.3
	8	54.0	34.0	97.5	61.8
	15	31.5	60.0	50.5	47.3
	24	30.5	45.0	47.5	41.0
	34	75.5	59.0	77.5	70.7
	37	89.0	53.0	82.5	74.8
	43	35.5	40.0	63.0	46.2
	44	49.0	72.0	35.0	52.0
	Mean	57.6	56.0	63.3	59.0
Pickle Lake	102	43.5	27.5	28.5	33.2
	112	46.0	76.0	80.0	67.3
	119	26.0	32.5	96.0	51.5
	122	48.5	61.5	82.5	64.2
	135	92.0	73.0	91.0	85.3
	137	35.5	33.0	29.0	32.5
	141	24.5	48.5	39.0	37.3
	142	43.5	89.5	41.0	58.0
	149	54.0	44.0	89.5	62.5
	Mean	45.9	53.9	64.1	54.6
Bearskin Lake	303	51.0	41.0	74.0	55.3
	308	25.0	91.0	37.0	51.0
	314	88.0	49.0	90.0	75.7
	319	37.0	79.0	43.5	53.2
	322	34.5	66.5	35.5	45.5
	326	38.0	63.0	84.0	61.7
	330	42.0	85.0	51.5	59.5
	337	93.0	34.0	17.5	48.2
	345	57.5	70.0	55.5	61.0
	Mean	51.8	64.3	54.3	56.8

Table 5.3. Average number of leaves per shoot for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	17	27	29	24
	219	20		14	17
	222	11	27	20	19
	229	20	16	25	20
	233	17	19	23	20
	238	14	24	25	21
	240	22	23	28	24
	242		11	18	15
	245	19	14	12	15
	Mean	18	20	22	20
Thunder Bay	1	25	18	16	20
	6	15	18	19	17
	8	20	14	32	22
	15	11	17	16	15
	24	9	12	13	11
	34	21	17	23	20
	37	25	17	23	22
	43	11	10	19	13
	44	17	27	14	19
	Mean	17	17	19	17
Pickle Lake	102	17	12	11	13
	112	15	20	22	19
	119	10	9	23	14
	122	17	22	26	22
	135	24	20	24	23
	137	12	11	10	11
	141	11	17	16	16
	142	16	28	15	20
	149	17	15	25	19
	Mean	15	17	19	17
Bearskin Lake	303	19	16	26	20
	308	10	25	14	16
	314	31	19	32	27
	319	15	22	16	18
	322	17	29	18	21
	326	16	21	28	22
	330	20	32	20	24
	337	30	13	11	18
	345	22	28	24	25
	Mean	20	23	21	21

Table 5.4. Average total abaxial leaf area per shoot (cm^2) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	649	1739	2368	1585
	219	1407		438	923
	222	349	2329	1176	1285
	229	1259	423	1566	1083
	233	808	1143	1489	1147
	238	519	1725	1787	1344
	240	1233	1480	1983	1565
	242		547	1585	1066
	245	1129	417	402	649
	Mean	919	1225	1422	1189
Thunder Bay	1	2446	1103	602	1384
	6	680	872	990	847
	8	809	428	2178	1138
	15	303	897	717	639
	24	410	682	710	601
	34	1560	1074	1607	1414
	37	2069	1049	1844	1654
	43	337	387	1018	581
	44	930	1673	558	1054
	Mean	1060	907	1136	1035
Pickle Lake	102	506	244	247	332
	112	503	1155	1190	949
	119	181	215	1555	650
	122	492	761	1169	807
	135	1551	1091	1327	1323
	137	394	313	203	303
	141	347	758	536	547
	142	552	1711	415	893
	149	801	532	1772	1035
	Mean	592	753	935	760
Bearskin Lake	303	859	538	1488	962
	308	334	2563	574	1157
	314	1678	668	1926	1424
	319	356	878	330	521
	322	389	1119	481	663
	326	501	1145	1924	1190
	330	575	1621	631	942
	337	2585	435	207	1076
	345	845	1385	940	1057
	Mean	902	1150	945	999

Table 5.5. Average total oven-dry leaf weight per shoot (g) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	1.970	6.080	8.900	5.650
	219	5.460		2.170	3.815
	222	1.120	10.710	4.570	5.467
	229	3.980	1.170	5.440	3.530
	233	2.910	3.990	5.460	4.120
	238	1.730	6.580	7.250	5.187
	240	4.170	4.970	8.130	5.757
	242		2.250	6.690	4.470
	245	3.710	1.580	1.220	2.170
	Mean	3.131	4.666	5.537	4.445
Thunder Bay	1	9.910	4.360	2.330	5.533
	6	2.110	2.690	3.290	2.697
	8	2.630	1.630	9.300	4.520
	15	1.060	3.630	3.000	2.563
	24	1.380	2.610	2.720	2.237
	34	5.750	3.780	6.340	5.290
	37	9.300	4.530	8.990	7.607
	43	1.290	1.470	3.750	2.170
	44	3.700	6.770	1.830	4.100
	Mean	4.126	3.497	4.617	4.080
Pickle Lake	102	1.710	1.030	1.020	1.253
	112	1.630	4.540	4.660	3.610
	119	0.590	0.660	6.170	2.473
	122	1.620	2.980	4.420	3.007
	135	6.610	4.510	6.150	5.757
	137	1.440	1.470	1.010	1.307
	141	1.530	3.150	2.520	2.400
	142	1.720	7.220	1.600	3.513
	149	2.830	2.200	7.950	4.327
	Mean	2.187	3.084	3.944	3.072
Bearskin Lake	303	3.520	2.200	6.130	3.950
	308	1.020	10.730	2.500	4.750
	314	6.730	2.680	9.090	6.167
	319	1.370	3.530	1.290	2.063
	322	1.490	4.250	1.750	2.500
	326	1.710	4.630	7.640	4.660
	330	2.220	6.760	2.430	3.803
	337	10.600	2.030	0.980	4.537
	345	2.850	5.820	3.080	3.917
	Mean	3.501	4.737	3.877	4.038

Table 5.6. Average oven-dry shoot weight (g) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	0.730	3.330	5.500	3.187
	219	2.650		0.910	1.780
	222	0.530	6.380	2.120	3.010
	229	2.340	0.660	3.800	2.267
	233	1.410	1.860	3.090	2.120
	238	0.940	4.760	5.380	3.693
	240	1.870	2.290	4.150	2.770
	242		0.930	4.320	2.625
	245	1.820	0.750	0.600	1.057
	Mean	1.536	2.620	3.319	2.492
Thunder Bay	1	5.520	2.280	0.900	2.900
	6	1.150	1.690	1.880	1.573
	8	1.350	0.590	6.450	2.797
	15	0.410	1.710	1.510	1.210
	24	0.520	1.190	1.200	0.970
	34	3.160	1.860	3.520	2.847
	37	5.240	1.780	4.930	3.983
	43	0.540	0.630	1.950	1.040
	44	1.490	3.270	0.590	1.783
	Mean	2.153	1.667	2.549	2.123
Pickle Lake	102	0.820	0.420	0.350	0.530
	112	0.720	2.420	2.960	2.033
	119	0.220	0.350	4.120	1.563
	122	0.880	1.970	3.330	2.060
	135	4.730	2.670	4.440	3.947
	137	0.560	0.530	0.390	0.493
	141	0.590	1.570	1.070	1.077
	142	0.780	4.750	0.780	2.103
	149	1.260	0.970	5.340	2.523
	Mean	1.173	1.739	2.531	1.814
Bearskin Lake	303	1.650	0.940	3.410	2.000
	308	0.290	6.070	0.750	2.370
	314	6.450	1.430	6.450	4.777
	319	0.700	2.470	0.710	1.293
	322	0.600	2.580	0.700	1.293
	326	0.730	2.130	4.210	2.357
	330	1.230	5.030	1.170	2.477
	337	6.190	0.850	0.260	2.433
	345	1.570	3.070	1.370	2.003
	Mean	2.157	2.730	2.114	2.334

Table 5.7. Average oven-dry root weight (g) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	1.070	1.850	3.150	2.023
	219	1.890		1.360	1.625
	222	0.900	3.930	2.000	2.277
	229	1.730	0.670	1.220	1.207
	233	1.860	1.390	2.360	1.870
	238	1.010	2.020	2.000	2.097
	240	1.220	2.210	2.400	1.943
	242		1.470	2.580	2.025
	245	1.630	0.830	0.540	1.000
	Mean	1.414	1.746	2.030	1.730
Thunder Bay	1	3.330	2.440	1.370	2.380
	6	0.870	1.300	1.470	1.213
	8	1.210	0.840	3.280	1.777
	15	1.030	1.170	2.000	1.400
	24	0.840	1.430	1.030	1.100
	34	1.740	1.340	2.240	1.773
	37	3.550	1.470	4.040	3.020
	43	0.820	0.900	1.290	1.003
	44	2.070	1.960	0.590	1.540
	Mean	1.718	1.428	1.923	1.690
Pickle Lake	102	1.340	0.710	0.790	0.947
	112	0.520	1.840	1.160	1.173
	119	0.390	0.710	2.010	1.037
	122	0.530	1.520	1.240	1.097
	135	1.910	1.590	1.570	1.690
	137	0.670	0.830	1.050	0.850
	141	0.930	1.440	1.380	1.250
	142	0.550	2.370	1.230	1.383
	149	1.180	0.900	5.530	2.537
	Mean	0.891	1.323	1.773	1.329
Bearskin Lake	303	2.380	1.460	1.990	1.943
	308	0.600	3.680	1.070	1.783
	314	3.270	1.610	4.680	3.187
	319	0.840	1.860	0.950	1.217
	322	0.950	2.380	0.620	1.317
	326	1.340	2.160	2.760	2.087
	330	1.300	3.310	1.180	1.930
	337	4.190	1.710	0.600	2.167
	345	0.920	1.960	1.050	1.310
	Mean	1.754	2.237	1.656	1.882

Table 5.8. Average oven-dry root/shoot weight ratio for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	0.396	0.197	0.219	0.271
	219	0.233		0.442	0.338
	222	0.545	0.230	0.299	0.358
	229	0.274	0.366	0.132	0.257
	233	0.431	0.238	0.276	0.315
	238	0.378	0.231	0.211	0.273
	240	0.202	0.167	0.195	0.188
	242		0.462	0.234	0.348
	245	0.295	0.356	0.297	0.316
	Mean	0.344	0.281	0.256	0.294
Thunder Bay	1	0.216	0.367	0.424	0.336
	6	0.267	0.297	0.284	0.283
	8	0.304	0.378	0.291	0.324
	15	0.701	0.219	0.443	0.454
	24	0.442	0.376	0.263	0.360
	34	0.195	0.238	0.227	0.220
	37	0.244	0.233	0.290	0.256
	43	0.448	0.429	0.226	0.368
	44	0.399	0.195	0.244	0.279
	Mean	0.357	0.304	0.290	0.317
Pickle Lake	102	0.530	0.490	0.577	0.532
	112	0.221	0.264	0.152	0.212
	119	0.481	0.703	0.195	0.460
	122	0.212	0.307	0.160	0.226
	135	0.168	0.221	0.148	0.179
	137	0.335	0.415	0.750	0.500
	141	0.439	0.305	0.384	0.376
	142	0.220	0.198	0.517	0.312
	149	0.289	0.284	0.416	0.330
	Mean	0.322	0.354	0.367	0.348
Bearskin Lake	303	0.460	0.465	0.209	0.378
	308	0.458	0.219	0.329	0.335
	314	0.248	0.392	0.301	0.314
	319	0.406	0.310	0.475	0.397
	322	0.455	0.348	0.253	0.352
	326	0.549	0.320	0.233	0.367
	330	0.377	0.281	0.328	0.329
	337	0.250	0.594	0.484	0.443
	345	0.208	0.220	0.236	0.221
	Mean	0.379	0.350	0.316	0.348

Table 5.9. Average petiole length (mm) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	18.5	18.5	25.0	20.7
	219	23.5		18.5	21.0
	222	16.0	27.5	23.5	22.3
	229	40.0	25.0	35.5	33.5
	233	18.5	21.0	20.0	19.8
	238	20.0	29.0	27.0	25.3
	240	20.5	21.5	23.5	21.8
	242		25.5	29.5	27.5
	245	26.0	16.0	19.5	20.5
	Mean	22.9	23.0	24.7	23.5
Thunder Bay	1	22.0	19.5	17.5	19.7
	6	14.5	19.0	20.5	18.0
	8	18.0	20.0	18.0	18.7
	15	26.5	25.0	26.0	25.8
	24	23.0	32.0	30.0	28.3
	34	19.5	15.5	16.0	17.0
	37	25.5	26.5	31.0	27.7
	43	18.0	24.0	19.0	20.3
	44	24.5	22.5	16.0	21.0
	Mean	21.3	22.7	21.6	21.9
Pickle Lake	102	18.5	19.5	21.5	19.8
	112	20.0	27.0	23.5	23.5
	119	11.5	15.5	22.0	16.3
	122	17.0	21.5	22.5	20.3
	135	16.5	20.0	19.0	18.5
	137	25.0	23.5	27.5	25.3
	141	24.0	23.0	33.5	26.8
	142	11.0	20.0	12.0	14.3
	149	23.0	21.0	31.5	25.2
	Mean	18.5	21.2	23.7	21.1
Bearskin Lake	303	12.0	11.5	11.5	11.7
	308	19.0	34.0	24.0	25.7
	314	21.5	21.0	22.0	21.5
	319	13.0	13.5	15.0	13.8
	322	12.0	18.5	12.5	14.3
	326	15.5	20.0	23.0	19.5
	330	21.0	27.5	21.0	23.2
	337	19.5	17.5	33.0	23.3
	345	17.0	25.5	20.0	20.8
	Mean	16.7	21.0	20.2	19.3

Table 5.10. Average single-leaf abaxial area (cm^2) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	65.9	92.7	107.0	88.5
	219	102.5		52.8	77.7
	222	46.3	125.6	104.2	92.0
	229	101.4	43.3	99.7	81.5
	233	78.0	91.6	121.4	97.0
	238	46.5	93.5	92.7	77.6
	240	78.8	99.2	123.8	100.6
	242		71.0	124.1	97.6
	245	89.3	49.4	50.7	63.1
	Mean	76.1	83.3	97.4	85.6
Thunder Bay	1	122.9	86.0	61.9	90.3
	6	58.6	72.0	79.9	70.2
	8	71.7	49.4	96.3	72.5
	15	37.6	80.1	81.6	66.4
	24	58.6	88.0	82.4	76.3
	34	105.9	80.0	114.9	100.3
	37	94.9	93.5	117.4	101.9
	43	44.9	56.9	86.8	62.9
	44	83.0	89.4	57.7	76.7
	Mean	75.3	77.2	86.5	79.7
Pickle Lake	102	46.3	27.7	32.9	35.6
	112	47.3	90.2	81.9	73.1
	119	29.3	29.3	102.2	53.6
	122	46.1	58.9	73.8	59.6
	135	84.6	68.6	82.5	78.6
	137	43.5	43.8	33.7	40.3
	141	51.4	60.8	70.4	60.9
	142	48.9	79.2	42.9	57.0
	149	63.1	44.9	98.3	68.8
	Mean	51.1	55.9	68.7	58.6
Bearskin Lake	303	80.3	62.4	83.4	75.4
	308	42.1	145.8	72.1	86.7
	314	73.1	48.5	80.5	67.4
	319	33.6	52.6	37.1	41.1
	322	36.1	52.4	39.4	42.6
	326	50.7	72.3	104.1	75.7
	330	45.7	80.4	49.6	58.6
	337	111.6	43.6	37.6	64.3
	345	56.2	68.3	60.4	61.6
	Mean	58.8	69.6	62.7	63.7

Table 5.11. Average single-leaf oven-dry weight (mg) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	175	285	380	280
	219	385		235	310
	222	125	520	380	342
	229	305	105	315	242
	233	250	290	430	323
	238	160	345	380	295
	240	240	290	440	323
	242		285	510	398
	245	265	165	125	185
	Mean	238	286	355	293
Thunder Bay	1	475	315	215	335
	6	165	215	255	212
	8	215	190	390	265
	15	120	290	295	235
	24	185	315	290	263
	34	350	255	430	345
	37	400	345	525	423
	43	140	190	300	210
	44	325	360	180	288
	Mean	264	275	320	286
Pickle Lake	102	140	110	120	123
	112	140	330	320	263
	119	85	85	390	187
	122	125	205	245	192
	135	340	260	355	318
	137	145	175	145	155
	141	190	230	285	235
	142	145	310	150	202
	149	215	190	395	267
	Mean	169	211	267	216
Bearskin Lake	303	310	225	325	287
	308	125	565	290	327
	314	295	170	395	287
	319	115	190	120	142
	322	125	190	130	148
	326	150	270	350	257
	330	155	295	170	207
	337	430	185	160	258
	345	165	290	190	215
	Mean	208	264	237	236

Table 5.12. Average specific leaf weight (mg/cm^2) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	2.66	3.07	3.55	3.09
	219	3.76		4.45	4.11
	222	2.70	4.13	3.65	3.49
	229	3.01	2.42	3.16	2.86
	233	3.18	3.17	3.56	3.30
	238	3.45	3.70	4.10	3.75
	240	3.06	2.92	3.57	3.18
	242		4.03	4.12	4.08
	245	2.96	3.38	2.47	2.94
	Mean	3.10	3.35	3.62	3.36
Thunder Bay	1	3.86	3.66	3.47	3.66
	6	2.82	2.99	3.19	3.00
	8	3.00	3.85	4.05	3.63
	15	3.20	3.62	3.61	3.48
	24	3.15	3.58	3.52	3.42
	34	3.31	3.19	3.74	3.41
	37	4.21	3.69	4.47	4.12
	43	3.12	3.35	3.46	3.31
	44	3.92	4.03	3.12	3.69
	Mean	3.40	3.55	3.63	3.53
Pickle Lake	102	3.02	3.97	3.65	3.55
	112	2.96	3.67	3.90	3.51
	119	2.90	2.90	3.82	3.21
	122	2.71	3.49	3.32	3.17
	135	4.02	3.79	4.30	4.04
	137	3.33	4.00	4.33	3.89
	141	3.69	3.78	4.05	3.84
	142	2.97	3.91	3.49	3.46
	149	3.41	4.23	4.02	3.89
	Mean	3.23	3.75	3.88	3.62
Bearskin Lake	303	3.86	3.61	3.90	3.79
	308	2.97	3.88	4.03	3.63
	314	4.04	3.52	4.91	4.16
	319	3.42	3.61	3.24	3.42
	322	3.46	3.63	3.30	3.46
	326	2.96	3.74	3.35	3.35
	330	3.40	3.67	3.43	3.50
	337	3.85	4.24	4.25	4.11
	345	2.94	4.26	3.15	3.45
	Mean	3.43	3.79	3.73	3.65

Table 5.13. Average stomatal density (#/mm^2) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	178	186	183	182
	219	194		190	192
	222	184	142	173	166
	229	173	195	194	187
	233	159	144	139	147
	238	243	214	179	212
	240	191	206	213	203
	242		245	227	236
	245	211	176	184	190
	Mean	192	188	187	189
Thunder Bay	1	205	221	176	200
	6	205	231	217	218
	8	220	200	260	227
	15	231	194	165	197
	24	201	202	218	207
	34	263	240	233	245
	37	252	248	219	240
	43	312	273	234	273
	44	208	281	225	238
	Mean	233	232	216	227
Pickle Lake	102	172	182	209	188
	112	208	196	195	200
	119	213	177	165	185
	122	281	312	260	285
	135	203	246	224	224
	137	225	234	273	244
	141	207	214	183	201
	142	184	193	197	191
	149	199	214	196	203
	Mean	210	219	212	214
Bearskin Lake	303	251	265	262	259
	308	163	132	131	142
	314	249	224	228	234
	319	192	213	191	199
	322	213	214	220	216
	326	193	214	215	207
	330	248	196	226	224
	337	162	154	150	156
	345	208	197	201	202
	Mean	209	201	203	204

Table 5.14. Average stomatal length (μm) for provenances and clones-within-provenances in the greenhouse provenance trial.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	29.0	28.9	30.1	29.3
	219	32.0		32.8	32.4
	222	30.7	33.7	31.5	32.0
	229	30.2	25.8	27.5	27.8
	233	28.0	33.4	29.2	30.2
	238	31.7	29.7	34.4	31.9
	240	29.4	30.6	32.6	30.9
	242		31.5	30.9	31.2
	245	26.8	25.7	29.4	27.3
	Mean	29.7	29.9	30.9	30.2
Thunder Bay	1	33.5	33.1	33.2	33.3
	6	31.6	28.9	33.0	31.2
	8	28.2	28.2	28.0	28.1
	15	32.1	29.6	34.1	31.9
	24	30.2	29.8	28.6	29.5
	34	30.7	28.3	28.5	29.2
	37	32.8	33.7	33.7	33.4
	43	25.6	28.2	27.7	27.2
	44	33.3	29.7	33.1	32.0
	Mean	30.9	29.9	31.1	30.6
Pickle Lake	102	28.6	27.6	28.8	28.3
	112	28.8	31.8	29.9	30.2
	119	30.7	33.2	33.2	32.4
	122	25.5	26.9	28.8	27.1
	135	31.9	31.9	29.7	31.2
	137	31.9	31.0	26.4	29.8
	141	27.7	28.0	30.5	28.7
	142	30.1	29.5	27.6	29.1
	149	28.2	26.3	31.2	28.6
	Mean	29.2	29.6	29.5	29.4
Bearskin Lake	303	28.6	28.3	25.6	27.5
	308	34.4	43.0	41.2	39.5
	314	30.0	29.4	29.3	29.6
	319	28.4	31.1	29.4	29.6
	322	32.1	32.8	32.3	32.4
	326	28.4	34.1	30.0	30.8
	330	27.3	30.3	27.8	28.5
	337	35.0	36.0	35.8	35.6
	345	27.4	26.9	28.1	27.5
	Mean	30.2	32.4	31.0	31.2

Table 5.15. Average transpiration rates ($\mu g/(cm^2 s)$) for provenances and clones-within-provenances in the greenhouse provenance trial on July 11, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	8.858	7.336	5.630	7.275
	219	7.677		7.497	7.587
	222		5.455	8.009	6.732
	229	7.355	6.053	6.468	6.625
	233	9.549	5.930	6.058	7.179
	238	7.513	7.703	7.352	7.523
	240	7.300	7.576	8.169	7.682
	242		7.818	7.597	7.708
	245	4.892	6.493	7.530	6.305
	Mean	7.592	6.795	7.145	7.177
Thunder Bay	1	8.500	8.912	7.734	8.382
	6	7.847	6.583	8.239	7.556
	8	7.411	8.654	6.944	7.670
	15	7.359	6.758	7.576	7.231
	24	5.596	5.023	5.235	5.285
	34	7.599	6.869	7.211	7.226
	37	9.051	8.287	8.020	8.456
	43	8.033	7.677	7.645	7.785
	44	8.400	7.152	9.015	7.189
	Mean	7.755	7.324	7.513	7.531
Pickle Lake	102	7.484	5.566	5.641	6.230
	112	6.451	8.287	6.522	7.087
	119	8.095	7.294	7.824	7.738
	122	9.202	5.581	6.956	7.246
	135	7.331	7.464	6.099	6.965
	137	8.753	8.963	7.211	8.309
	141	6.345	5.690	7.989	6.675
	142	7.724	7.861	5.113	6.899
	149	7.743	7.927	7.135	7.602
	Mean	7.681	7.181	6.721	7.194
Bearskin Lake	303	7.392	4.755	7.054	6.407
	308	7.191	8.191	9.160	7.903
	314	6.668	5.814	6.248	6.243
	319	8.705	7.614	6.852	7.724
	322	8.552	8.809	8.225	8.529
	326	7.238	8.345	7.328	7.637
	330	7.882	5.001	6.218	6.367
	337	8.553	9.423	7.400	8.459
	345	7.362	7.817	7.093	7.424
	Mean	7.838	7.310	7.286	7.478

Table 5.15. Average transpiration rates (μg/(cm²s)) for provenances and clones-within-provenances in the greenhouse provenance trial on July 12, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	9.556	8.025	12.975	10.185
	219	8.936		12.475	10.706
	222	8.829	7.429	15.545	10.601
	229	7.919	4.923	12.295	8.379
	233	9.114	7.001	9.423	8.513
	238	9.200	7.486	14.060	10.249
	240	8.429	8.927	15.505	10.954
	242		9.237	13.320	11.279
	245	9.233	7.594	12.945	9.924
	Mean	8.902	7.577	13.171	9.883
Thunder Bay	1	10.845	8.642	14.665	11.384
	6	10.372	8.438	14.860	11.223
	8	8.995	9.243	15.935	11.391
	15	8.507	8.127	15.080	10.571
	24	7.545	5.378	10.417	7.780
	34	9.234	6.348	14.150	9.911
	37	11.435	9.712	15.260	12.136
	43	9.601	7.755	12.295	9.884
	44	10.755	8.204	16.020	11.660
	Mean	9.699	7.983	14.298	10.660
Pickle Lake	102	7.745	6.297	12.860	8.967
	112	8.055	8.894	10.051	9.000
	119	9.596	7.338	15.535	10.823
	122	9.823	6.714	11.780	9.439
	135	10.910	8.782	9.454	9.715
	137	10.134	9.328	15.055	11.506
	141	7.792	6.319	14.770	9.627
	142	8.550	6.392	12.305	9.082
	149	9.643	9.130	15.430	11.401
	Mean	9.139	7.688	13.027	9.951
Bearskin Lake	303	9.458	5.592	15.175	10.075
	308	9.602	8.918	16.820	11.780
	314	7.980	6.624	15.110	9.905
	319	10.489	9.849	13.810	11.383
	322	11.130	9.328	15.335	11.931
	326	8.891	9.145	9.905	9.314
	330	8.256	5.931	12.665	8.951
	337	9.956	9.217	13.915	11.029
	345	9.069	9.902	15.095	11.355
	Mean	9.425	8.278	14.203	10.635

Table 5.17. Average transpiration rates ($\mu g/(cm^2 s)$) for provenances and clones-within-provenances in the greenhouse provenance trial on July 13, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	8.693	8.104	6.261	7.686
	219	8.143		6.004	7.074
	222	8.122	6.977	7.880	7.660
	229	7.390	3.596	5.262	5.416
	233	7.593	6.279	5.013	6.295
	238	8.227	8.052	7.826	8.335
	240	7.644	7.120	8.308	7.691
	242		7.245	7.411	7.328
	245	8.527	6.494	7.223	7.415
	Mean	8.042	6.846	6.798	7.229
Thunder Bay	1	9.888	7.973	7.107	8.323
	6	9.687	6.345	7.719	7.917
	8	8.051	7.508	7.742	7.767
	15	7.491	6.172	7.316	6.993
	24	6.460	5.677	4.810	5.649
	34	8.738	7.359	7.577	7.891
	37	10.490	8.469	8.047	9.002
	43	8.434	7.809	4.901	7.048
	44	9.637	6.898	7.751	8.095
	Mean	8.764	7.134	6.996	7.631
Pickle Lake	102	6.403	3.942	4.510	4.953
	112	7.417	7.705	6.137	7.086
	119	8.123	6.987	7.507	7.539
	122	9.300	7.128	6.927	7.785
	135	10.032	8.343	6.664	8.346
	137	9.525	8.012	6.828	8.122
	141	6.527	6.664	6.938	6.710
	142	7.684	5.601	4.097	5.794
	149	9.222	6.733	7.298	7.751
	Mean	8.248	6.791	6.323	7.121
Bearskin Lake	303	8.586	5.812	8.134	7.511
	308	9.083	8.843	8.067	8.664
	314	8.162	6.228	7.640	7.343
	319	9.242	8.452	6.923	8.206
	322	10.032	8.635	7.204	8.624
	326	7.763	8.204	6.121	7.363
	330	6.289	6.949	5.564	6.267
	337	9.441	7.127	6.181	7.583
	345	8.563	6.742	7.375	7.560
	Mean	8.573	7.443	7.023	7.680

Table 5.18. Average transpiration rates ($\mu g/(cm^2 s)$) for provenances and clones-within-provenances in the greenhouse provenance trial on July 14, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	5.101	4.398	2.927	4.142
	219	4.699		2.950	3.825
	222	5.136	5.126	4.707	4.990
	229	6.628	2.779	2.565	3.991
	233	3.746	3.468	2.517	3.244
	238	6.383	4.018	5.127	5.176
	240	4.808	5.611	4.883	5.101
	242		5.908	3.055	4.812
	245	3.815	3.205	2.552	3.191
	Mean	5.039	4.313	3.476	4.276
Thunder Bay	1	6.510	6.560	3.736	5.602
	6	6.024	4.539	4.342	4.968
	8	4.249	5.074	3.827	4.383
	15	6.316	4.738	3.551	4.868
	24	3.187	2.278	1.936	2.467
	34	5.902	2.508	4.552	4.321
	37	6.995	6.458	3.941	5.798
	43	4.636	3.605	1.668	3.303
	44	4.366	5.131	3.622	4.373
	Mean	5.354	4.543	3.464	4.454
Pickle Lake	102	4.081	2.233	1.495	2.603
	112	4.981	6.079	3.563	4.874
	119	4.587	4.376	4.184	4.382
	122	4.922	2.907	4.343	4.057
	135	4.049	4.835	3.438	4.107
	137	5.295	5.289	3.369	4.651
	141	4.710	2.729	3.639	3.693
	142	4.894	3.661	1.858	3.471
	149	2.897	3.970	3.417	3.428
	Mean	4.491	4.009	3.256	3.919
Bearskin Lake	303	4.249	3.316	5.015	4.193
	308	5.621	5.372	4.218	5.070
	314	4.892	3.494	4.565	4.317
	319	4.907	6.184	3.154	4.748
	322	3.870	5.958	3.531	4.453
	326	4.137	6.083	2.619	4.280
	330	4.918	1.947	2.345	3.070
	337	6.064	4.932	2.967	4.654
	345	5.442	4.608	4.607	4.886
	Mean	4.900	4.655	3.669	4.408

Table 5.19. Average stomatal conductance (cm/s) for provenances and clones-within-provenances in the greenhouse provenance trial on July 11, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	1.239	0.947	0.658	0.948
	219	1.018		0.929	0.974
	222		0.662	1.094	0.878
	229	0.932	0.724	0.869	0.842
	233	1.328	0.743	0.800	0.957
	238	0.955	0.982	0.989	0.975
	240	0.961	0.952	1.231	1.048
	242		1.041	0.972	1.007
	245	0.611	0.826	1.051	0.829
	Mean	1.006	0.860	0.955	0.940
Thunder Bay	1	1.170	1.179	1.013	1.121
	6	1.058	0.808	1.170	1.012
	8	0.941	1.170	0.884	0.998
	15	0.939	0.843	0.964	0.915
	24	0.715	0.612	0.624	0.650
	34	0.980	0.879	0.980	0.946
	37	1.241	1.083	1.027	1.117
	43	1.059	1.032	0.980	1.024
	44	1.131	0.899	1.250	1.093
	Mean	1.026	0.945	0.988	0.986
Pickle Lake	102	0.989	0.668	0.709	0.789
	112	0.833	1.098	0.829	0.920
	119	1.083	0.947	1.019	1.016
	122	1.282	0.686	0.891	0.953
	135	0.979	0.973	0.784	0.912
	137	1.203	1.272	0.933	1.136
	141	0.803	0.701	1.087	0.864
	142	0.998	0.993	0.616	0.869
	149	1.015	1.050	0.896	0.987
	Mean	1.020	0.932	0.863	0.938
Bearskin Lake	303	0.975	0.579	0.955	0.836
	308	1.083	1.083	1.200	1.122
	314	0.837	0.727	0.847	0.804
	319	1.179	0.982	0.975	1.045
	322	1.154	1.179	1.106	1.146
	326	0.960	1.106	0.960	1.009
	330	1.036	0.604	0.840	0.827
	337	1.155	1.268	0.970	1.131
	345	0.958	0.987	0.943	0.963
	Mean	1.037	0.946	0.977	0.987

Table 5.20. Average stomatal conductance (cm/s) for provenances and clones-within-provenances in the greenhouseprovenance trial on July 12, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	1.088	1.079	1.079	1.082
	219	1.081		1.075	1.078
	222	1.006	0.937	1.331	1.091
	229	0.849	0.524	1.089	0.821
	233	1.065	0.880	1.026	0.990
	238	1.059	1.024	1.297	1.127
	240	0.979	1.065	1.828	1.291
	242		1.199	1.218	1.209
	245	1.103	1.022	1.073	1.066
	Mean	1.029	0.966	1.224	1.073
Thunder Bay	1	1.306	1.067	1.212	1.195
	6	1.206	0.988	1.480	1.225
	8	1.030	1.240	1.326	1.199
	15	1.027	0.947	1.392	1.122
	24	0.812	0.655	0.828	0.765
	34	1.158	0.836	1.456	1.150
	37	1.420	1.297	1.279	1.332
	43	1.243	1.132	1.184	1.186
	44	1.356	0.987	1.357	1.233
	Mean	1.173	1.017	1.279	1.156
Pickle Lake	102	0.851	0.736	1.255	0.947
	112	0.883	1.119	1.026	1.009
	119	1.058	0.970	1.563	1.197
	122	1.115	0.837	1.349	1.100
	135	1.321	1.201	0.995	1.172
	137	1.163	1.333	1.319	1.272
	141	0.892	0.809	1.576	1.092
	142	0.978	0.704	1.013	0.898
	149	1.132	1.220	1.439	1.264
	Mean	1.044	0.992	1.282	1.106
Bearskin Lake	303	1.096	0.684	1.468	1.083
	308	1.265	1.275	1.426	1.322
	314	0.904	0.851	1.428	1.061
	319	1.262	1.450	1.346	1.353
	322	1.431	1.288	1.351	1.357
	326	0.988	1.253	0.817	1.019
	330	0.963	0.777	1.125	0.955
	337	1.210	1.317	1.262	1.263
	345	1.076	1.384	1.397	1.286
	Mean	1.133	1.142	1.291	1.189

Table 5.21. Average stomatal conductance (cm/s) for provenances and clones-within-provenances in the greenhouse provenance trial on July 13, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	1.177	1.193	0.891	1.087
	219	1.066		0.854	0.960
	222	1.063	1.060	1.160	1.094
	229	0.973	0.490	0.745	0.736
	233	0.995	0.881	0.704	0.860
	238	1.065	1.225	1.166	1.152
	240	1.070	1.114	1.251	1.145
	242		1.110	1.079	1.095
	245	1.121	0.851	1.043	1.005
	Mean	1.066	0.990	0.988	1.015
Thunder Bay	1	1.426	1.233	1.070	1.243
	6	1.316	0.929	1.165	1.137
	8	1.046	1.161	1.179	1.129
	15	0.951	0.944	1.124	1.006
	24	0.816	0.764	0.673	0.751
	34	1.164	0.948	1.153	1.088
	37	1.469	1.334	1.240	1.348
	43	1.198	1.063	0.660	0.974
	44	1.294	1.023	1.184	1.167
	Mean	1.187	1.044	1.050	1.094
Pickle Lake	102	0.799	0.556	0.595	0.650
	112	0.994	1.229	0.895	1.039
	119	1.072	1.045	1.126	1.081
	122	1.325	0.935	1.036	1.099
	135	1.377	1.296	0.988	1.220
	137	1.345	1.299	1.011	1.218
	141	0.847	0.863	0.998	0.903
	142	1.008	0.807	0.556	0.790
	149	1.247	1.016	1.104	1.122
	Mean	1.113	1.005	0.923	1.014
Bearskin Lake	303	1.146	0.766	1.276	1.063
	308	1.241	1.308	1.255	1.268
	314	1.056	0.863	1.127	1.015
	319	1.228	1.310	1.023	1.187
	322	1.358	1.289	1.088	1.245
	326	1.015	1.267	0.847	1.043
	330	0.771	0.888	0.808	0.822
	337	1.297	1.088	0.884	1.090
	345	1.186	0.996	1.097	1.093
	Mean	1.144	1.086	1.045	1.092

Table 5.22. Average stomatal conductance (cm/s) for provenances and clones-within-provenances in the greenhouse provenance trial on July 14, 1988.

Provenance	Clone	Block 1	Block 2	Block 3	Mean
Northern Wisconsin	201	1.089	0.910	0.672	0.890
	219	1.027		0.694	0.861
	222	1.029	1.039	0.959	1.009
	229	1.320	0.474	0.575	0.790
	233	0.769	0.679	0.481	0.643
	238	1.336	0.821	1.114	1.090
	240	0.884	1.057	1.051	0.997
	242		1.215	0.969	0.956
	245	0.712	0.620	0.584	0.639
	Mean	1.021	0.852	0.758	0.877
Thunder Bay	1	1.385	1.337	0.963	1.228
	6	1.270	0.823	0.894	0.996
	8	0.870	1.021	0.967	0.953
	15	1.344	0.883	0.880	1.036
	24	0.570	0.424	0.430	0.475
	34	1.240	0.473	1.000	0.904
	37	1.657	1.339	0.976	1.324
	43	0.896	0.721	0.305	0.661
	44	0.860	0.978	0.885	0.908
	Mean	1.121	0.889	0.818	0.943
Pickle Lake	102	0.782	0.372	0.326	0.493
	112	0.965	1.221	0.717	0.968
	119	0.894	0.896	1.013	0.934
	122	0.898	0.565	0.925	0.796
	135	0.860	1.065	0.670	0.865
	137	1.164	1.077	0.810	1.017
	141	0.881	0.538	0.729	0.716
	142	0.974	0.687	0.420	0.694
	149	0.528	0.695	0.828	0.684
	Mean	0.883	0.791	0.715	0.796
Bearskin Lake	303	0.851	0.670	1.126	0.882
	308	1.123	1.128	1.065	1.105
	314	0.949	0.699	0.966	0.871
	319	1.036	1.294	0.640	0.990
	322	0.768	1.320	0.859	0.982
	326	0.767	1.269	0.588	0.875
	330	1.038	0.359	0.435	0.611
	337	1.260	0.892	0.680	0.944
	345	0.990	0.856	0.956	0.934
	Mean	0.976	0.943	0.813	0.911