PLUS-TREE SELECTION OF BLACK SPRUCE IN NORTHWESTERN ONTARIO FOR SUPERIOR GROWING SPACE EFFICIENCY

by

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Plus-tree selection of black spruce (*Picea mariana* (Mill.) B.S.P.) based on increment of wood volume per unit of crown (growing space efficiency) has the potential to improve yield per hectare and avoid biased selection of trees that have a competitive advantage in natural stands. In 1981, and again in 1983, 200 and 400 trees from two 60 year-old upland black spruce stands located in Northwestern Ontario were scored for various growth parameters, crown dimensions and competition indices. Regression analysis showed that the competition indices were poorer indicators of basal area increment (b.a.i.) than the crown parameters. The crown parameter that best predicted b.a.i. was crown area (c.a.); r^2 values of 0.45 and 0.57 respectively were calculated for the two black spruce stands although the slopes differed significantly. To test the effectiveness of baseline selection of black spruce based on the regression of b.a.i. vs. c.a., the top 10 trees were selected from the second stand by this method and compared to each of the top 10 trees chosen by a height vs. age baseline method and a purely random method. Only one tree was selected in common by each of the baseline methods. Trees selected by b.a.i. vs. c.a. baseline were far more variable in their size than those selected by height vs. age. Scale drawings and statistical analysis of the selected trees did not reveal any easily-identified crop ideotype of black spruce plus-trees expressing growing space efficiency. Wind-pollinated seed of the 29 selected trees was collected and used to establish a short-term and a long-term progeny test to investigate heritability of growing space efficiency. The short-term test was conducted in a greenhouse over one growing season and included light intensity as a treatment, while the long-term progeny test was planted in 1984 and included spacing as a treatment. Discriminant analysis of Marks Lake progeny helped to identify a weak trend where the tallest progeny came from short-crowned parents. Results of the short-term progeny test demonstrated strong family differences, strong family x light interaction, but no selection method differences. Some of the family differences in the progeny could be accounted for by the maternal effect of seed weight, although after removal of this effect by analysis of covariance, still no differences could be detected between selection methods. Parent and progeny correlations for height and crown features were weak and often negative, which suggests heritability estimates for characters related to growing space efficiency are likely to be as low as estimates for growth in general. The premature results of this study imply that if trees selected for superior growing space efficiency have inherent advantages in lower light intensities within mature stands, their juvenile progeny do not express these qualities. Characters responsible for growing space efficiency are not heritable or have not yet expressed themselves.

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INTRODUCTION

Ontario's economic development was spurred by the exploitation of the large continuous stands of black spruce (*Picea mariana* (Mill) B.S.P.) within the boreal forest region in the early 1900s (Rowe, 1972). Wood fiber demand is steadily rising, as is the demand for high quality black spruce pulp. For this reason black spruce remains a vital part of Ontario's economy. The accelerated harvest of natural timber reserves often requires artificial means of regeneration to keep pace with the depletion of the natural resource. The gains in quality and quantity of the wood supply from cultural practices associated with this "second forest" is enhanced if the growing stock comes from superior seed sources (Rauter, 1979). Superior seed is developed through tree improvement programs where initial phenotype or plus-tree selection plays an important role.

Black spruce is genetically variable in its growth rate, but not in its morphological characteristics such as stem straightness and branch angle. Selection of superior black spruce trees should, therefore, logically concentrate on growth parameters (Morgenstern, 1975). Plus-tree selection of black spruce based upon height growth employing single-tree selections and high selection differentials has not proven satisfactory and has been replaced by a low-intensity "occular" initial selection followed by family selection of open-pollinated progeny based upon height growth.

An alternate approach to plus-tree selection for improving height growth of individual trees is to improve tree growing space efficiency. Brown and Goddard (1961), Thomas (1980), and Stanton and Canavera (1983) indicate that plus-trees identified by their superior basal area increment (b.a.i.) per unit crown area (c.a.) defined from linear regressions may provide stock that are inherently superior in growing space efficiency. Stands comprised of individuals that express superior growing space efficiency would show higher mean tree volumes at any density and this would give greater volume yields per hectare relative to average stands, thus shifting the emphasis from tree improvement to stand improvement.

The primary objective of this thesis was to evaluate plus-tree selection for growing space efficiency as a method for increasing volume per hectare of black spruce. A secondary objective was to identify a parent tree form or crown shape that was related to growing space efficiency, thus simplifying plus-tree selection field procedures.

Information on heritability and possible genetic gains through selection for growing space efficiency is nonexistant. A return to intensive plus-tree selection might be warranted if the heritability of the characters that are responsible for growing space efficiency prove adequate for black spruce.

LITERATURE REVIEW

TREE IMPROVEMENT AND THE ROLE OF PLUS-TREE SELECTION

Genetic systems of boreal conifers promote outcrossing and maintain high levels of genetic variation (Hamrick et al., 1979). For this reason, most boreal conifers are amenable to tree improvement programs that are designed to exploit genetic variation (Morgenstern, 1975).

Genetic variation of boreal conifers can follow geographic patterns that are continuous (clinal), discontinuous (ecotypic) or random (resulting from genetic drift) (Stebbins, 1950). Tree improvement programs have been established that exploit geographic variation through the selection of superior provenances and the establishment of seed collection zones (Rauter, 1979; Teich, 1973). Genetic variation is also expressed locally between individuals (Wright, 1976) which may be partially a result of selection pressures caused from inter-tree competition (Stern, 1969). Specialized tree improvement programs try to exploit variation between individuals within a region by carefully selecting trees with superior phenotypes from natural stands to provide material for seed orchards or breeding experiments.

Initial phenotypic selection from the forest is based on a selection methodology designed to screen candidates that exhibit desirable characters. Initial selection (Falconer, 1981) can lead directly to seed orchard development or can be followed by additional breeding and selection methods (i.e., family selection from progeny trials). Candidate trees that meet the criteria are often called "plus-trees" (Wright, 1976; Morgenstern, 1975).

In general, southern pine species and Monterey pine (*Pinus radiata* D. Don) plus-tree selection programs appear successful (Dorman, 1976; Cotterill and Zed, 1980). The effectiveness of plus-tree selection is questionable for Douglas fir (*Pseudotsuga menziesii* (Mirb) Franco) (Silen and Mandel, 1981), jack pine (*Pinus banksiana* Lamb.) (Canavera, 1975) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Samuel and Johnstone, 1979). Although not used extensively with hardwoods, plus-tree selection was judged ineffective with black cherry (*Prunus serotina* Ehrh.) (Pitcher, 1982), and several southern hardwoods (Purnell and Kellison, 1983) (from Stanton and Canavera, 1983).

PLUS-TREE SELECTION METHODS

The philosophy underlying plus-tree selection is that the favorable deviation of plus-trees from the population mean is due at least partly to genetic rather than environmental or random effects (Falconer, 1981). Occular, check-tree and baseline plus-tree selection methods differ in the sample method used to determine the population mean and the specified deviation from the mean.

Occular methods rely upon a subjective assessment where trees that appear to be better than average are chosen as plus-trees without measuring the candidate or neighbouring trees. The occular method is useful for improving qualitative, morphological or multiple characters. But the majority of economic characters of interest to foresters, such as growth rates, are quantitative rather than qualitative. Improved growth rates reduce rotation ages and increase yield and economic return to silvical investments (Davis, 1966).

When a more objective method than the occular method is desired, either the check-tree or base line method may be used. The check-tree method is similar to the occular method and compares candidate trees to their immediate neighbours. Plus-trees must exceed their neighbours' measure of performance by a specified amount, usually an arbitrary point of truncation that will give the desired selection differential (Ledig, 1974). The selection differential is the difference between the normal and selected population means (Falconer, 1981). Check-tree methods are limited to pure, even-aged stands. The small sample of neighbours may include siblings which significantly increases the probability of rejecting genetically superior trees (Ledig, 1974).

Base line methods of plus-tree selection rely upon the sampling of a large enough segment of the parent population such that a base line is constructed from least-squares regression where the character of interest (usually height growth) is the dependent variable (age is usually the independent variable) (Ledig, 1974). The base line (regression line) defines the population mean and plus-trees would be among the greatest positive residuals or would exceed some other point of truncation. For example, if a site index baseline, from a regression of height vs. age, showed the average 50 year-old tree was 15 meters, plus-trees of that age would be at least 17 meters tall. The large samples required can make the base line method costly, but this method is not restricted to pure, even-aged stands and there is no risk of disregarding plus-trees that are relatives in close proximity to each other.

BLACK SPRUCE SELECTION IN NORTHWESTERN ONTARIO

In many areas of the boreal forest region black spruce is the most common species (Rowe, 1972), having a range from Newfoundland to Alaska (Hoise, 1967). The wood produces high yields of excellent quality pulp (Ladell, 1970). Losses due to decay seldom exceed 3% of total volume (Basham and Morawski, 1964). The tree's generally good form results in easy logging, in low handling costs and in good utilization. All these qualities combine to make black spruce a very valuable tree species.

Black spruce varies clinally with latitude across its range with noticeable amounts of variation within a region and large amounts of variation between individuals within stands sufficient to warrant tree improvement work (Fowler and Mullin, 1977; Morgenstern, 1975; 1978). There is an absence of proven ecotypic variation between upland and lowland sites.

Black spruce is primarily used for pulp and paper, and all phenotypes usually express good form (Morgenstern, 1975). Therefore, tree improvement effort has been directed toward increasing total yield. When the plus-tree selection program began in Ontario, an intensive selection strategy was adopted that involved a site index (height vs. age), base-line method. A high selection differential was chosen that limited candidates to the best sites because it was felt that phenotypic expression of height on poor sites would not show large, easily measured differences (Morgenstern, 1975).

Morgenstern (1973) estimated the heritability expressed by 4 year-old seedlings' height growth to be 17% with a corresponding gain of 8%. These values are generally considered to be adequate to justify expenditures if seedling results are maintained to maturity (Carlisle and Teich, 1971). The selection differential required to realize this genetic gain was quite high.

Initial targets set for the location of plus-trees were not met in Northwestern Ontario because of budget priorities, lack of understanding and lack of enthusiasm of personnel, as well as other problems commonly associated with the initiation of any new program (Kokocinski, personal communication). The high selection differential required many man-hours, thus less intensive selection procedures were recommended to help reduce costs and meet targets (Morgenstern, 1975).

In recent years, the intensive site-index baseline method has been replaced in favour of a low intensity comparison tree (occular) method. Trees were selected based upon relative performance determined visually from observations made of the surrounding forest at 40 meter intervals along a grid established within a stand (Kokocinski, 1979). Open-pollinated progeny trials were established and family selections are to be made 20 years after establishment (Rauter, 1979).

GROWING SPACE EFFICIENCY: AN ALTERNATIVE CRITERION FOR PLUS-TREE SELECTION

One alternative approach to (single-tree) plus-tree selection and thus to improving tree growth, is to improve tree growing space efficiency. The focus is shifted from individual tree improvement to stand improvement. Increases in yield per hectare are possible because productivity per tree could be maintained in dense stands. Plus-trees would possess the potential of producing more volume or basal area increment (b.a.i.) per unit of crown size and/or growing space than competing trees of the same age.

In addition, plus-tree selection is not biased in favour of trees with chance, competitive advantages, a problem with other methods of plus-tree selection (Brown and Goddard, 1961).

A difficulty of this alternate selection approach lies in the definition of growing space. Assmann (1970) defined growing space as the tree's horizontal crown projection plus its appropriate allocation of unoccupied area. For the past 20 years, this topic has been explored by ecologists and forest mensurationists in applications of single tree growth modelling (Munro, 1974). Many competition indices (see Alemdag, 1978) have been developed to predict individual tree growth on the basis of growing space defined by several factors that can be considered as either extrinsic, distance-dependent measures of competing trees (e.g., Spurr, 1962; Opie, 1968) or intrinsic measures of subject tree crowns (e.g., Krajicek et al., 1961; Hatch, 1975; Arney, 1973).

Brown and Goddard (1961) estimated 35 year-old Loblolly pine (*Pinus taeda* L.) 10 year b.a.i. from few 90° increment cores bored at d.b.h. Ten year b.a.i. was regressed against a measure of crown area (crown length x width) for fifty trees. The strong relationship ($r^2 = 0.69$) made possible a baseline, defined by the linear function, for the selection of plus-trees. Basal area of co-dominant and dominant trees in .04 or .01 hectare plots centered around a subject tree failed to correlate strongly ($r^2 = .005$ to $.26$) with the subject tree b.a.i., and hence were not adequate for the construction of baselines for selection of crop ideotypes.

Similarly, Thomas (1980) tested eight distance-dependent competition indices (Heygi, 1975; Glen et al., 1976) with operational potential as baselines for selecting plus-trees of *Tsuga heterophylla* (Rafn.) Sarg.

(western hemlock). Various measures of crown area, crown radius and crown length were made from the ground and from large-scale aerial photographs (after Mitchel, 1975). The crown measurements were included with the competition indices, and each was regressed with 10 year b.a.i. of subject trees as the dependent variable. The subject trees were from several large permanent sample plots on Vancouver Island. Crown area measurements were more closely related to b.a.i. than were the extrinsic competition indices.

Alemdag (1978) compared six competition indices for their ability to predict b.a.i. of *Picea glauca* (Moench) Voss. He found the results to be inconsistent as did Thomas (1980) and Brown and Goddard (1961). The inconsistencies arise from the arbitrary selection and weighing of competing individuals included by the competition index. Many of the competition indices examined by Alemdag (1978) involved tedious measurements and complex calculations not feasible in an operational plus-tree selection program.

As part of my undergraduate thesis (Van Damme, 1982), a high quality stand of black spruce was identified and 200 subject trees were sampled along a systematic grid. Crown length, crown radius, tree height and d.b.h. measures were taken for each subject tree. Two 90° increment cores were taken at one meter above the ground for each subject tree and were used to estimate b.a.i. Competing trees were defined as trees that lay within a plot radius determined as a factor of 0.25m/cm of d.b.h. for each subject tree that acted as a plot center. Distance and d.b.h.'s of these competing trees were tallied to give estimates of fixed, polyareal, and Spurr's (1962) point densities. The subject tree crown measures and competition indices of surrounding densities were regressed with b.a.i. as the dependent variable.

My results agreed with Thomas (1980) and Brown and Goddard's (1961) work. The extrinsic competition indices of surrounding density failed to adequately predict the b.a.i. of the subject tree (r^2 = 0.02 to 0.04). The measure of crown area (c.a.) was weakly yet significantly ($a < 0.05$) correlated to point density (r^2 = 0.09). Crown radius x crown length (c.a.) correlated strongly (r^2 = 0.51). For these reasons, the b.a.i. vs. c.a. regression showed promise as a baseline for selection of plus-trees of black spruce. It was felt that trees selected by the b.a.i. vs. c.a. baseline would be unbiased by competitive advantage and are possibly trees that possess superior growing space efficiency.

CROP IDEOTYPES AND GROWING SPACE EFFICIENCY

A crop ideotype is a plant model which is expected to yield a greater quantity of product when developed as a cultivar and grown as a crop. Many agriculturists have shown small erect leaves are common to high yielding grain cultivars grown under dense conditions because leaf size and arrangement allow more light to penetrate the canopy (Donald, 1968). A grain crop ideotype, therefore, is a plant with small erect leaves.

Cannell (1978) distinguishes crop ideotypes that do well when competing with other plants from isolation ideotypes that grow vigorously under open conditions. Isolation ideotypes would possess tall broad crowns. Choice of isolation or crop ideotypes would be based upon management objectives. Cannell (1978) suggests a tree's crown structure could define crop ideotypes. Tree crop ideotypes will vary with utilization needs but a pulpwood crop ideotype should give high fiber yields per hectare. Thus, a pulpwood crop ideotype would show high levels of growing space efficiency.

Long narrow crowns contribute to high leaf area ratios which may be especially beneficial to trees growing in dense plantation conditions (Farmer, 1978; Cannell, 1978). Perhaps a black spruce pulpwood crop ideotype is a tree with a long narrow crown.

PROGENY TRIALS: ASSESSMENT OF PLUS-TREE SELECTION CRITERIA AND METHODS

Most quantitative traits, such as height growth, are controlled by multiple genes with additive effects that are subject to large amounts of environmental modification (Wright, 1976). Selection for growth characters is very difficult because the genetic contribution to the phenotypic expression is unknown (Stern, 1969; Wright, 1976; Falconer, 1981). The genetic contribution to the phenotypic expression can be estimated with progeny trials. Progeny trials allow estimates of heritability.

Heritability quantifies the resemblance of the parent's character expression to the character expression of the progeny as well as to the similarity among the siblings' character expressions. Heritability is defined more precisely as the contribution of the additive genetic variance relative to the total character variance (Falconer, 1981). Estimates of heritability can be determined by parent-progeny regression or by analysis of sibling variance (Falconer, 1981; Jacquard, 1983).

Wright's (1976) review of the literature indicated that the heritability of characters varies enormously from species to species. Measures of growth, controlled by many alleles, usually express low heritability when compared to branch angles (Shelbourne, 1969), phenological characters and other characters under the control of a few alleles (Falconer, 1981). For example, heritability of height for *Populus deltoides* Bortr. was 0.06 while date of flushing was 0.90 (Wright, 1976). Similarly, Banister (1980) reports heritability values from 0.4 to 0.5 for stem crookedness, sweep, whorl number and branch angle for juvenile *Pinus radiata* D. Don. Riemenschnieder (1980) estimated heritability of *Pinus banksiana* Lamb. height growth to range from 0.12 to 0.23.

Heritability values apply only to the population, trait and environment for which the value was estimated. Many published heritability estimates of forest tree growth characters have unclear components of variance. Resultant heritability and genetic gain values have limited use for comparing tree improvement methods (Namkoong, 1966). Namkoong (1966) describes methods to adjust heritability estimates to allow comparison of tree improvement methods (e.g., seedling vs. clonal seed orchards). Namkoong's (1966) analysis of published material found no single method to be superior to others.

Hanover and Burton (1969) found heritability determined for one year-old full sib *Pinus monticola* Dougl. height growth was 0.084, based upon the female parents, while the heritability based upon the male parents was 0.197. When different female parents were used, the heritability estimate for height was 0.50. Both experiments used eight females and four males. These findings demonstrate how specific heritability estimates are, and how important it is to consider large samples of families to make inferences of population heritabilities. Hanover and Burton (1969) experiment indicated that specific and general combining abilities of the few parents influenced the overall heritability estimates. Heritability estimates will also be different if clonal material is used rather than material germinated from seed (Wright, 1976; Jacquard, 1983).

Paternal and maternal effects can confound heritability estimates based on young progeny. Bingham (1966) reports paternal effects can be significant for wheat growth and yield, but the contribution of pollen grains to endosperm and seedling development is uncertain for trees. Seed weight is considered a maternal character (Saward, 1974; Squillace, 1957) that is positively correlated to seedling survival and growth (Burger, 1964; Kandya, 1978; Wang, 1979; Chauhan and Raina, 1980). Seed weight bias, that could be removed as a covariate, is often overlooked in juvenile progeny trials.

Juvenile progeny trials may test characters that express low juvenile-mature correlation. If juvenile-mature correlations are low, heritability estimates will be misleading. Lambeth (1980) examined eight different studies with eight different coniferous species for juvenile-mature correlations of height growth. He found the juvenile-mature correlations to be consistently strong with remarkable colinearity after the seedlings were planted for 3 years. In the first 3 years the seedlings showed a very erratic performance, perhaps as a result of planting shock or seed weight bias.

Ying and Morgenstern (1979) found strong correlation between successive measurements of white spruce (*Picea glauca* (Moench) Voss) progeny tests at 11 and 22 years. This agrees with Lambeth's work. This would suggest that realistic heritability estimates and family selection could be carried out in plantations of white spruce that are much younger than 1/3 of rotation age recommended by Johnsson (1964). The sooner heritability estimates and family selection can be made, the faster improved breeding stock is made available, which improves economic efficiency of the breeding method.

Very little work has been done on coniferous, juvenile-mature correlations for characters other than height or volume growth. Pollard and Logan (1978) suggest needle primordia and stem unit number (number of needles per length of stem) could replace height measures of very young spruce seedlings as estimators of growth potential. Their experiments demonstrate that needle primordia numbers express no genotype x environment interaction and accurately predict the following year's height growth. If needle primordia number is found to strongly correlate with mature height or volume and is independent of seed weight, reliable heritability estimates and family selection could be made at very early stages of juvenile development.

Franklin (1979) suggests that published juvenile-mature correlations based on phenotypic values of periodic height and volume growth are less appropriate than genotypic estimates of these characters. Twenty to forty-year progeny trial heritability estimates were modelled over time for douglas fir, loblolly pine (*Pinus taida* L.), ponderosa pine (*Pinus ponerosa* Laws) and slash pine (*Pinus elliotii* Engelm). The ratio of additive genetic variance to total variance (heritability) fluctuated with plantation development and tree ontogeny. All four species had a similar pattern. Heritability estimates were lowest just at crown closure after a sharp decline from peak juvenile estimates. Heritability estimates then rose to another peak five to ten years after crown closure but gradually declined afterwards when some trees became suppressed by the plantation canopy.

Franklin (1979) speculates that the changing heritability estimates reflect genotype x spacing and genotype x time interactions. When genotypes best adapted for capturing the site as seedlings (isolation ideotypes) fully express their superiority, the additive genetic variance to total variance ratio (heritability) is the highest. But, when crown closure begins, different genotypes best adapted to the intraspecific competitive conditions (crop ideotypes) begin to overtake the isolation ideotypes. This reduces the additive genetic variance to total variance ratio (see Cannell 1978, 1982). Franklin's (1979) work shows phenotypic correlations are highest between ages within each heritability peak. Similar correlations made between heritability peaks were often negative. For these reasons, he recommends meaningful family selection and heritability estimates must wait until 1/2 rotation age unless variably spaced progeny trials are used. Variably spaced trials would reach crown closure at different ages; therefore, spacing and ontogenetic effects may be isolated from one another. Heritability estimates and family selection might be possible in the closely spaced plots at an earlier age than the more widely spaced plots.

Comstock and Moll (1963) warn that heritability estimates are also affected by genotype x site interaction. Characters that express low genetic stability (i.e., a high genotype x environment interaction) will upwardly bias heritability estimates if the progeny design is not replicated across a variety of sites. Owino et al. (1977) estimated this upward bias to be as high as 60% for heritability estimates based upon mass selection progeny trials of loblolly pine because of the significant genotype x site interactions.

Significant genotype x site interactions have been demonstrated for many coniferous species (Bell et al., 1979; Steinbeck, 1966; Shelbourne, 1972; Sorensen and Franklin, 1977). Cannell (1982) found strong genotype x inter-tree spacing interactions in four year-old *Picea sitchensis* (Bong.) Carr. Genotype x light interactions have also been documented by Bourdaue (1963) and Townsend et al. (1972). This would suggest that many heritability estimates may be too high because variance resulting from genotype x environment interaction was not accounted for.

The specific nature of the heritability estimate explains why there are conflicting or uncertain reports on plus-tree selection efficacy as a tree improvement method. For example, Holst and Teich (1969) and Morgenstern et al. (1975) thought heritability estimates from progeny trials were high enough to merit plus-tree selection for white spruce height growth but Khalil (1975), based upon different progeny trials, felt plus-tree selection of white spruce was ineffective.

Tree improvement experimentation often utilizes conventional statistical methods of comparison where improved varieties are compared with controls for various measures of performance when heritability estimates are impractical or might be misleading. For example, Stanton and Canavera (1983) used an Analysis of Variance to compare the first year growth of progeny from four different selection methods with a control of random selection. They felt that plus-tree selection to improve volume growth appeared ineffective because the height growth of the year-old progeny from select parents were no different from the random controls.

Heritability, although a fluctuating, design-specific value, is still used extensively by tree breeders for the assessment of breeding and plus-tree selection methods. The efficiency of plus-tree selection methods and other breeding programs is determined by the cost of selection and establishment of subsequent breeding programs compared to the benefits realized through genetic gain (Porterfield, 1977; Nickles, 1970). Genetic gain is simply the product of character heritability and the selection differential. Generally, if heritability of a character is very low, family selection from progeny trials gives greater gain per dollar of development than does plus-tree selection (Morgenstern, 1975; Falconer, 1981). The efficiency of mass selection is directly proportional to the heritability of the selection character (Wright, 1976).

METHODS

STUDY AREAS

Two study areas were chosen 60 km west of Thunder Bay, Ontario. The first area, chosen in the fall of 1981, is near the Matawin River and the second area, chosen in the spring of 1983, is adjacent to the Marks Lake road (Fig. 1). Both study areas were in high quality, even-aged, 65 year-old upland black spruce stands of fire origin. The timber was cruised with a 10-point prism sample, soils pits were dug, and ground cover vegetation was identified for both areas (Appendix 1).

Figure 2 is a scaled profile of soil and stand conditions in both study areas. The Marks Lake area soil is till over bedrock from 0.5 m to more than 1.0 m in depth. The Matawin River area has deep clays covered with deep fine sands in a small portion of the southwest corner. Although the soils are quite different, both areas have mesic (fresh) moisture regimes reflected by the excellent tree growth. Both stands have very high site indices according to Plonski (1974), but species composition and stocking levels are quite different. The Marks Lake area has a stocking of 60% and a species composition of 60% black spruce, 30% jack pine and 10% poplar (*Populus tremuloides* Michx.). The Matawin area, with more homogeneous soils, has a stocking of 120% and a species composition of 90% black spruce with 10% jack pine and minor amounts of poplar (Plonski, 1974). The Marks Lake area has patches of alder (*Alnus crispa* (Ait.) Pursh) but the Matawin River area has no understory.

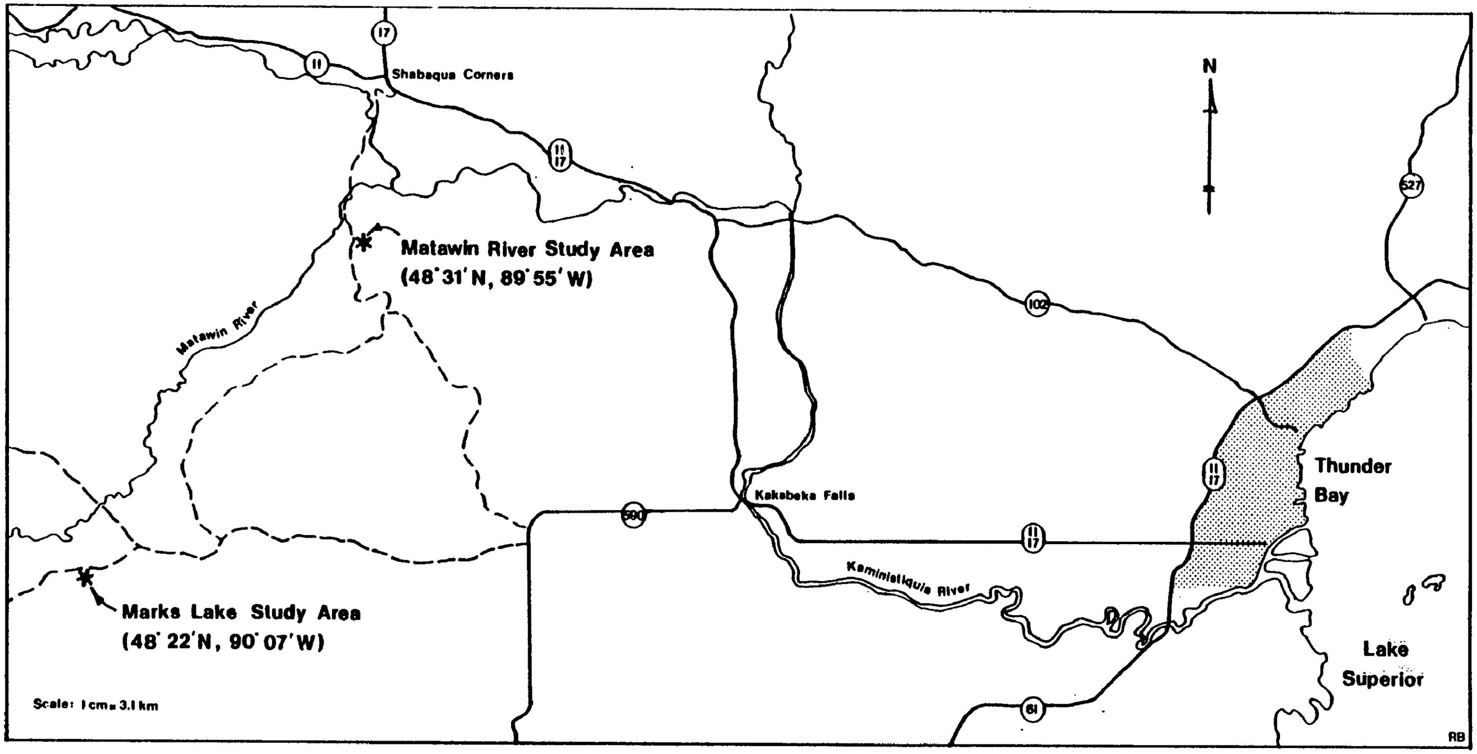
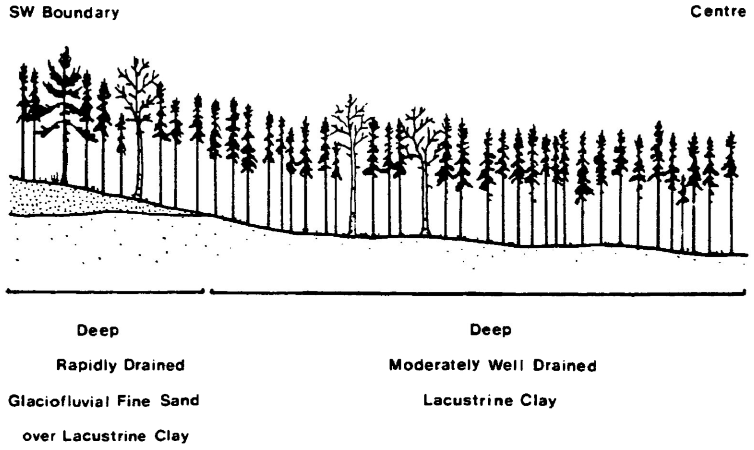


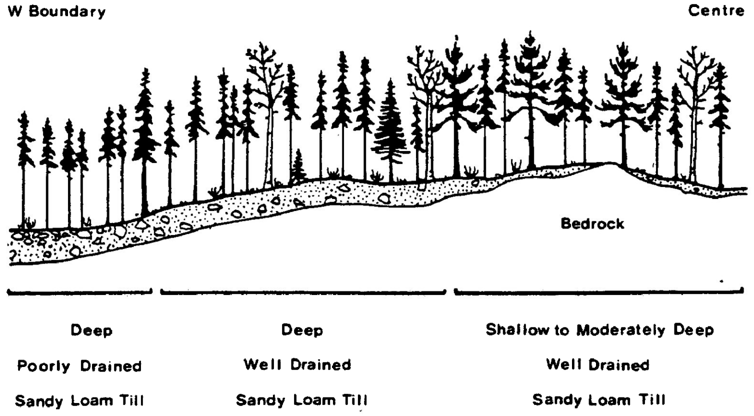
Fig. 1 Map showing location of the Marks Lake and Matawin River study areas

Matawin River Study Area



Species	Sb, Po,
Age	65 yrs
Height	15 m
Stocking	120%
Site Class	Ia
Avg. dbh	13.8 cm
Basal Area	45 m^2/ha
Density	3,000 stems/ha

Marks Lake Study Area



Species	Sb, Pj, Po,
Age	65 yrs
Height	16 m
Stocking	60%
Site Class	Ia
Avg. dbh	16.5 cm
Basal Area	28m^2/ha
Density	1,300 stems/ha

RB

Fig. 2 Stand and soil profiles for the Marks Lake and Matawin River study areas

SUBJECT TREE IDENTIFICATION: FIELD AND LAB PROCEDURES

In the Matawin River and Marks Lake study area, 251 trees and 398 trees, respectively, were chosen as subject trees along a systematic grid (Figs. 3 and 4). The point of commencement and end of line for each compassed line of the grid were blazed, tagged by number and azimuth and marked with flagging tape. Subject trees along the lines were flagged with orange tape. Aluminum tags were nailed at eye level, facing the direction of travel, and numbered consecutively on the Matawin River area (e.g., 193). In the Marks Lake area, subject trees were tagged similarly, but numbered by line and consecutive number (e.g., 9-7). These systematic grid samples allowed subject trees to be easily located for future cone or scion collection.

Black spruce trees that originated from the same fire qualified as subject trees if they were within one meter of the compassed line, had a diameter at d.b.h. greater than 9.0 cm, and expressed good form. Subject tree crown length and tree height was measured by one person with a Suunto clinometer to the nearest tenth of a meter. D.b.h. was measured with a diameter tape to the nearest millimeter. The crown radius was measured at four approximate cardinal points with the aid of a right-angled prism held perpendicular to the edge of the crown and ground. This device helped to assure that measures from the centre of the tree bole went to a point plumb with the crown edge without requiring plumb lines and additional manpower (Figs. 5 and 6). The prism device was easily used by one person who made all the measurements of subject tree crown radius in both study areas. This procedure reduced the personal bias from the subjective definition of crown edge.

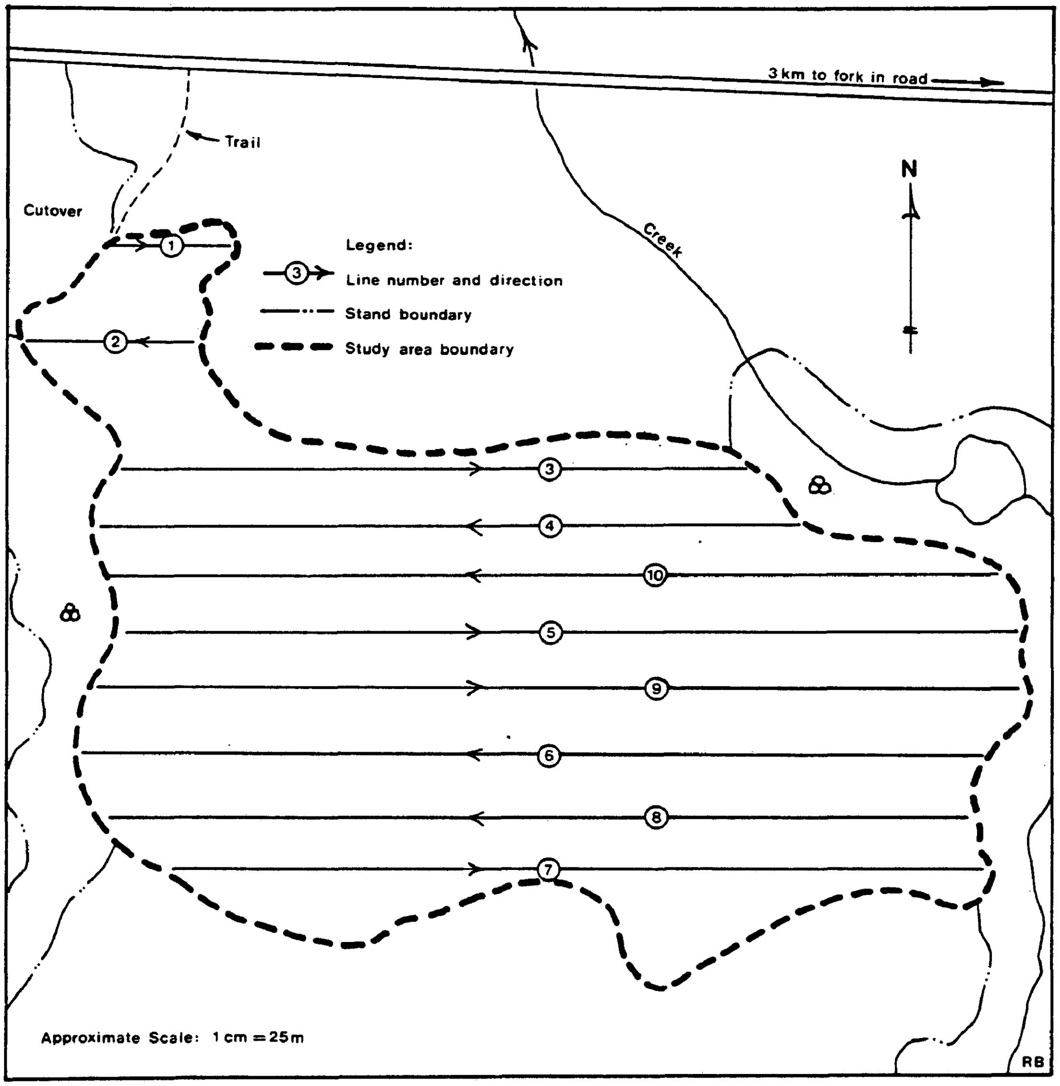


Fig. 3 Sketch map of Marks Lake study area (systematic grid)

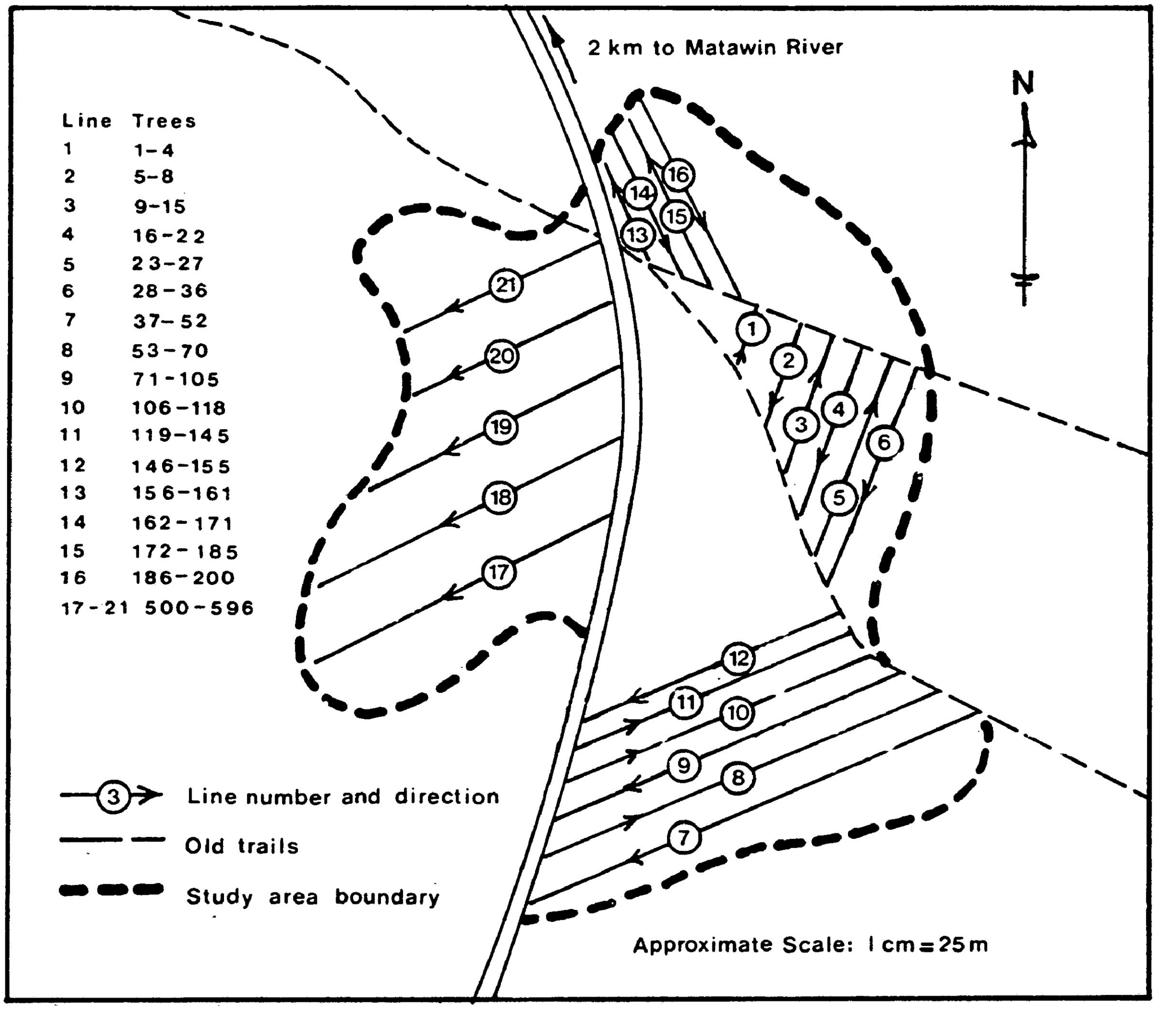


Fig. 4 Sketch map of Matawin River study area (systematic grid)

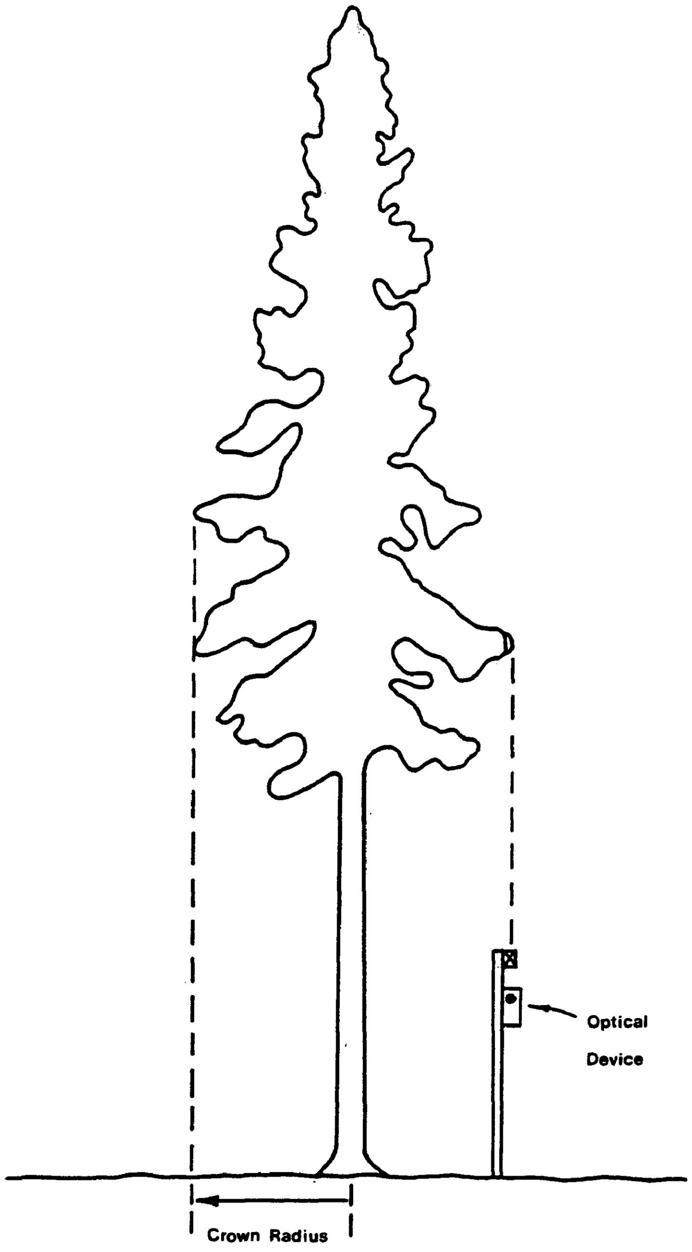


Fig. 5 Crown radius measurement of a subject tree

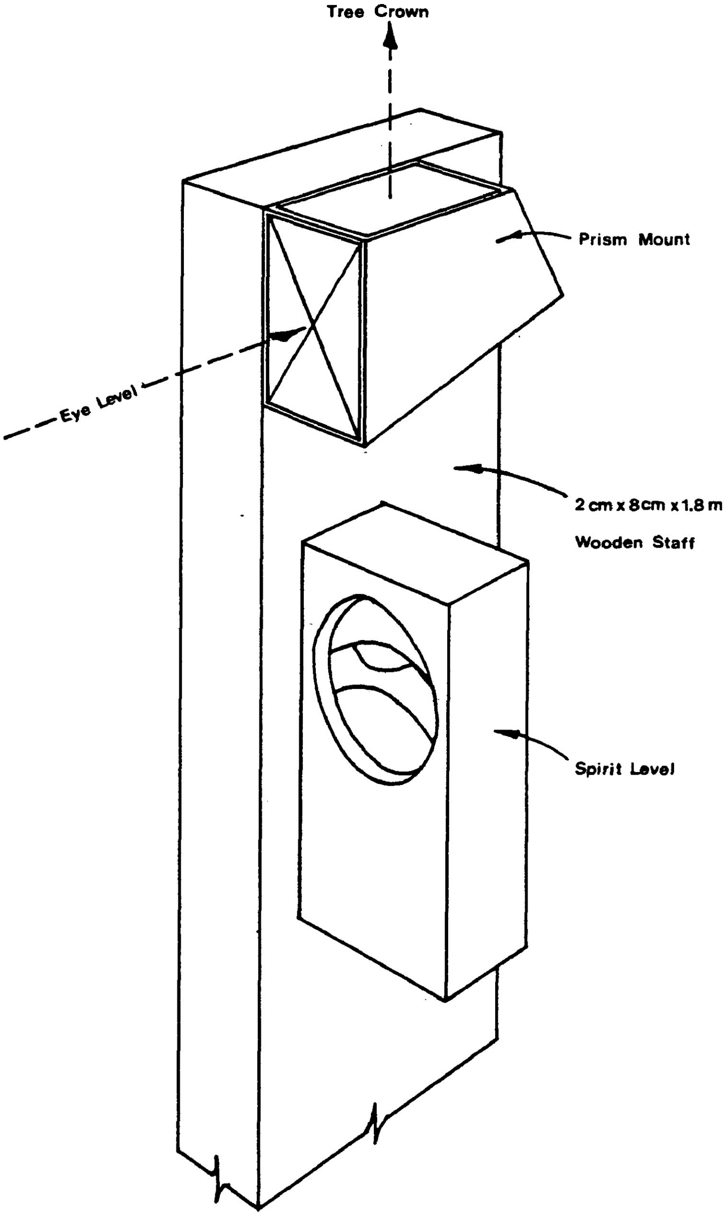


Fig. 6 Detail of right-angled prism for measuring crown radius

Two increment cores were taken at right-angles at 1 m above ground level and were stored in labelled plastic straws. Then, estimates of the subject tree current ten year periodic b.a.i. were made from the cores in the lab. B.a.i. was calculated as an average of two radial measures of the ten most recent growth rings from the cores, which were then converted to a circle area. Matawin River subject tree core measurements were made using a digitized micrometer system while calibrated dissecting microscopes measured the Marks Lake cores. Care had to be taken to exclude frost rings from the annual count along Marks Lake cores.

All field and core data (Appendices 2, 3 and 4) were entered on the Lakehead University's VAX 11/780 computer system. Fortran programs compiled the data which were analyzed later with S.P.S.S. programs (Norman et al., 1975).

PARENT TREE IDENTIFICATION AND SEED COLLECTION

To test the effectiveness of plus-tree selection based on the b.a.i. vs. c.a. method, parents were selected by three methods. Ten plus-trees from the b.a.i. vs. c.a. regression, ten plus-trees from the height vs. age regression and ten randomly selected trees were identified as parents that would provide seed for the progeny trials. Linear regression of b.a.i. upon c.a. (average crown radius x crown length) provided a baseline from which plus-tree parents were selected. Plus-trees were subject trees with the greatest positive residual from the regression line. These plus-trees were assumed to represent phenotypes with superior growing space efficiency. Similarly, linear regression of height upon age identified conventional plus-trees that are among the tallest subject trees in the stand comparable to the Ontario Ministry of Natural Resources' methodology of the early 1970s.

Parent trees were located along the Matawin River grid system and marked with orange spray paint in February, 1983. The tops of plus-tree parents were shot off with a 0.22 calibre target rifle. Most of the random trees were felled. Unfortunately, the seeds collected from the Matawin River were made unviable because of high oven temperatures used to extract the seed from the cone. Loss of seed viability necessitated extension of the analysis to the Marks Lake study area because the already-sampled parents from the Matawin River study area were damaged with few cones remaining after the initial collection.

Parents were identified, and cones were collected from the Marks Lake population in May, 1983. Sixty cones per tree were required, and some parents were rejected because of poor cone yield. This constraint increased the proportion of the selected individuals from 2.5% to approximately 5% of the population. Tree 10-13 was scored as a plus-tree by both the height vs. age and b.a.i. vs. c.a. method, so a total of 29 parent trees provided the seed for the progeny trial. Each parent tree number identified the family of the wind-pollinated seed that was stored in separate bottles after careful extraction by hand from the cones following the U.S.D.A. (1974) procedure.

Multiple range S.N.K. tests (Steel and Torrie, 1980), Hubbs' diagrams or "Dice-grams" (Sokal and Rohlf, 1981), and scaled diagrams were used to compare the six parent groups to find a common, easily identified character or character combination associated with plus-trees or crop ideotypes. The S.N.K. tests also helped defined the magnitude of difference between selection method groups.

Subject tree character allometric functions (linear regressions) were considered to find simpler, more efficiently measured characters that might replace b.a.i. or c.a. measurements for plus-tree selection. Lastly, b.a.i. vs. c.a. regressions for subject trees from both the Matawin River and Marks Lake area were tested for homogeneity of slope.

Plus-trees assumed to express superior growing space efficiency were selected by three other baselines but were not included in the progeny test. It was felt that the four methods would select parents with similar crown or form characters and these could be compared in hopes of identifying a crop ideotype. One baseline had tree volume, estimated by volume equations (Honer et al., 1983), dependent upon crown radius. The remaining two baselines showed the same relationship as the first two but the variables were transformed to the natural log. The transformation helped to linearize the baselines and reduce heteroscedasticity of variance found for the untransformed regressions.

SEED WEIGHT

Five lots of ten seeds were weighed on an analytical balance for each family. Seed was returned to storage after weighing and the seed planted in family units may not have been the seed that was weighed. The weights were recorded to the nearest tenth of a milligram and keyed into the VAX 11/780 to be used as a covariate of progeny performance (Appendix 5). In addition, seed weight was regressed against parent characters to test for growth and seed weight correlation. Mean seed weights from both study areas were tested against each other with a t-test to identify significant differences. ANOVAs of seed weight data with selection methods as treatments and families nested within selection methods tested for differences in seed weight between selection methods and families (Anderson, 1974).

PROGENY ESTABLISHMENT AND ANALYSIS

On 1 August, 1983 a short-term progeny trial was established in the Lakehead University greenhouse. Ten progeny from each of the ten parents within each of the three primary selection methods were randomly assigned within each of three blocks. The greenhouse had an 18-hour, 26°C day and a 6-hour, 18°C night environment.

Two seeds from each family were sown into 4 cavity/book Spencer-Lamier (tm) containers filled with a premoistened 50% peat, 50% vermiculite growth medium. Each cavity was marked with a plastic pot marker showing the family number. No pre-sowing germination treatments were used. The seeds germinated within a week to ten days after sowing.

Surplus seedlings were thinned or transplanted to empty cavities on 8 September, 1983. A shade box with a single layer of nylon screen reduced the light intensity over one block to 56%. Another box, placed over the second block, had two layers of screen which reduced the light intensity to 33%. The third block remained free of shade (Fig. 7). Irrigation, when required, was alternated with 20-20-20 fertilizer at 100-150 ppm. Flats were rotated bi-monthly to help reduce edge effects.

The seedlings were harvested one block per day between 7 December, 1983 and 9 December, 1983. Damping-off may have been responsible for high levels of mortality in some families during the four-month growth period. Family portraits were made with a photocopy machine, consisting of five surviving seedlings per family per block. Tops were cut at the root collar

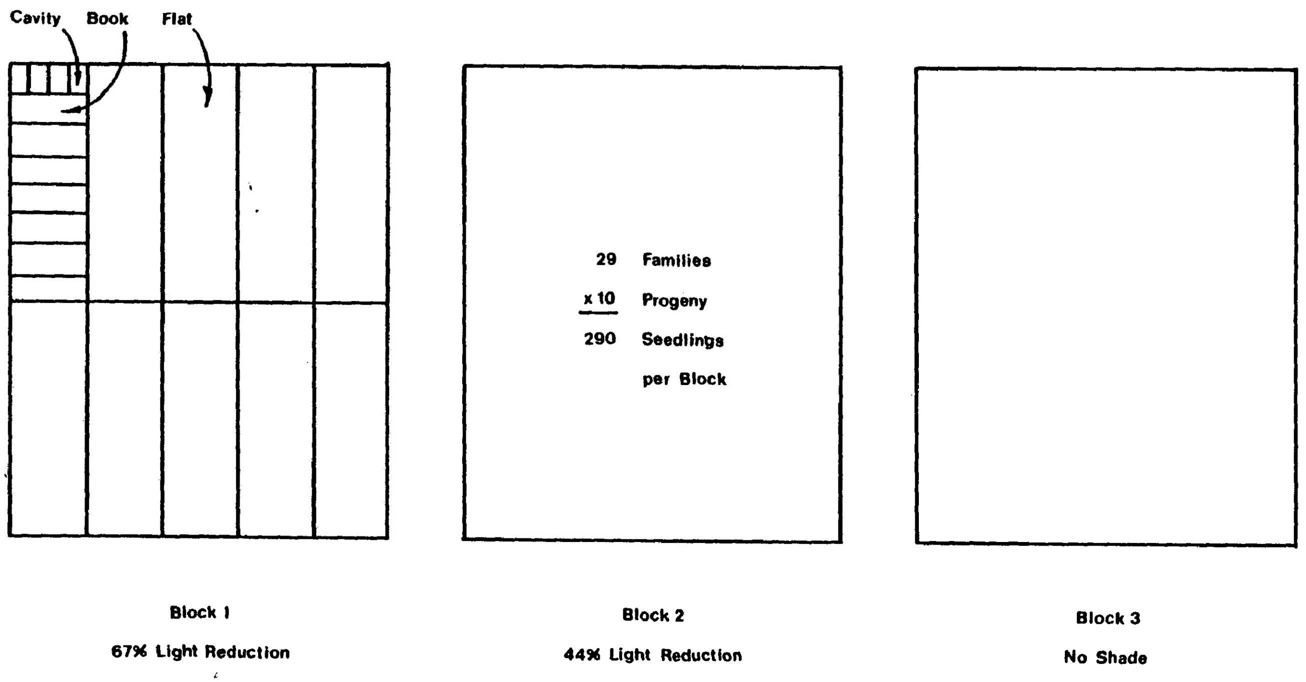


Fig. 7 Schematic diagram of greenhouse layout for progeny trial

and roots and tops were separately stored in labelled paper bags and then dried in an oven (115°C) for 24 hours.

Top and root oven-dry weights were recorded to a tenth of a milligram. Linear measures of seedling height (HT), foliated length (FL), foliated width (FW), and needle length (NL) (Fig. 8) with a potential resolution of 0.008 mm, were digitized from the family portraits on a Houston Instruments "Hi-pad" digitizer interfaced with an Apple-IIe microcomputer (Appendix 6). The digitized information was transferred from the Apple-IIe disk with Softerm® (terminal emulation and data transfer package programs) to the VAX 11/780 via a telephone modem (Micromodem II).

The fundamental assumption of the experiment was that all progeny grown in the Spencer-Lamier (tm) cavities had equivalent growing space. Progeny from parents expressing superior growing space efficiency should be larger than progeny from the tallest or randomly selected parents if the characters responsible for growing space efficiency proved heritable. ANOVAs tested for significant differences in progeny size.

The analysis of each progeny character followed a nested factorial design. The linear model, degrees of freedom and expected mean squares (E.M.S.) are shown in Tables 1 and 2. This analysis is somewhat unique with families being nested within selection methods. Covariance analysis (Cochran and Cox, 1957; Steel and Torrie, 1981) of selection method differences adjusted for mean family seed weights followed the nested factorial analysis. To compare our work with material published by Stanton and Canavera (1983), the data were artificially organized into randomized blocks where selection methods were treated as main effects and family means were experimental units (Anderson, 1974). All of the analyses were done on the VAX 11/780 with the S.P.S.S. programs.

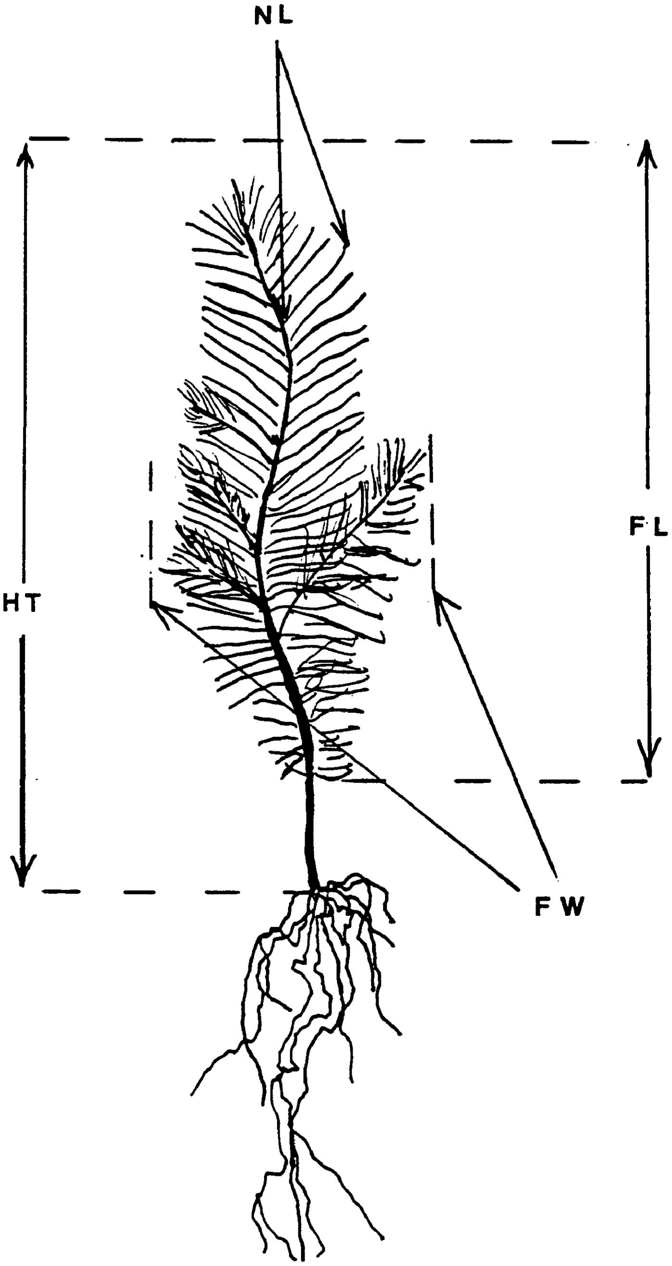


Fig. 8 Linear measurements of 4 month-old seedlings from greenhouse progeny trial

TABLE 1

LINEAR MODEL FOR NESTED ANOVA

Ho There is no difference between selection methods and families for seedling dry weight, leaf area and needle length, height and leaf area production over one growing season.

The Linear Model

$$Yijkl = u + Bi + \sigma(i) + Sj + BSij + F(j)k + BFi(j)k + E(ijk)l$$

where

u = overall mean

fixed Bi = effect of the 1th block C = 1...b b = 3

$\sigma(i)$ = restriction error associated with blocks

fixed S(j) = effect of jth slection method J = 1...s s = 3

random F(j)k = effect of kth family within the jth selection method k = 1...f f = 10

BSij = effect of block x selection interaction

BFi(j)k = effect of block x family interaction

E(ijk)l = effect of lth seedling within the kth family within the jth selection method within the lth block l = 1...n n = 5

TABLE 2

NESTED ANOVA EXPECTED MEAN SQUARES WITH CORRESPONDING SOURCES OF VARIATION AND DEGREES OF FREEDOM

Source of Variation	Degrees of Freedom	Expected Mean Square*
Blocks (Shade)	(b-1) = 2	$\sigma^2 + 10\sigma^2 BF + 300\phi_{BS} + 300\sigma^2 + 300\phi_B$
Restriction Error	0	$\sigma^2 + 10\sigma^2 BF + 300\phi_{BS} + 300\sigma^2 0$
Selection	(S-1) = 2	$\sigma^2 + 30\sigma^2_F + 300\phi_S$
Block x Selection	(b-1) (S-1) = 4	$\sigma^2 + 10\sigma^2_{BF} + 300\phi_{BS}$
Families within Selection	S(f-1) = 27	$\sigma^2 + 30\sigma^2 F$
Block x Families Within Selection	S(f-1) (b-1) = 54	$\sigma^2 + 10\sigma^2 BF$
Error	bsf(n-1) = 360	σ^2
Total	sfbn-1 = 449	

*Arrows indicate appropriate F-test.

Juvenile heritability estimates that would allow calculations of genetic gain were not possible to make because crown height and diameter cannot be determined for young seedlings. Literature suggests that crown architecture is important but the juvenile progeny have not yet developed crowns. For this reason we can only make inferences concerning heritability. Regressions between progeny characters and analogous parent characters were run to show trends that might approximate heritability estimates when fully developed crowns of progeny can be compared with their parents.

Discriminant analysis techniques were explored as a method of developing better plus-tree selection methods. A portion of the data was used as an example. A discriminant analysis of three parent groups determined a posteriori and based on progeny performance was run in hopes of identifying pooled parent characters that were associated with superior progeny height. The groups consisted of the parents producing the tallest ten, median nine and shortest ten families of progeny from the shade-free block.

LONG-TERM PROGENY TRIAL

The assessment of progeny based upon one growth season is very weak. The impact of the genotype x environment interaction over the seasons (Franklin, 1979; Owino, 1976) combined with the problem of maternal effects and juvenile/mature correlations make heritability estimates at this young age highly academic. For these reasons, a long-term progeny trial on Lakehead University property was also initiated.

Progeny from the Marks Lake study area were established in the Lakehead University greenhouse and out-planted in June of 1984 in a variably spaced, plaid pattern. The analysis is similar to a split plot design (Lin and Morse, 1975). The design will allow investigations of (1) plant and row spacing and plot density effects upon seedling growth and development, (2) the family x spacing interaction, and (3) selection method x spacing interaction. Long-term heritability estimates will be possible at various stages of crown closure within five to eight years.

Three major blocks were established on an old field cleared of brush and treated with herbicides (Fig. 9). Two between-row spacings (1.0 and 2.0 m) by three within-row plant spacings (2.0, 1.0 and 0.5 m) gave six treatment combinations per block. Within each major treatment combination, 27 families with five replicates (1-0 seedlings) were randomized and planted with shovels. Guard plants of nursery 1-0 stock were planted with potiputkis to fill periodic gaps caused by mortality. Appendix 3 shows the ANOVA with expected mean squares for this design.

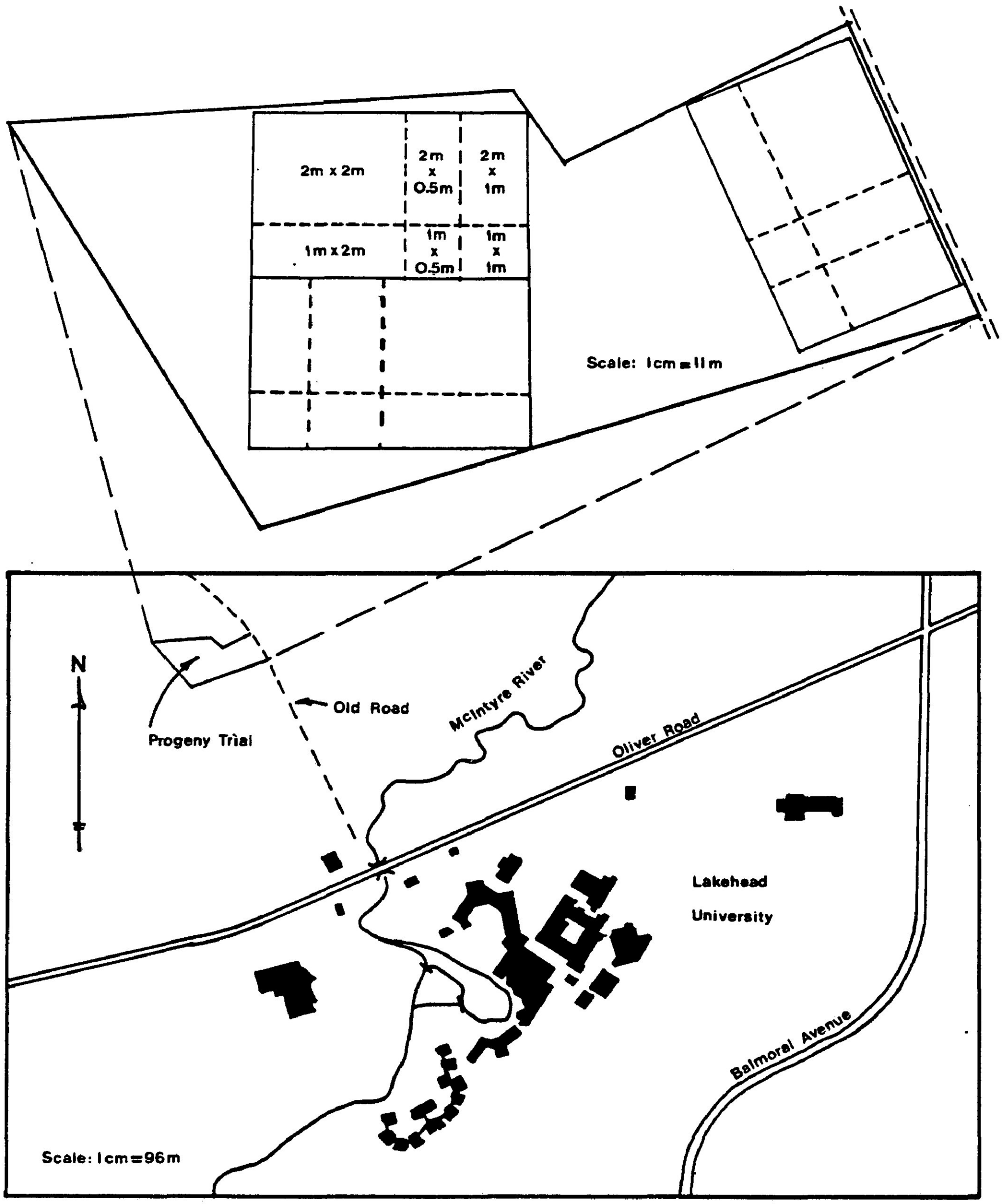


Fig. 9 Location and planned layout of proposed variably spaced progeny trial

RESULTS

MARKS LAKE AND MATAWIN RIVER SUBJECT TREE SUMMARY STATISTICS AND ALLOMETRIC FUNCTIONS

Relationships between morphological features are often described by allometric functions. Subject tree allometric functions derived from linear regressions of data from both study areas were used to identify individual variables that could form baselines for plus-tree selection. Subject tree allometric functions were also used to strengthen the stand and tree descriptions available from summary statistics.

In both study areas the subject b.a.i. and crown measurements were more variable than the height and d.b.h. measurements. Table 3 shows summary statistics for subject tree measurements. The Marks Lake area has larger trees, probably as a result of the lower stand density; however, the patterns of variation, as measured by the coefficient of variation, are nearly identical.

For both study areas, correlation matrices generated from S.P.S.S. programs were used to calculate the coefficient of determination (r^2) which is a measure of the goodness-of-fit for the linear allometric functions of subject tree characters. Table 4 is a listing of the allometric functions (linear regressions) calculated for this study and the corresponding coefficients of determination. The regressions listed in Table 4 were either required as baselines for plus-tree selection or helped identify related characters that could form new, simpler baselines for plus-tree selection. All characters are highly correlated with one

TABLE 3

SUMMARY STATISTICS FOR THE MARKS LAKE AND MATAWIN RIVER AREA (IN PARENTHESES) SUBJECT TREES

Character	Mean	S [1]	Sy [2]	Coefficient of Variation
Age*	54	4.60	0.23	0.08
	(50)	(5.02)	(0.31)	(0.10)
dbh	16.5	3.23	0.16	0.20
	(13.5)	(2.81)	(0.18)	(0.20)
Height (m)	16.5	1.89	0.10	0.11
	(14.6)	(2.07)	(0.13)	(0.14)
b.a.i.* (cm^2)	28.5	16.99	0.85	0.60
	(19.9)	(14.3)	(0.90)	(0.72)
crown length (m)	6.7	2.74	0.14	0.41
	(5.5)	(2.21)	(0.14)	(0.40)
crown radius (m)	1.0	0.38	0.02	0.38
	(0.8)	(0.25)	(0.02)	(0.31)
crown area (m^2)	7.5	5.88	0.30	0.78
	(5.1)	(3.33)	(0.21)	(0.66)

*from increment cores taken one meter above ground level.

[1] S = standard deviation.

[2] Sy = standard error of the mean.

TABLE 4

SUMMARY OF IMPORTANT REGRESSIONS FOR MARKS LAKE AND MATAWIN RIVER SUBJECT TREES

Regression	Coefficient of Determination (r^2)	
	Mattawin River*	Marks Lake**
height vs. age	0.02[1]	0.02
b.a.i. vs. c.a.	0.45	0.57
ln (b.a.i.) vs. ln (c.a.)	0.41	0.56
$\sqrt{\text{b.a.i.}}$ vs. $\sqrt{\text{c.a.}}$	N/A	0.58
c.a. vs. d.b.h.	0.75	0.83
crown length vs. crown radius	0.60	0.78
b.a.i. vs. d.b.h.	0.65	0.56
b.a.i. (1976-81) vs. b.a.i. (1971-76)	0.79***	N/A
volume vs. crown radius	N/A	0.41
ln (vol.) vs. ln (c.r.)	N/A	0.41

* n = 251

** n = 398

***n = 200

[1] All regressions were significant ($\alpha = 0.05$) except for height vs. age.

another (r^2 = .39 to .83) except for height and age (r^2 = 0.02). Due to the even-aged nature of the fire-origin stands, no significant relationship between height and age would be expected. The Matawin River study area subject trees' 1976-1981 five-year b.a.i. was strongly correlated to the 1971-1976 b.a.i. (r^2 = 0.79) which suggests that the pattern of tree growth has not changed notably in the last 10-year period.

The linear regressions that were to be used as baselines for plus-tree selection of parents for progeny testing received separate, detailed analyses. Heteroscedasticities of variance for b.a.i. vs. c.a. and volume vs. c.r. regressions were found when the standardized residual plots were examined. The increased spread of the standardized residuals with an increase in standardized dependent variables gives a funnel-shaped pattern indicative of heteroscedasticity (Fig. 10). Heteroscedasticity makes the construction of confidence intervals uncertain (Chatterjee and Price, 1977). A square-root transformation of the data improved the goodness-of-fit (r^2 = .57 to r^2 = .58) but was less successful than a natural log transformation (ln) in removing heteroscedasticity. Figure 10 shows the funnel-shaped pattern of standardized residuals on the left side and the random pattern of the standardized residuals on the right side which indicates that heteroscedasticity has been removed from data transformed to the natural log (ln (b.a.i.) vs. ln (c.a.)).

While both study areas have similar patterns of goodness-of-fit for the subject tree regressions, the slopes and intercepts of the regression lines are different (Fig. 11). A t-test of the transformed regression lines showed the slopes to be significantly different between the Marks Lake and Matawin River study areas for the ln (b.a.i.) vs. ln (c.a.) and

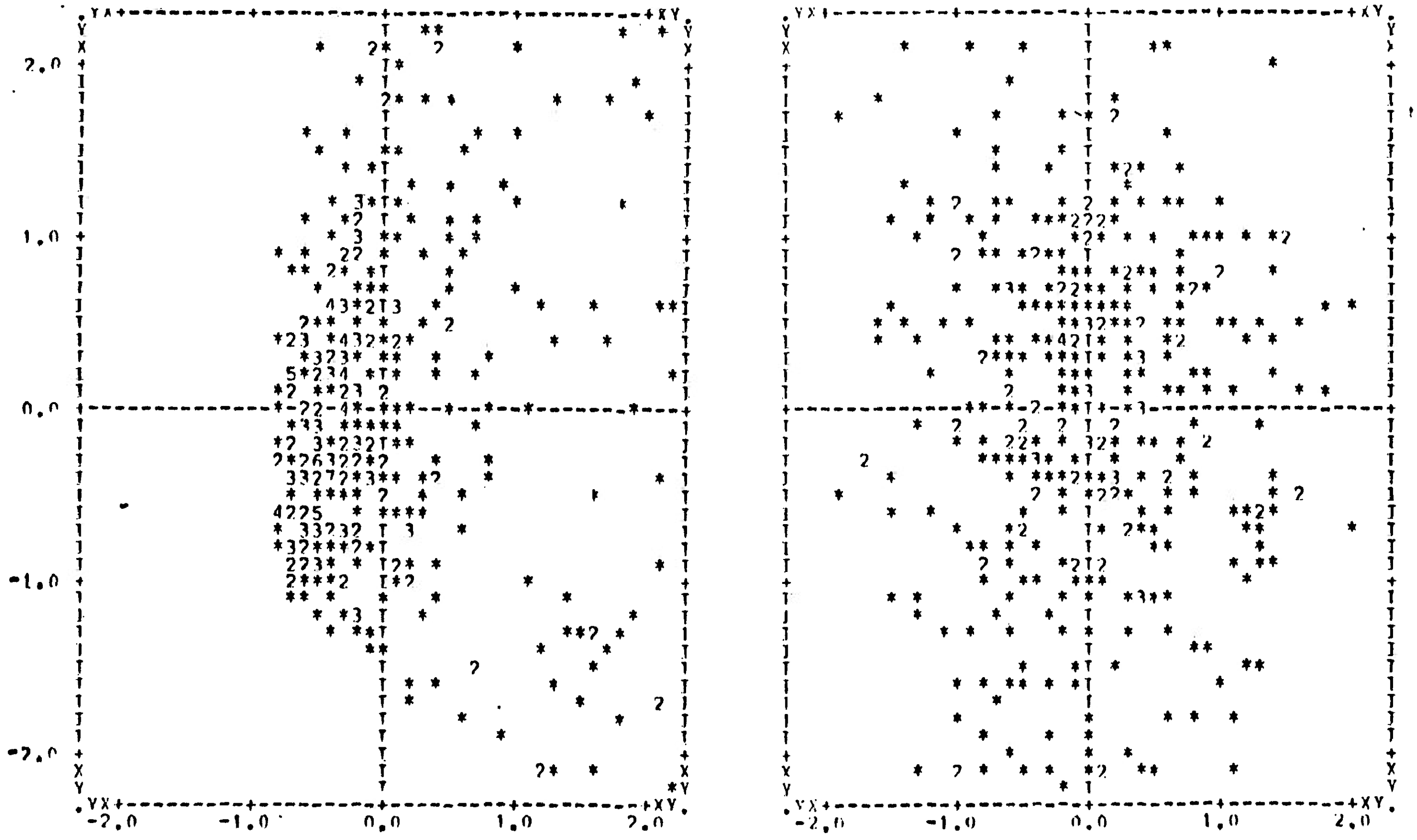


Fig. 10 Plot of standardized residuals for b.a.i. vs. c.a. on the left and ln (b.a.i.) vs. ln (c.a.) on the right. The random pattern of the transformed data's standardized residual plots indicates that the heteroscedasticity has been removed.

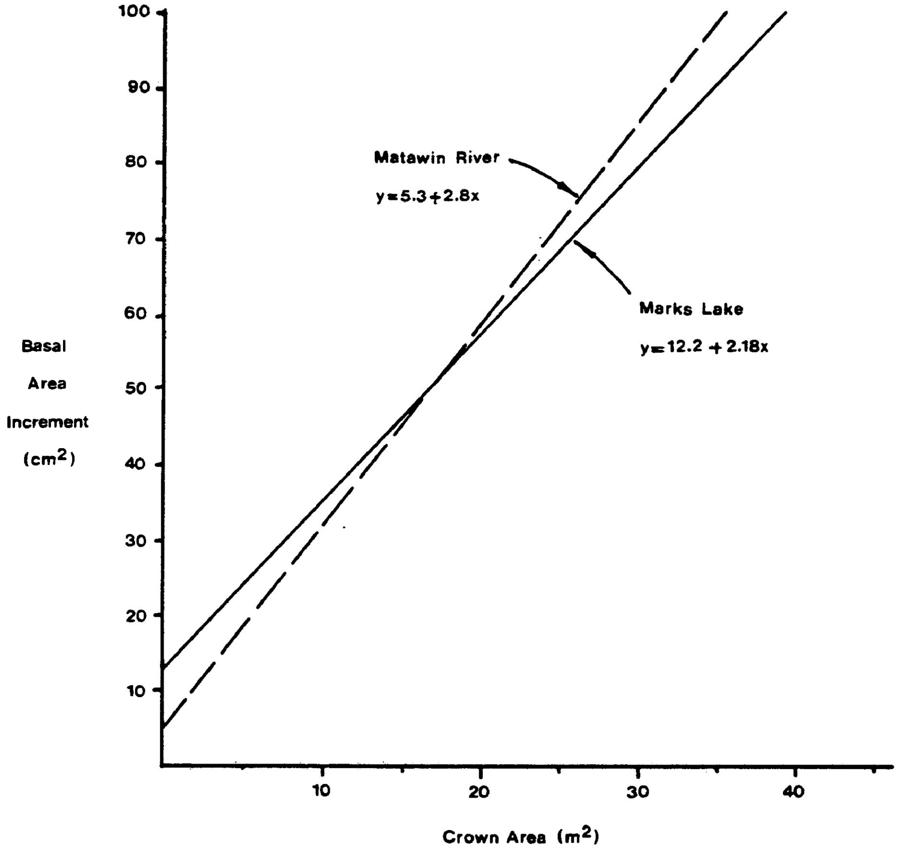


Fig. 11 Regression lines of b.a.i. vs. c.a. for the Marks Lake and Matawin River subject trees

ln (vol.) vs. ln (c.r.) regressions. A t-test is not valid for the untransformed data because of the heteroscedasticity of variance.

CHARACTERISTICS OF MARKS LAKE TREES SELECTED RANDOMLY, SELECTED FOR SUPERIOR GROWING SPACE EFFICIENCY AND SELECTED FOR SUPERIOR HEIGHT GROWTH

Six groups of ten trees each selected from the Marks Lake area were compared with one another. The selection methods for each group included a random method, a method based on superior height growth, and four methods were designed to select trees with superior growing space efficiency. Scaled diagrams (Fig. 12) were drawn with the objective of identifying crop ideotypes or common characters associated with superior growing space efficiency. The six groups of selected trees are listed in Table 5 and the tree measurements are found in Appendix 2.

The random selection group acted as a control. However, one experimental difficulty was encountered. Many of the random trees and approximately 20 trees selected for their superior b.a.i. per unit c.a. were rejected since they did not have sufficient cones to provide the necessary seed quantities for the progeny test. There was concern that large trees with more space and light would be favoured because they usually have a larger cone yield (Schmidtling, 1974). A t-test showed no significant differences between the mean values of the best trees from the b.a.i. vs. c.a. regression and the mean values of trees actually sampled that had somewhat poorer performance yet adequate seed. Therefore, the favouring of larger trees did not appear to significantly affect the selection differential calculated as the difference between the population mean and selected mean. Selection differentials for each group are listed with the summary statistics on inset tables of Figures 13 a-i. A t-test indicated

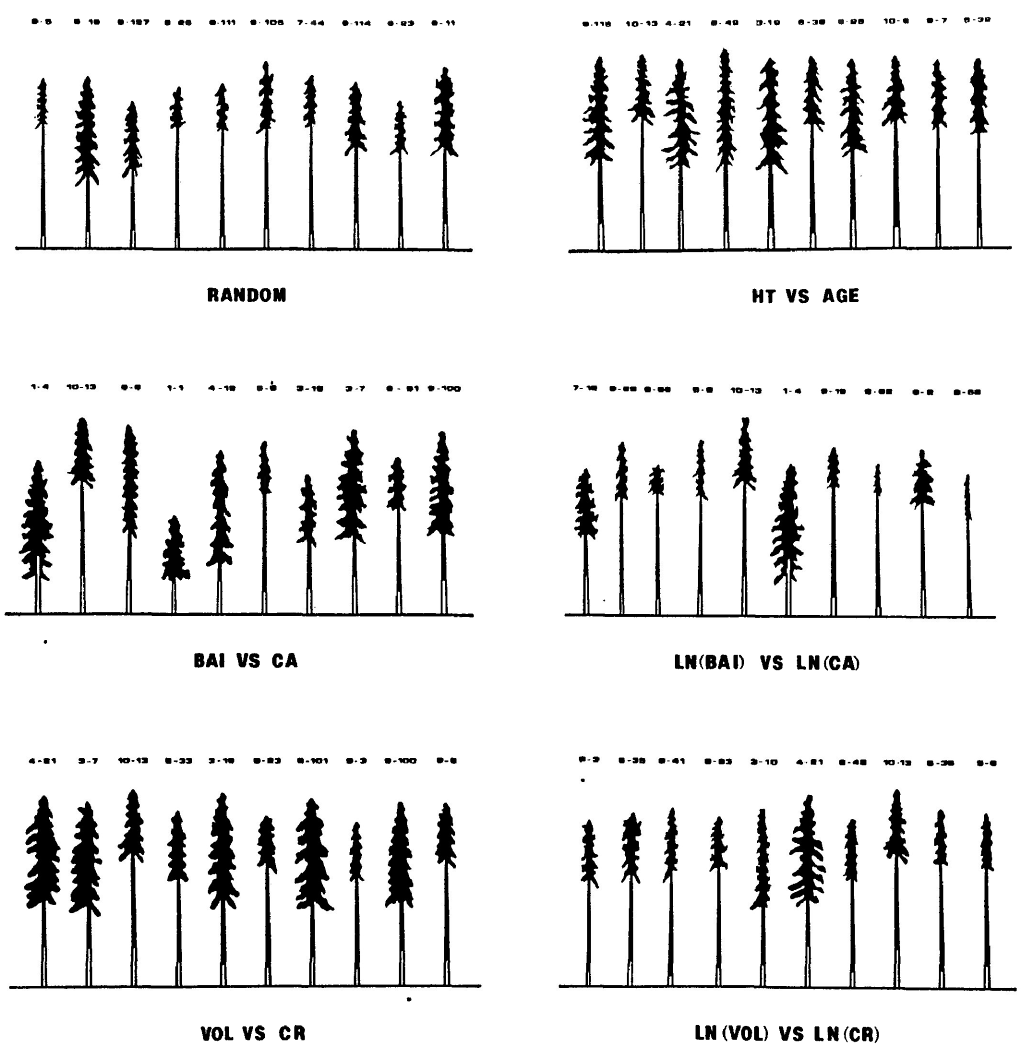


Fig. 12 Scaled diagrams of trees selected for superior qualities by six methods which include a randomly selected control group. Clear histograms in tree stem depict relative b.a.i.

TABLE 5

TREES SELECTED FROM MARKS LAKE PARENT POPULATION BY SIX METHODS

Random	Height vs. Age	b.a.i. vs. c.a.	ln b.a.i. vs. ln c.a.	ln vol. vs. ln c.r.	Vol. vs. c.r.
9-5	9-116	d 1-4	7-12	h 9-3	b 4-21
6-19	a[1] 10-13	a 10-13	5-29	i 5-33	f 3-7
9-127	b 4-21	8-6	8-56	8-41	a 10-13
5-25	8-49	1-1	e 5-8	9-23	i 5-33
9-111	c 3-19	4-19	a 10-13	3-10	c 3-19
9-105	6-38	e 5-8	d 1-4	b 4-21	9-23
7-44	6-28	3-15	9-19	8-42	9-101
9-144	10-6	f 3-7	9-62	a 10-13	h 9-3
6-23	9-7	8-51	9-2	5-35	g 9-100
9-11	5-32	g 9-100	8-58	e 5-8	9-6

[1] Family members prefixed by letters are selected by more than one method.

METHOD	MEAN	S.D.	MAX.	MIN.	S. DIFF.
R	18.35	1.85	22	15.8	+1.8
H	21.9	2.83	27.6	18.6	+5.5
B	20.82	3.88	27	15.7	+4.3
LB	17.52	3.72	23.5	11.4	+1.0
LV	21.69	2.69	27.6	18.3	+5.2
V	24.25	1.996	27.6	21.3	+7.8

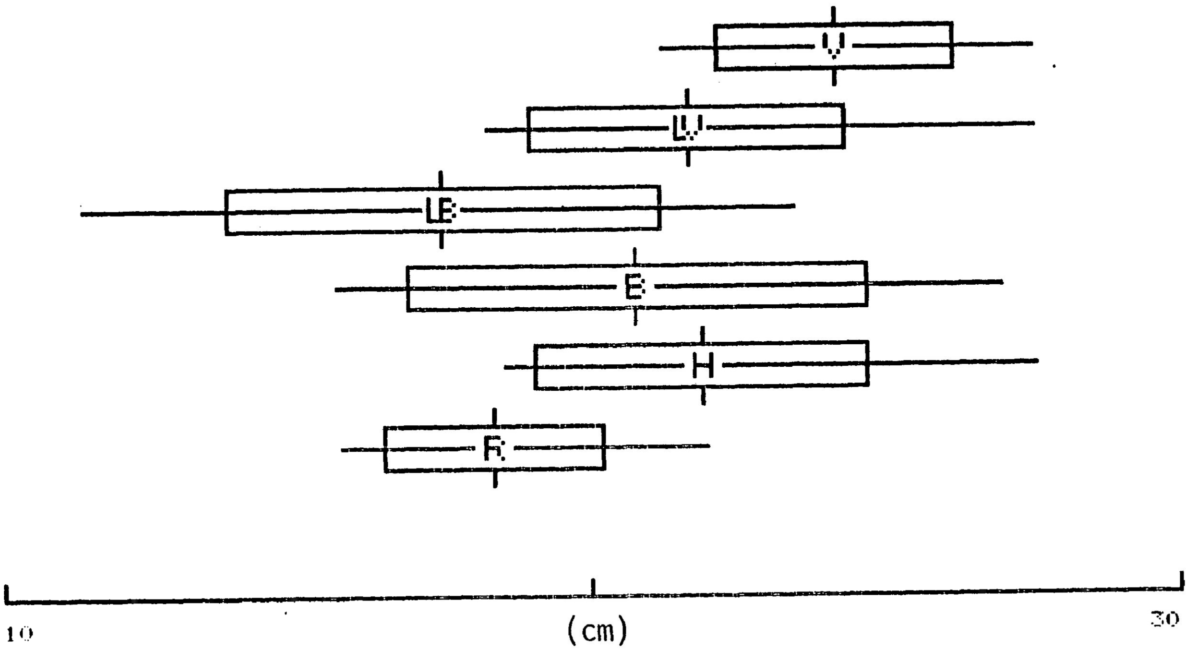


Fig. 13a Hubbs' diagram of d.b.h. (cm) for random (R), height vs. age (H), b.a.i. vs. age (B), ln (b.a.i.) vs. ln (c.a.) (LB), ln (vol.) vs. ln (c.r.) (LV), and volume vs. c.r. (V) selection methods. Inset shows descriptive statistics and selection differential (S. Diff.).

METHOD	MEAN	S.D.	MAX.	MIN.	S. DIFF.
R	17.9	1.41	20.1	15.6	+1.5
H	20.58	.47	21.6	20.1	+4.2
B	17.48	3.15	21.1	10.7	+1.0
LB	17.01	1.86	21.1	14.8	+0.5
LV	19.01	1.09	21.1	17.6	+2.6
V	19.5	1.13	21.1	17.6	+3.0

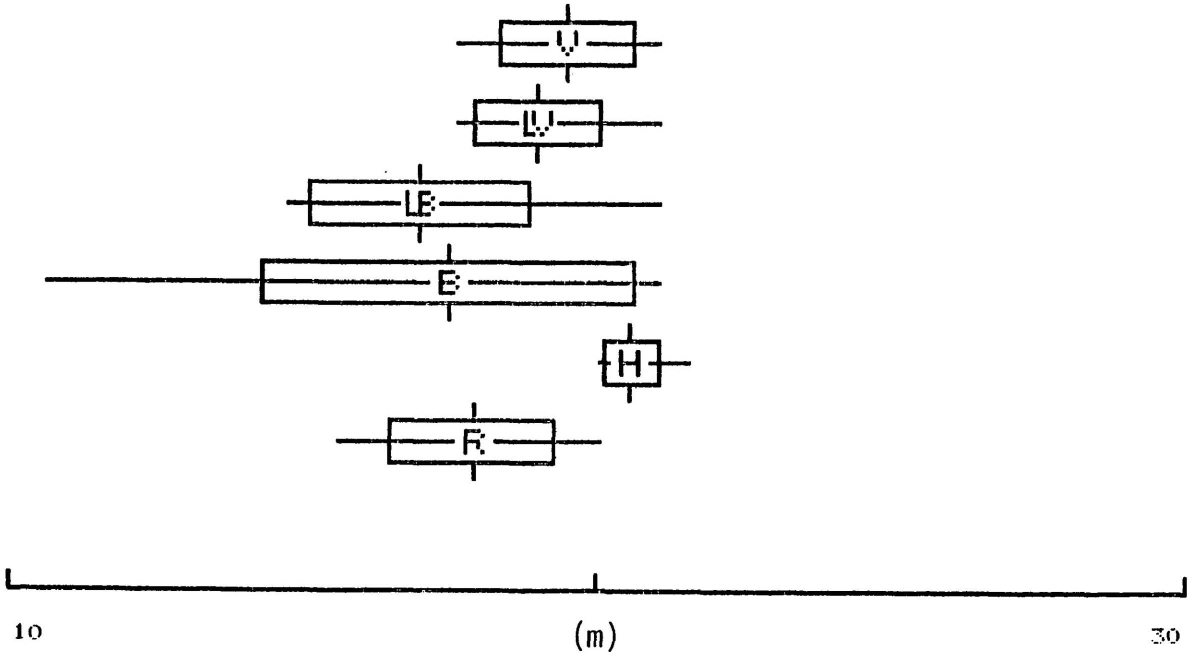


Fig. 13b Hubbs' diagram of height (m) for random (R), height vs. age (H), b.a.i. vs. age (B), ln (b.a.i.) vs. ln (c.a.) (LB), ln (vol.) vs. ln (c.r.) (LV), and volume vs. c.r. (V) selection methods. Inset shows descriptive statistics and selection differential (S. Diff.).

METHOD	MEAN	S.D.	MAX.	MIN.	S. DIFF.
R	7.02	2.46	12.3	4.3	+0.1
H	9.47	2.19	12.5	7	+2.8
B	8.81	2.69	12.5	5.5	+2.5
LB	5.83	2.68	12.2	3	-1.0
LV	7.47	2.06	11.5	5.5	+1.0
V	9.05	2.74	12.5	5.5	+2.2

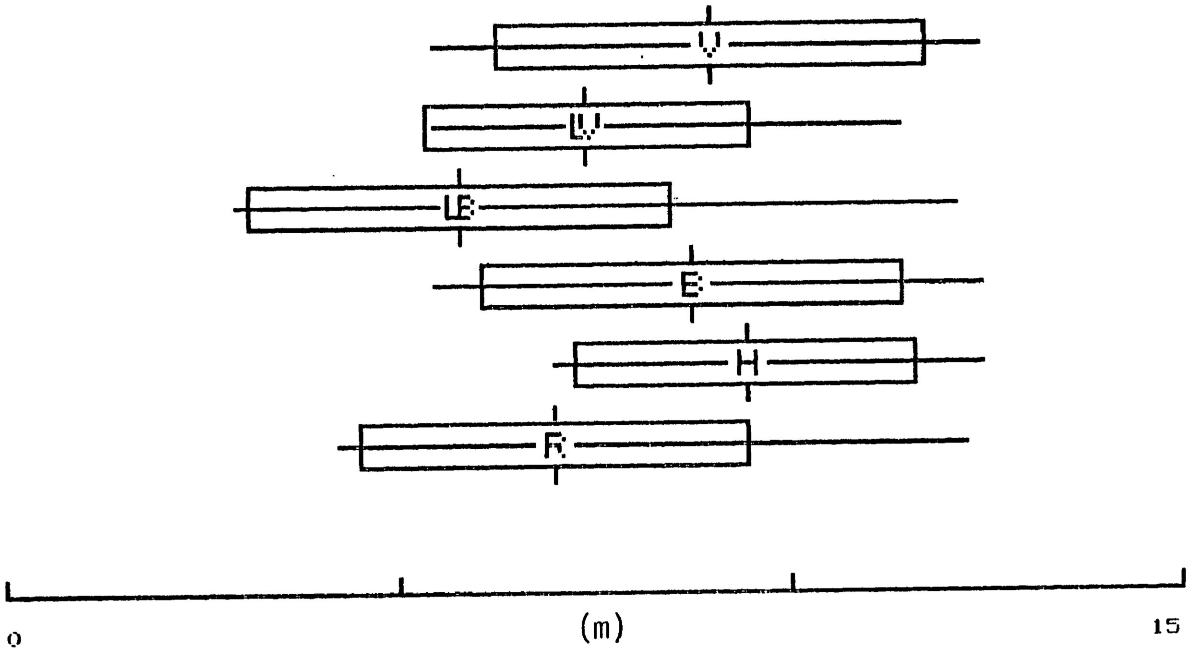


Fig. 13c Hubbs' diagram of crown length (m) for random (R), height vs. age (H), b.a.i. vs. age (B), ln (b.a.i.) vs. ln (c.a.) (LB), ln (vol.) vs. ln (c.r.) (LV), and volume vs. c.r. (V) selection methods. Inset shows descriptive statistics and selection differential (S. Diff.).

METHOD	MEAN	S.D.	MAX.	MIN.	S. DIFF.
R	1.08	.25	1.43	.68	+0.5
H	1.39	.35	2.03	.85	+6.2
B	1.36	.37	1.93	.65	+0.4
LB	.899	.51	1.75	.23	-0.1
LV	1	.42	2.03	.65	0.0
V	1.46	.44	2.03	.73	+0.5

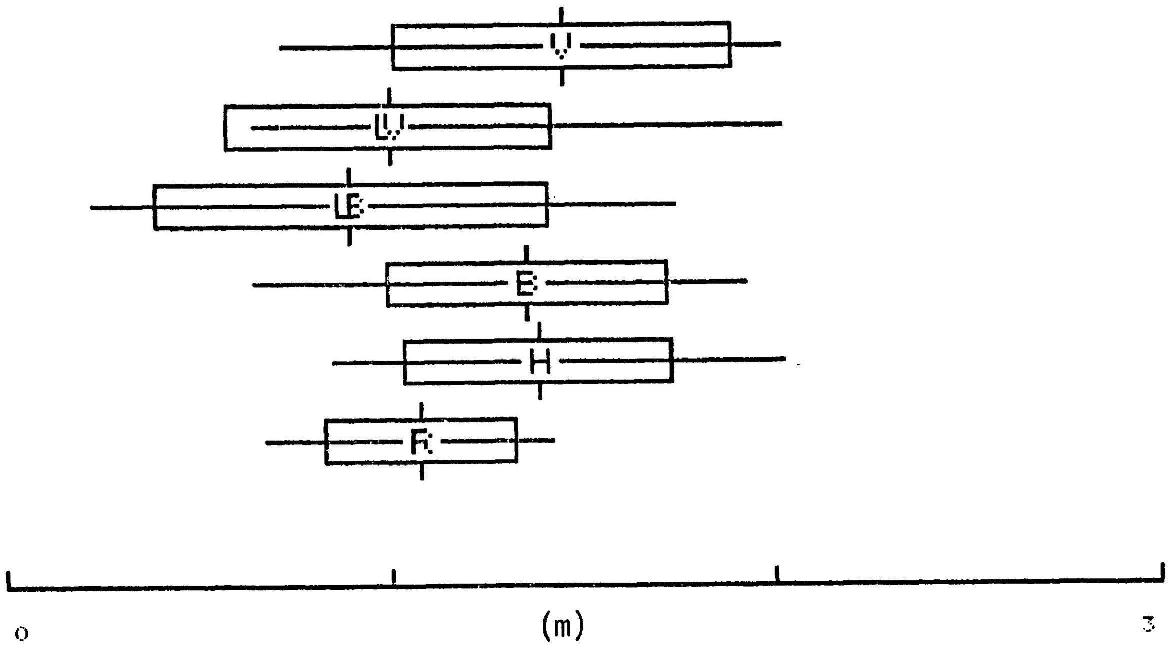


Fig. 13d Hubbs' diagram of crown radius (m) for random (R), height vs. age (H), b.a.i. vs. age (B), ln (b.a.i.) vs. ln (c.a.) (LB), ln (vol.) vs. ln (c.r.) (LV), and volume vs. c.r. (V) selection methods. Inset shows descriptive statistics and selection differential (S. Diff.).

METHOD	MEAN	S.D.	MAX.	MIN.	S. DIFF.
R	7.98	4.49	17.53	3.37	+ 0.5
H	13.59	5.72	23.29	6.2	+ 8.1
B	12.56	6.38	22.52	3.77	+ 5.0
LB	6.18	6.29	21.35	1.01	- 1.2
LV	7.93	5.7	23.29	3.77	+ 6.4
V	14.17	7.65	23.29	4.71	+ 6.7

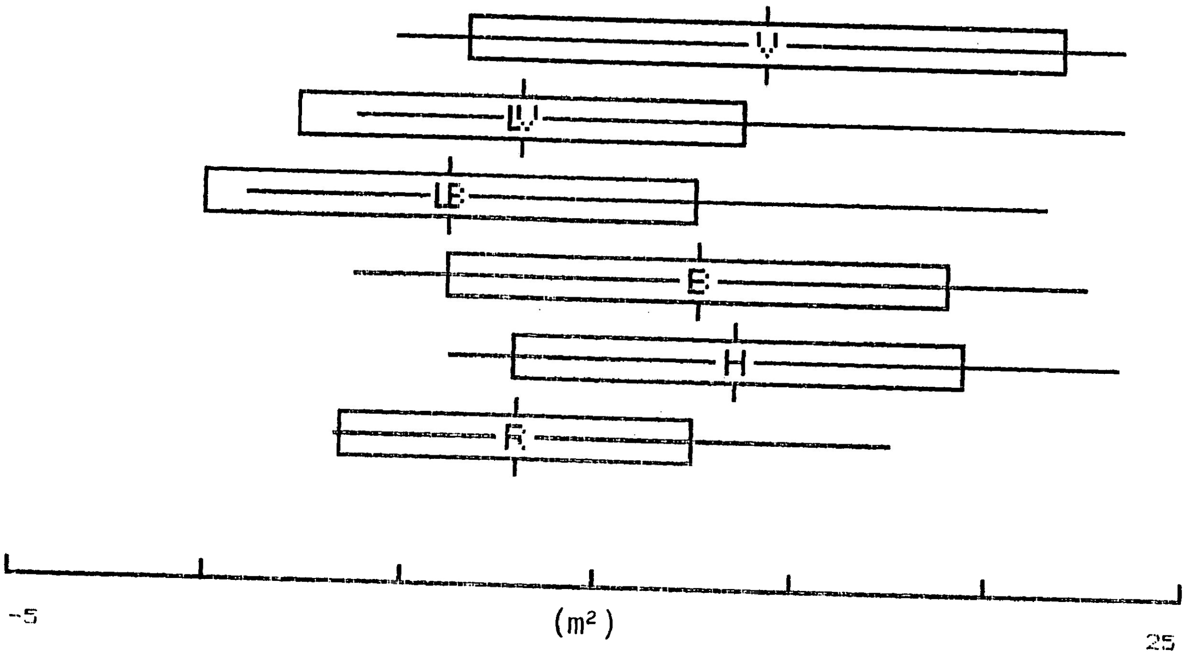


Fig. 13e Hubbs' diagram of crown area (length x radius) (m²) for random (R), height vs. age (H), b.a.i. vs. age (B), ln (b.a.i.) vs. ln (c.a.) (LB), ln (vol.) vs. ln (c.r.) (LV), and volume vs. c.r. (V) selection methods. Inset shows descriptive statistics and selection differential (S. Diff.).

METHOD	MEAN	S.D.	MAX.	MIN.	S. DIFF.
R	34.52	11.88	54.33	21.47	+ 6.0
H	49.62	18.82	82.36	28.98	+21.1
B	68.63	20.81	115.58	44.24	+40.1
LB	50.78	32.06	115.58	15.97	+22.3
LV	44.75	20.43	82.36	21.22	+16.3
V	58.28	19.48	82.47	28.67	+29.8

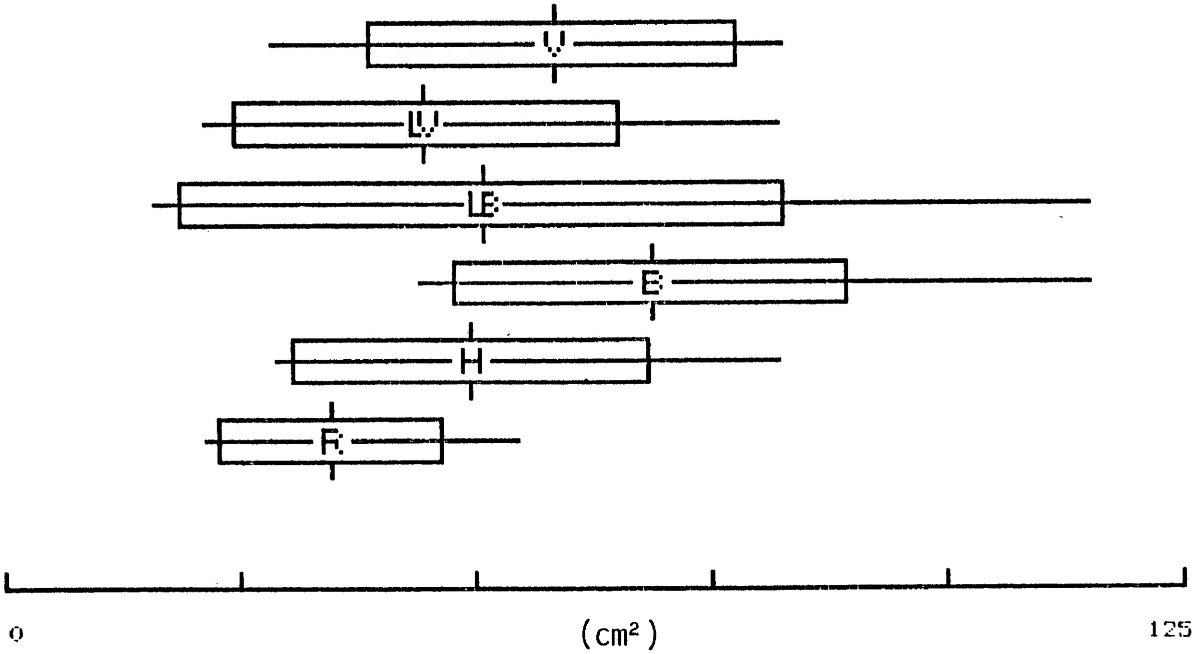


Fig. 13f Hubbs' diagram of b.a.i. for random (R), height vs. age (H), b.a.i. vs. age (B), ln (b.a.i.) vs. ln (c.a.) (LB), ln (vol.) vs. ln (c.r.) (LV), and volume vs. c.r. (V) selection methods. Inset shows descriptive statistics and selection differential (S. Diff.).

METHOD	MEAN	S.D.	MAX.	MIN.	S. DIFF.
R	.205	.052	.31	.14	0.0
H	.328	.087	.51	.23	+0.2
B	.273	.123	.48	.1	+0.1
LB	.19	.091	.38	.07	+0.1
LV	.303	.089	.51	.21	+0.1
V	.38	.075	.51	.27	+0.2

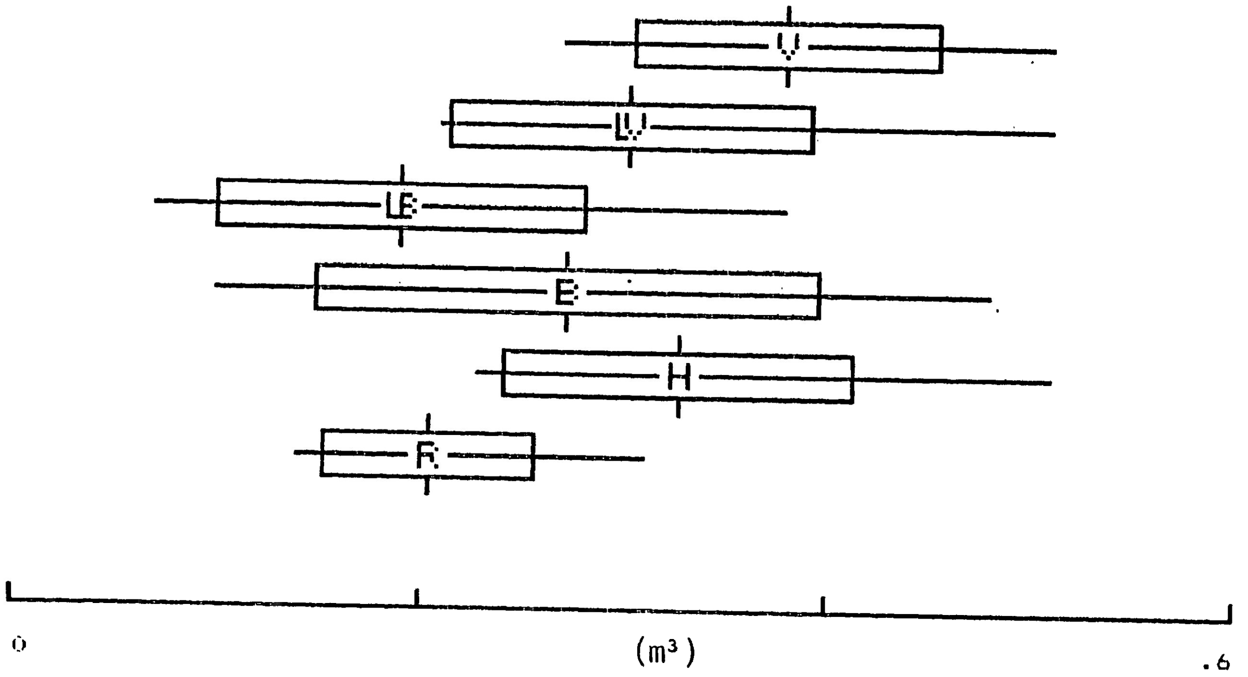


Fig. 13g Hubbs' diagram of volume for random (R), height vs. age (H), b.a.i. vs. age (B), ln (b.a.i.) vs. ln (c.a.) (LB), ln (vol.) vs. ln (c.r.) (LV), and volume vs. c.r. (V) selection methods. Inset shows descriptive statistics and selection differential (S. Diff.).

METHOD	MEAN	S.D.	MAX.	MIN.	S. DIFF.
R	4.9	1.36	6.67	1.88	+1.1
H	4.02	1.75	8.11	2.08	+0.2
B	6.37	2.41	11.74	3.66	+2.6
LB	11.25	3.83	16.3	5.41	+1.4
LV	6.39	2.4	11.74	3.43	+2.6
V	4.95	2	8.11	2.08	+1.1

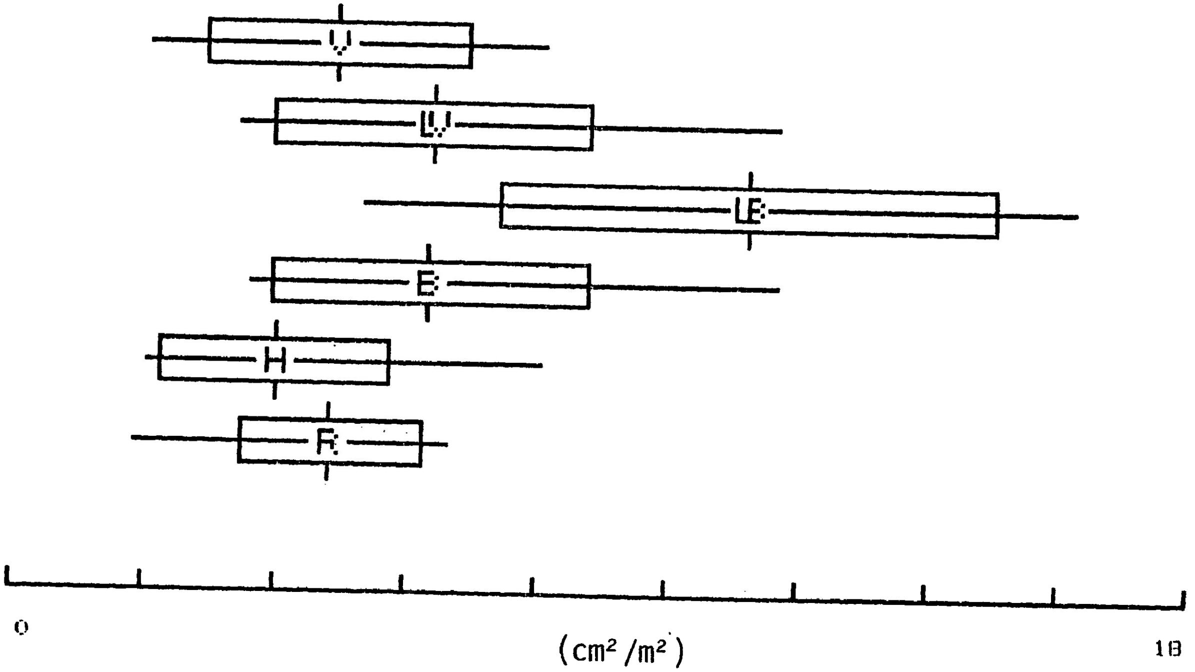


Fig. 13h Hubbs' diagram of b.a.i./c.a. for random (R), height vs. age (H), b.a.i. vs. age (B), ln (b.a.i.) vs. ln (c.a.) (LB), ln (vol.) vs. ln (c.r.) (LV), and volume vs. c.r. (V) selection methods. Inset shows descriptive statistics and selection differential (S. Diff.).

METHOD	MEAN	S.D.	MAX.	MIN.	S. DIFF.
R	.197	.054	.294	.122	0.0
H	.239	.038	.293	.155	+0.1
B	.205	.077	.321	.068	0.0
LB	.247	.096	.42	.102	+0.1
LV	.313	.033	.373	.252	+0.2
V	.273	.046	.373	.22	+0.4

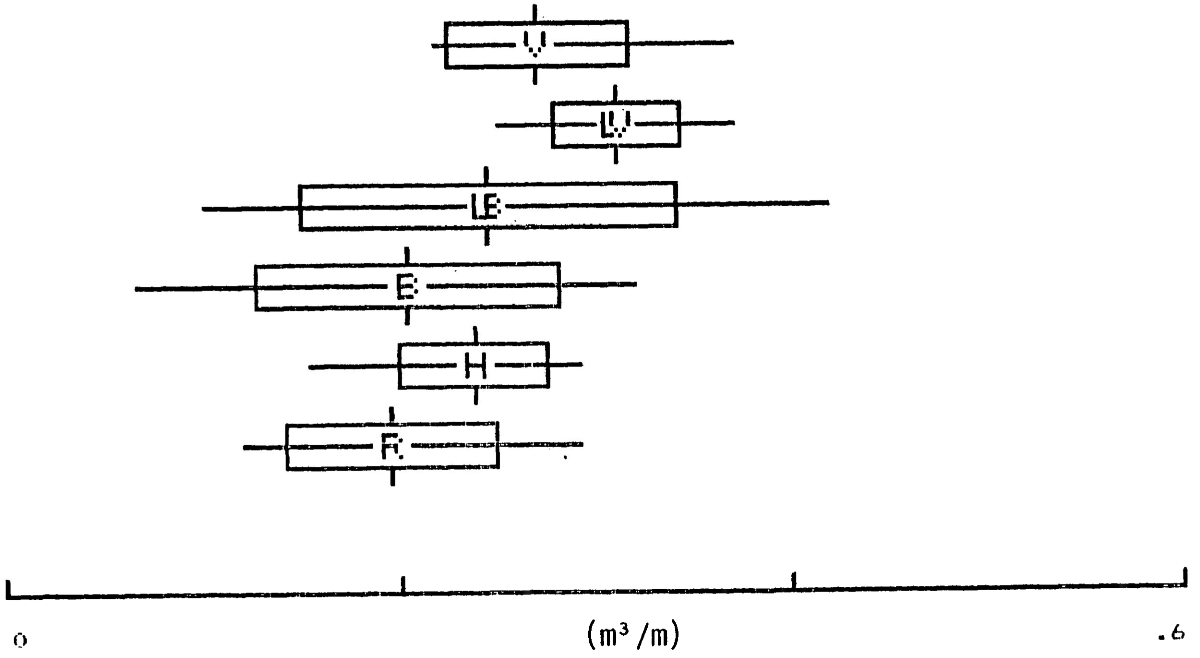


Fig. 13i Hubbs' diagram of vol/c.r. for random (R), height vs. age (H), b.a.i. vs. age (B), ln (b.a.i.) vs. ln (c.a.) (LB), ln (vol.) vs. ln (c.r.) (LV), and volume vs. c.r. (V) selection methods. Inset shows descriptive statistics and selection differential (S. Diff.).

that randomly selected trees seemed to adequately represent the population mean for most characters except height growth and d.b.h. The randomly selected trees were significantly taller than the stand average because the taller trees had more seed. Thus, this difference reduced the sensitivity of the progeny trial to a certain degree. The selection differential would be reduced if the mean of the random selection group was used to represent the population mean, as is the case for some tree improvement trials (Wright, 1976).

Some trees were selected by more than one baseline method. Trees selected by more than one method are indicated in Table 5. For example, tree 10-13 was selected by all five baselines. Six other trees were selected by at least two selection methods (4-21, 5-8, 3-19, 9-100, 3-7, 9-3). If we assume that b.a.i. vs. c.a., ln (b.a.i.) vs. ln (c.a.), vol. vs. c.r. and ln (vol.) vs. ln (c.r.) methods select trees with superior growing space efficiency, then common trees would probably be expected to be present in the groups.

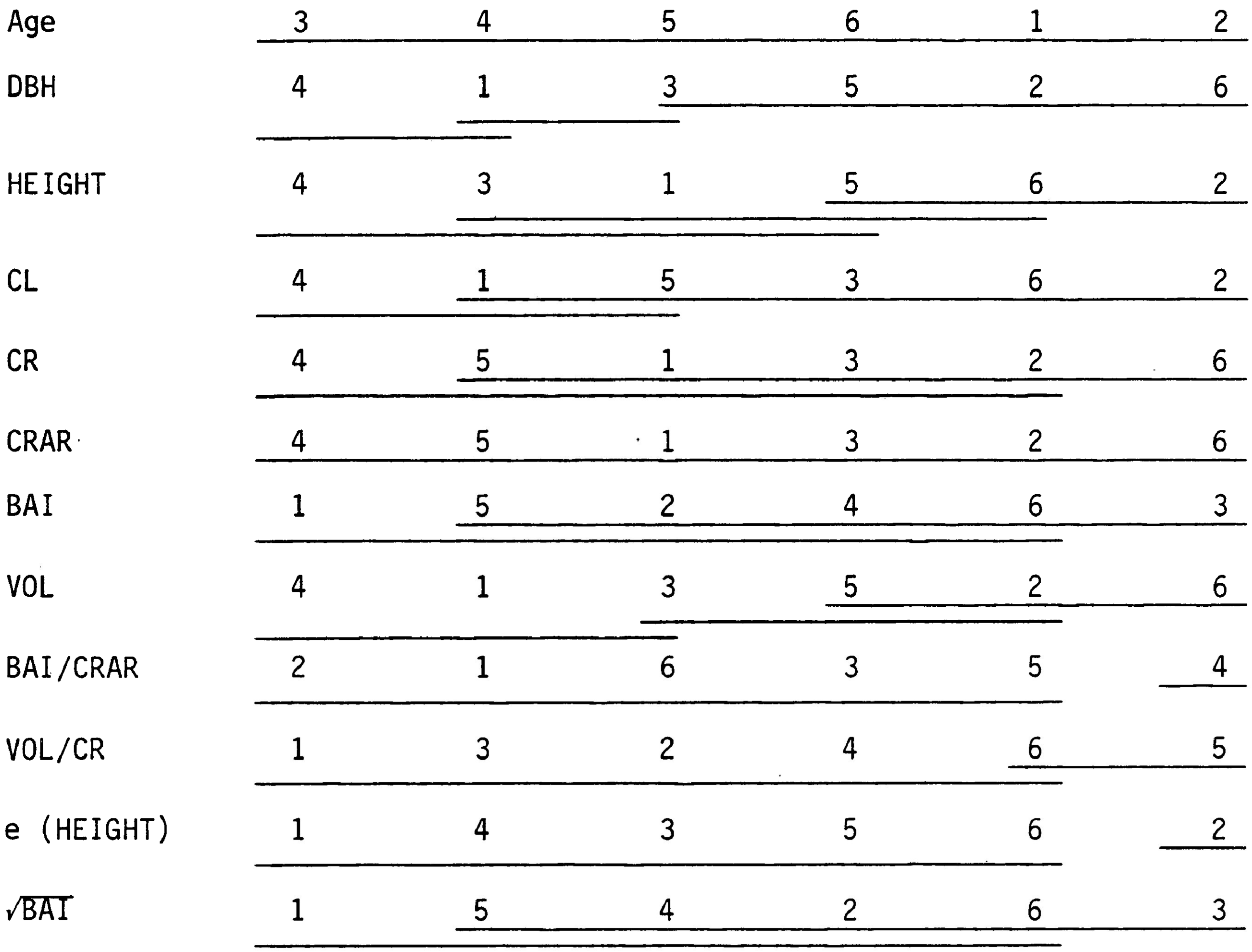
Trees drawn to Scale (Fig. 12), Hubbs' diagrams (Figs. 13 a-i) and S.N.K. multiple range tests were used to reveal common factors between trees in the various selection groups. Figure 12 is a scaled diagram that shows the ten trees selected by each of the six methods with the corresponding family number shown above each tree. Tree height, crown length, and crown radius are drawn to scale but the silhouette is an artistic impression. Clear histograms fill the lower tree stem showing relative ten-year b.a.i.

Hubbs' diagrams (Figs. 13a-i) have a horizontal bar defining the range of observations for a given character. The vertical bar marks the mean of the character and the box shows one standard deviation to either side of the mean. These diagrams, drawn by an Apple IIe computer, allow one to assess the significance of observed differences visually without the constraints of a fixed level of confidence. S.N.K. multiple range tests make comparisons at the 95% level of confidence; however, the level of confidence is less than 95% when all the comparisons between subsets of groups are considered at once. Figure 14 shows the six selection methods coded from 1 to 6 and listed by each character. Selection method groups that do not express significant differences from each other for a given character as determined by the S.N.K. tests are underscored and form a subset.

Generally, the trends observed from the scaled diagrams are supported by the more detailed Hubbs' diagrams and S.N.K. tests. The scaled diagrams are useful for observing broad multivariate trends that cannot be distinguished in Hubbs' diagrams and S.N.K. tests.

The random group has the lowest mean b.a.i. but the S.N.K. tests show that the random group b.a.i. is significantly different from only the b.a.i. vs. c.a. group. All methods designed to select superior growing space efficiency have patterns of tree size variation similar to the random group. The height vs. age group showed least tree size variation. Cochran's C test (Winer, 1971) found heterogeneity of variance between groups for height and b.a.i. Height was transformed to the anti-log of e, and b.a.i. was transformed to the square root to remove the heterogeneity of variance. When this was done, the height vs. age group was significantly

CHARACTER - Smallest to largest mean



Legend

1 - Random
2 - Height vs. Age
3 - BAI vs. CRAR
4 - ln BAI vs ln CRAR
5 - ln Vol. vs. ln CR
6 - Vol. vs. CR

Fig. 14 S.N.K. test of mean values for selection method groups. Groups that are not significantly different from each other are underscored and form a subset.

taller than any other group but the transformation did not alter the ranking of groups for b.a.i. by the S.N.K. tests. The transformed subsets are shown at the bottom of Figure 14.

Crown dimensions of the height vs. age group and the vol. vs. c.r. group were larger than those of the other four selection groups. The S.N.K. tests indicated that the differences in crown area were not significant but the trees selected by ln (b.a.i.) vs. ln (c.a.) had a mean crown length that was significantly less than most other groups (height vs. age, vol. vs. c.r., and b.a.i. vs. c.a.).

The analysis did not identify characters unique to groups that were assumed to express superior growing space efficiency. Differences in mean character values were less acute than differences in tree size variation. Both b.a.i. vs. c.a. and ln (b.a.i.) vs. ln (c.a.) methods selected a broad range of tree sizes in a pattern similar to that of random selection but with significantly superior b.a.i.'s. When compared with all the other groups, ln (b.a.i.) vs. ln (c.a.) selected trees with significantly superior b.a.i. per unit crown area. Trees selected by height vs. age were uniform in size and were the tallest trees. The greater variation in the sizes selected by the b.a.i. vs. c.a. method is easy to see in Figures 12-13b.

SEED CHARACTERISTICS

Seed weight may exert maternal influences upon seedling development. For this reason, family seed weights were recorded before the seeds were planted. Table 6 summarizes the mean seed weights from five randomly chosen seed lots of 10 seeds for each family from both the Matawin River and Marks Lake areas. Families are designated by the mother tree number.

TABLE 6

SUMMARY OF FAMILY SEED WEIGHT MEANS FROM 5 LOTS OF 10 SEEDS EACH

Selection Method	Population			
	Matawin River		Marks Lake	
	Family Number	Mean Seed Weight (mg)	Family Number	Mean Seed Weight (mg)
Random	159	1.094	9-5	1.176
	180	1.014	6-19	.860
	82	1.006	9-127	.958
	14	1.074	5-25	1.116
	501	.984	9-111	1.062
	51	.952	9-105	.858
	21	1.092	7-44	1.162
	87	.914	9-114	.990
	560	1.278	6-23	.932
All Families		1.034		.991
Height vs. Age	48	1.022	9-116	1.018
	93	1.032	10-13	.922
	27	1.026	4-21	1.028
	88	.992	8-49	.904
	139	1.148	3-19	.836
	513	.942	6-38	1.022
	37	.890	6-23	.872
	138	.948	10-6	.868
	61	1.006	9-2	1.060
	518	1.154	5-32	1.192
All Families		1.016		.999

TABLE 6 - continued

Selection Method	Population			
	Matawin River		Marks Lake	
	Family Number	Mean Seed Weight (mg)	Family Number	Mean Seed Weight (mg)
B.a.i. vs. crown area	93	1.032	1-4	.840
	30	1.146	10-13	.942
	175	.903	8-6	.806
	515	.912	1-1	.878
	6	1.030	4-19	.932
	138	1.145	5-8	1.112
	7	1.056	3-15	1.186
	15	1.128	3-7	1.078
	501	1.026	8-51	1.122
	25	1.141	9-100	.760
All Families		1.054		.968
All Selection Methods & Families		1.036		.982

Nested analysis of seed weight variances were run to see if it was necessary to use seed weight as a covariate of progeny performance. The ANOVAs (Tables 7 and 8) showed family differences were highly significant; therefore, seed weight would likely be required as a covariate in progeny analysis. Selection method group seed weight differences were non-significant.

Regressions of seed weight upon parent characters were run to elucidate the importance of certain maternal factors such as tree height or crown area that might influence seed weight. The regressions of seed weight upon parent characters were non-significant; this might explain why the ANOVAs showed no differences between selection groups because selection groups were defined by the parent characters. Table 9 presents the r^2 values for the seed weight regressions.

The Matawin River seed weight (1.03 mg) was significantly heavier than the Marks Lake seed weight (0.98 mg) as determined by a t-test. Cochrane's C test (Winer, 1971) showed the Matawin River seed weights expressed heterogeneity of variance between families. Transforming the Matawin River seed weights to the third power overcame this problem which can adversely affect ANOVA results. For this reason, the mean squares in the Matawin River ANOVA are much larger than the Marks Lake mean square values (Tables 7 and 8).

PROGENY PERFORMANCE

Open-pollinated seed was planted in the greenhouse to compare the performance of progeny from random, height vs. age, and b.a.i. vs. c.a. selected parents. The hypothesis was that progeny from parents that

TABLE 7

NESTED ANALYSIS OF VARIANCE FOR SELECTION METHODS FOR FAMILY SEED WEIGHT FROM THE MATAWIN RIVER POPULATION (TRANSFORMED TO THE 3RD POWER)

Source of Variation	Degree of Freedom	Mean Square	Ratio	$\alpha = 0.05$ Table F[1]
Selection Method	2	21.5545×10^{10}	0.4081	3.35
Families within Selection	27	52.8267×10^{20}	11.843**	1.55
Error	120	4.46022×10^{20}		
Total	149			

[1] F Values from Steel/Torrie (1980)

** = significance at $\alpha = 0.01$

TABLE 8

NESTED ANALYSIS OF VARIANCE FOR SELECTION METHODS FOR FAMILY SEED WEIGHT FROM THE MARKS LAKE POPULATION

Source of Variation	Degree of Freedom	Mean Square	Ratio	$\alpha = 0.05$ Table F[1]
Selection Method	2	290.1267	0.332	3.35
Families within Selection	27	795.2044	23.8657**	
Error	120	33.3200		
Total	149			

[1] F Values from Steel/Torrie (1980)

** = significance at $\alpha = 0.01$

TABLE 9

SUMMARY OF SEED WEIGHT CORRELATIONS WITH PARENT TREE MORPHOLOGY AND POINT DENSITY[1]

Regression	Coefficient of Determination (r^2)	
Parents	Matawin River (n = 28)	Marks Lake (n = 14)
Seed weight vs. point density	$0.15^{n.s.}$	N.A.
Seed weight vs. parent height	$0.06^{n.s.}$	$0.01^{n.s.}$
Seed weight vs. parent b.a.i.	$0.01^{n.s.}$	$0.02^{n.s.}$
Seed weight vs. crown area	$0.06^{n.s.}$	$0.21^{n.s.}$

[1] Spurr (1962).

n.s. = not significant.

expressed superior growing space efficiency should have progeny showing superior growth given uniform growing space if the characters responsible for superior growing space efficiency are both heritable and are expressed at early stages of development. The seedlings were grown under different light intensities to assess one component of phenotypic plasticity and how this might be related to growing space efficiency. It was thought that progeny from parents with superior growing space efficiency might perform best under shaded conditions because the parents' superior growing space efficiency may be linked to growth mechanisms operating under the reduced light intensities within a forest canopy.

The seedlings' responses to the different light intensities were obvious after two months and very pronounced by harvest time. The block with no shade had seedlings with numerous lateral branches and a dense needle complement. The block with maximum shade (33% light intensity) had small seedlings with almost no lateral branches and sparse, short needles. Seedlings in the block with medium shade (56% light intensity) expressed forms that were intermediate between those from the fully shaded and shade-free blocks. Figure 15 is a photocopy that shows 5 progeny of family 9-5 (random selection group) from each light treatment block. The differences in morphology corresponding to the different light intensities are easy to observe.

While differences between family groups within light treatment blocks were easy to observe by harvest time, differences between selection methods were not obvious. Inset tables on Figures 16a-h present summary statistics for selection method groups by each light treatment.

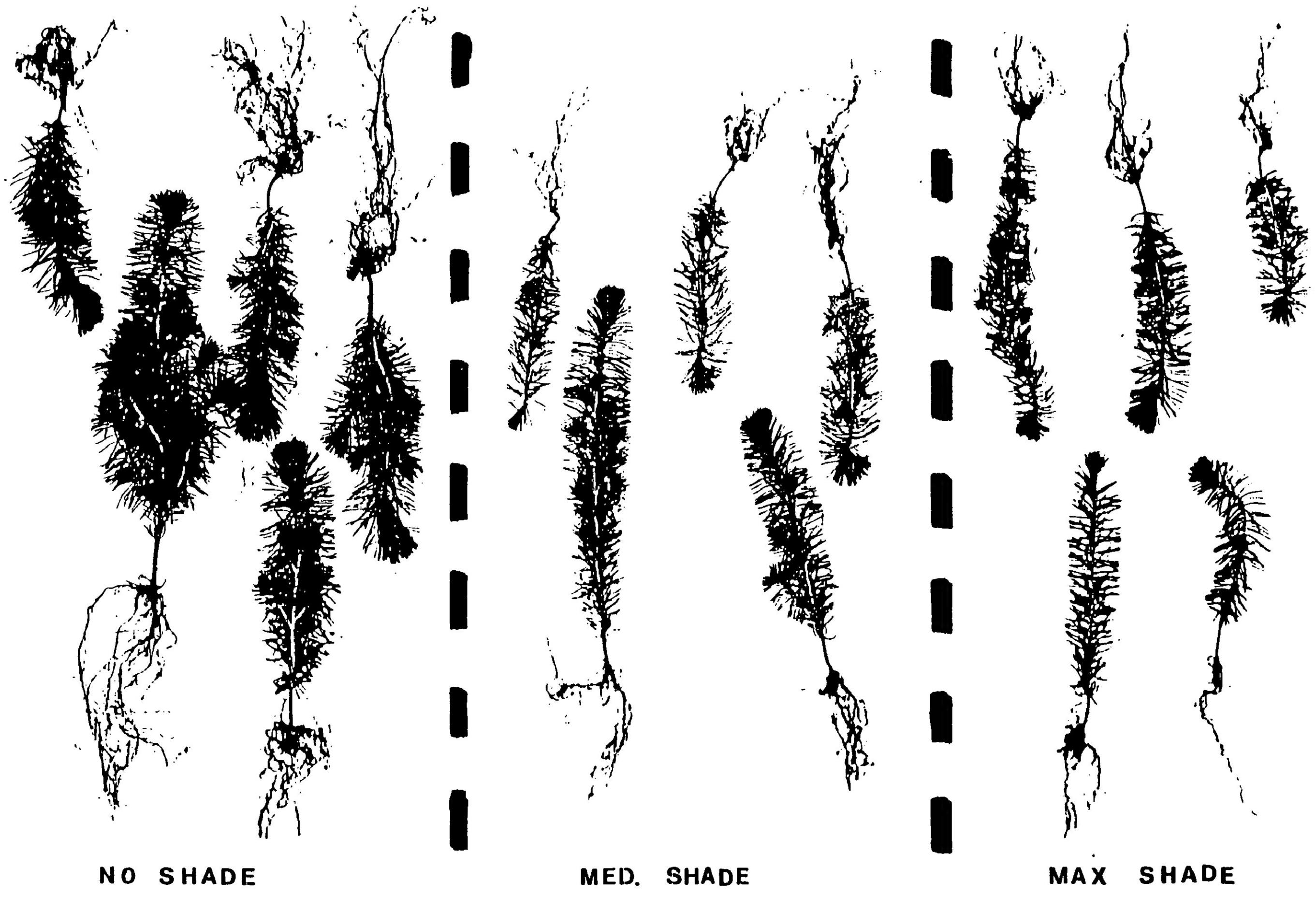
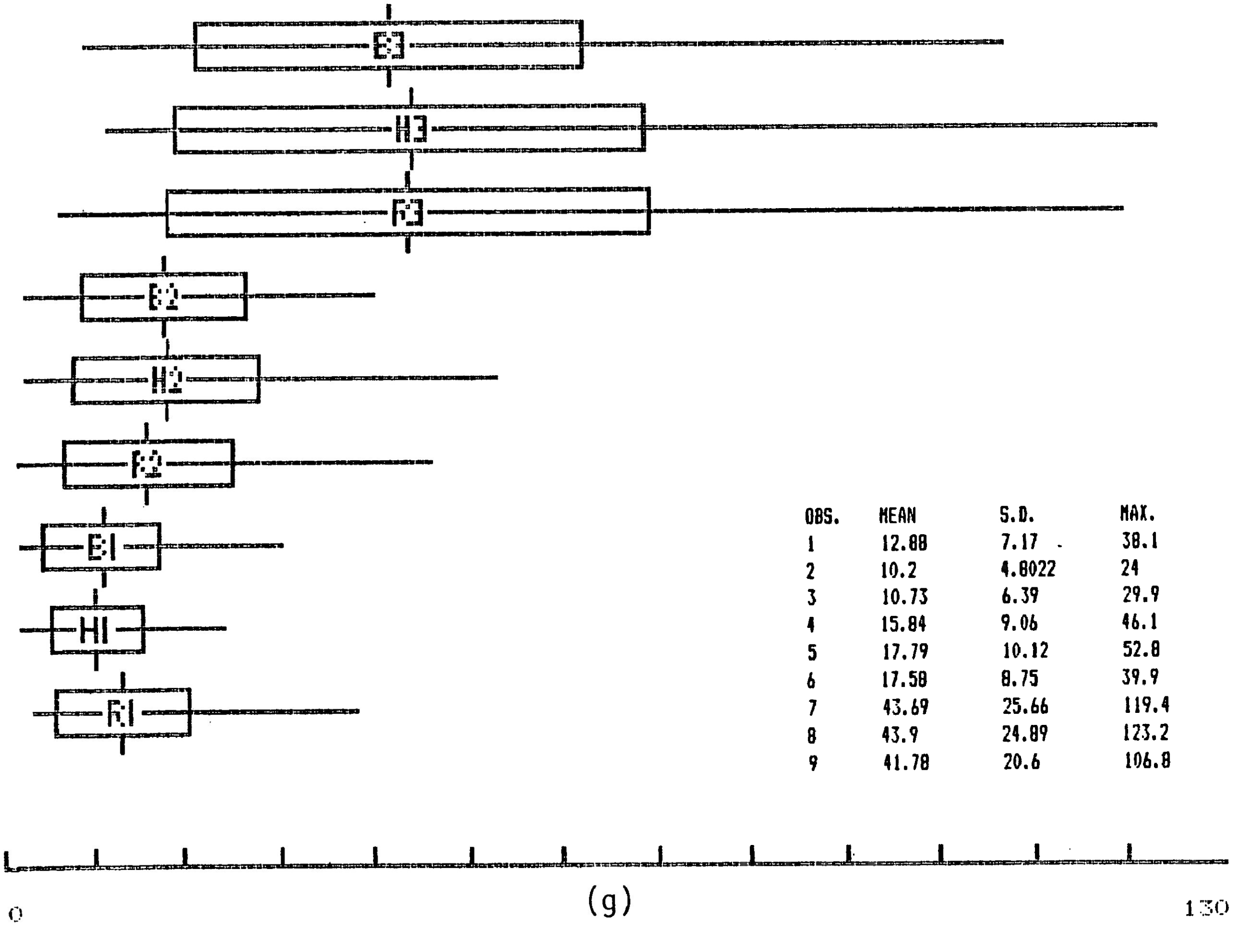


Fig. 15 Photoreduction of three family portraits (photocopies) taken of family 9-5 from the random selection group on December 7, 1983. The bold dashes delineate light treatment blocks of no shade, medium shade (56% light intensity) and maximum shade (33% light intensity).

Hubbs' diagrams (Figs. 16a-h) were drawn to compare mean progeny performance of the selection groups in each of the light intensities from the unbalanced data set. Figures 16a-h provide a visual comparison of the selection method differences as they are influenced by light intensity. Hubbs' diagrams help illustrate and support the results shown by the ANOVAs and offer an advantage by graphically showing the size of differences between progeny characters rather than restricting one's interpretation of differences to an arbitrarily chosen level of significance. Figure 16g identifies a weak trend. Although the differences are small, progeny from select parents have needles that are slightly longer than progeny from randomly selected parents. Because only one needle was measured for each seedling, the value of this result is very questionable. If this trend is correct, one might expect the select progeny with longer needles to show a growth advantage in the future because of the increased leaf area.

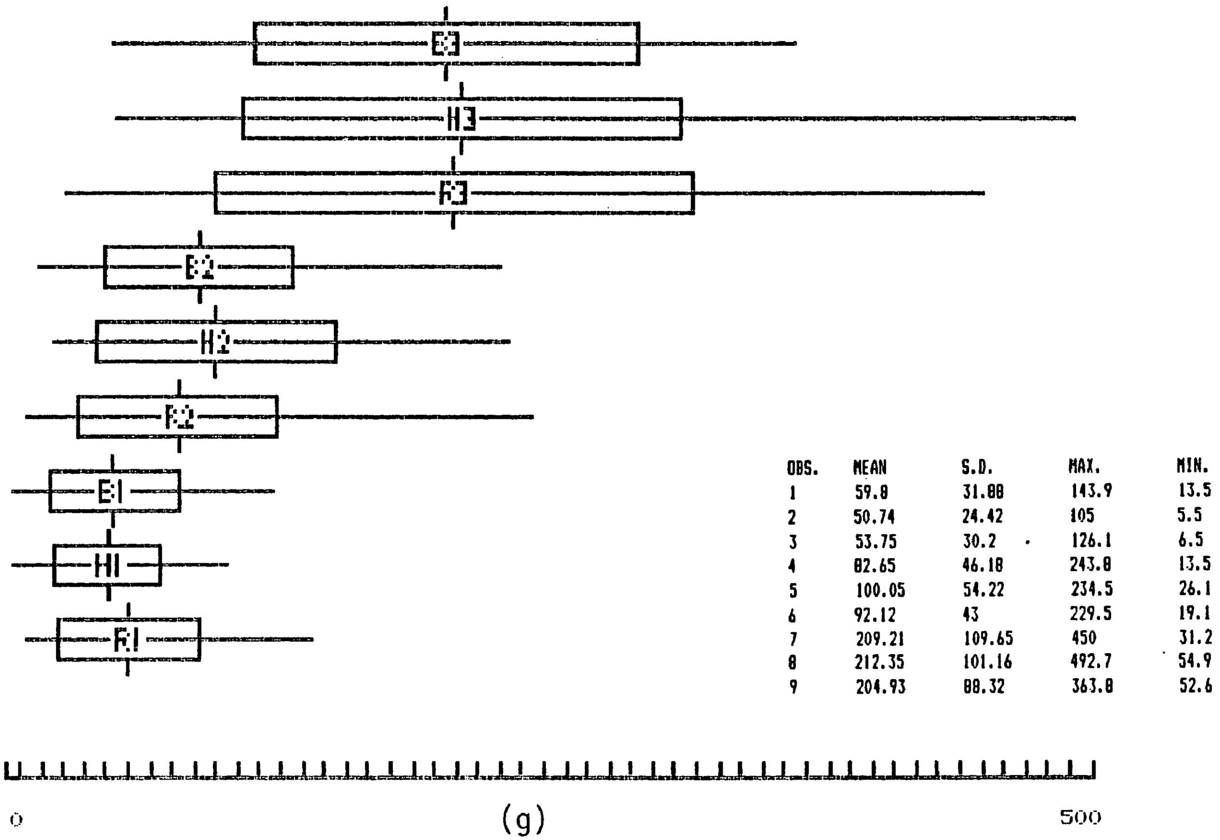
Two months after germination, mortality from damping off was evident and widespread among the progeny. Algal growth in some cavities created a hard cap with interfered with irrigation. A more controlled irrigation regime combined with covering the surface of the cavities with vermiculite has since been found to reduce damping off and algal growth.

The seedling mortality seemed independent of light effects but some families were more affected than others. The resulting unequal replications caused the ANOVAs to be unbalanced (Appendix 6). Regression techniques corrected for this problem in the nested factorial ANOVA. By eliminating one family from each selection method and reducing the replications from five to three, the design could be analyzed as fully balanced (Appendix 7).



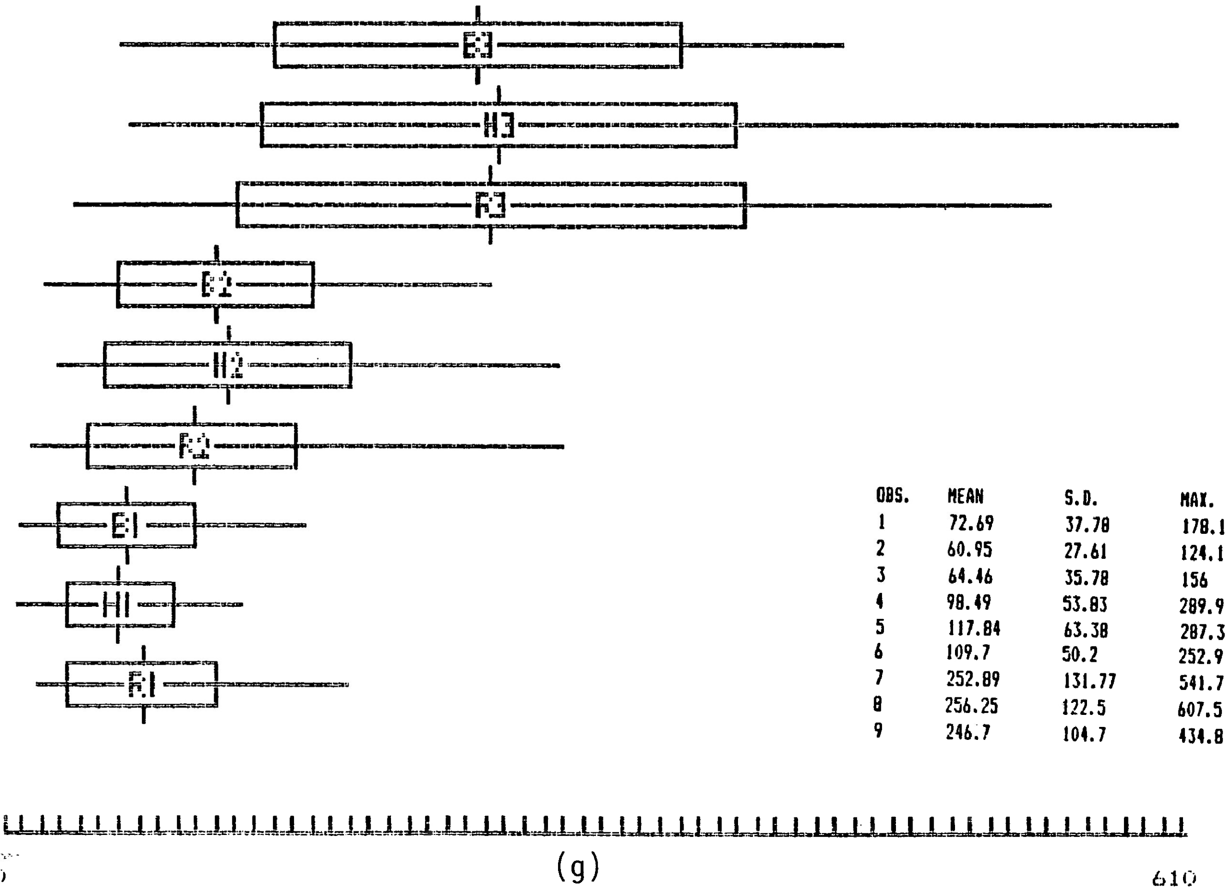
OBS.	MEAN	S.D.	MAX.	MIN.
1	12.88	7.17	38.1	3.4
2	10.2	4.8022	24	2
3	10.73	6.39	29.9	2
4	15.84	9.06	46.1	1.6
5	17.79	10.12	52.8	2.4
6	17.58	8.75	39.9	2.4
7	43.69	25.66	119.4	6.2
8	43.9	24.89	123.2	11.2
9	41.78	20.6	106.8	8.9

Fig. 16a Hubbs' diagram of root dry weight of progeny grown in 33% light intensity (R1, H1, B1), 56% light intensity (R2, H2, B2), and 100% light intensity (R3, H3, B3) where R = random selection, H = height vs. age selection, and B = b.a.i. vs. c.a. selection.



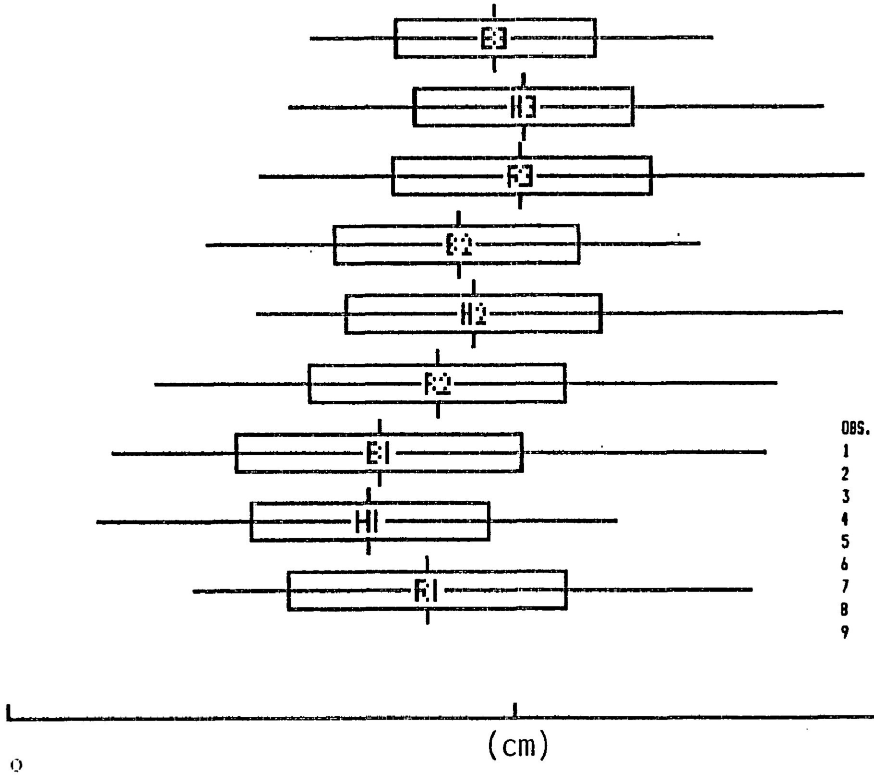
OBS.	MEAN	S.D.	MAX.	MIN.
1	59.8	31.88	143.9	13.5
2	50.74	24.42	105	5.5
3	53.75	30.2	126.1	6.5
4	82.65	46.18	243.8	13.5
5	100.05	54.22	234.5	26.1
6	92.12	43	229.5	19.1
7	209.21	109.65	450	31.2
8	212.35	101.16	492.7	54.9
9	204.93	88.32	363.8	52.6

Fig. 16b Hubbs' diagram of top dry weight of progeny grown in 33% light intensity (R1, H1, B1), 56% light intensity (R2, H2, B2), and 100% light intensity (R3, H3, B3) where R = random selection, H = height vs. age selection, and B = b.a.i. vs. c.a. selection.



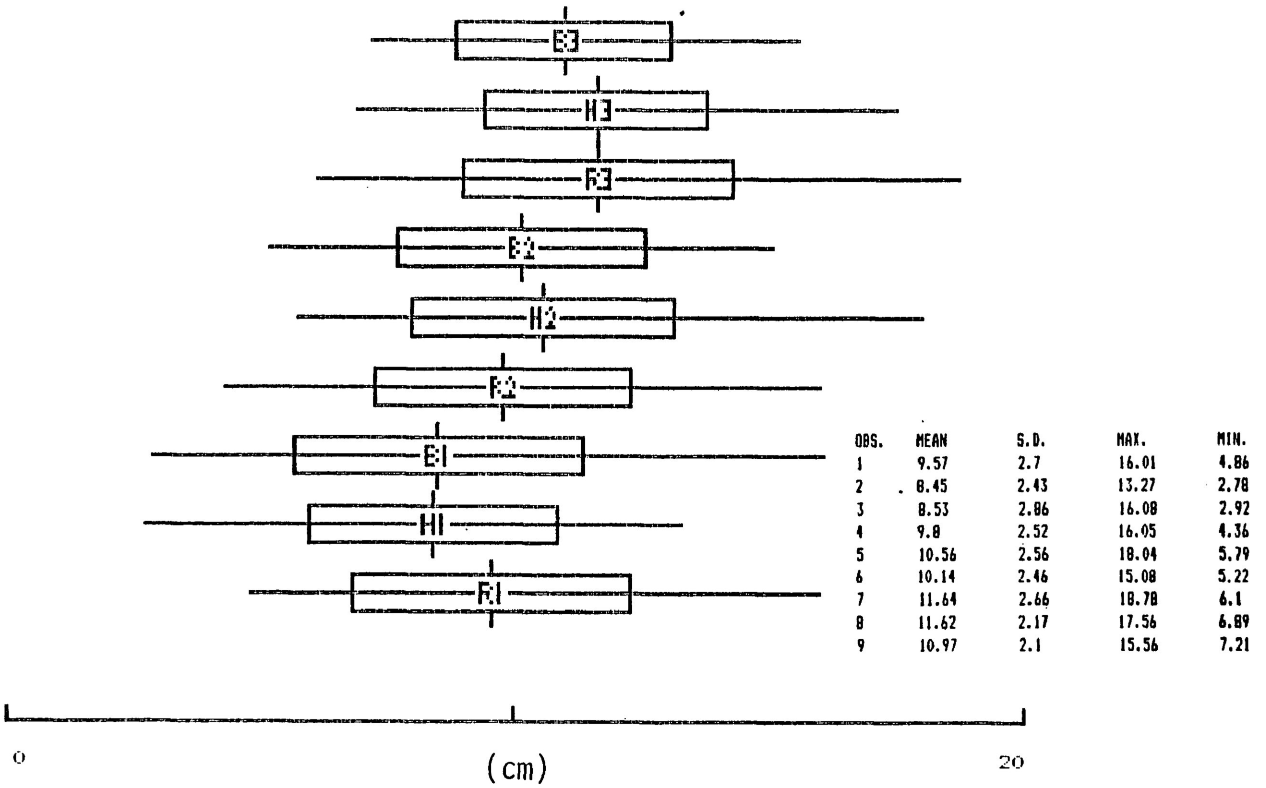
OBS.	MEAN	S.D.	MAX.	MIN.
1	72.69	37.78	178.1	17.6
2	60.95	27.61	124.1	7.5
3	64.46	35.78	156	10.7
4	98.49	53.83	289.9	15.6
5	117.84	63.38	287.3	28.5
6	109.7	50.2	252.9	23.6
7	252.89	131.77	541.7	37.4
8	256.25	122.5	607.5	66.1
9	246.7	104.7	434.8	61.5

Fig. 16c Hubbs' diagram of total dry weight of progeny grown in 33% light intensity (R1, H1, B1), 56% light intensity (R2, H2, B2), and 100% light intensity (R3, H3, B3) where R = random selection, H = height vs. age selection, and B = b.a.i. vs. c.a. selection.



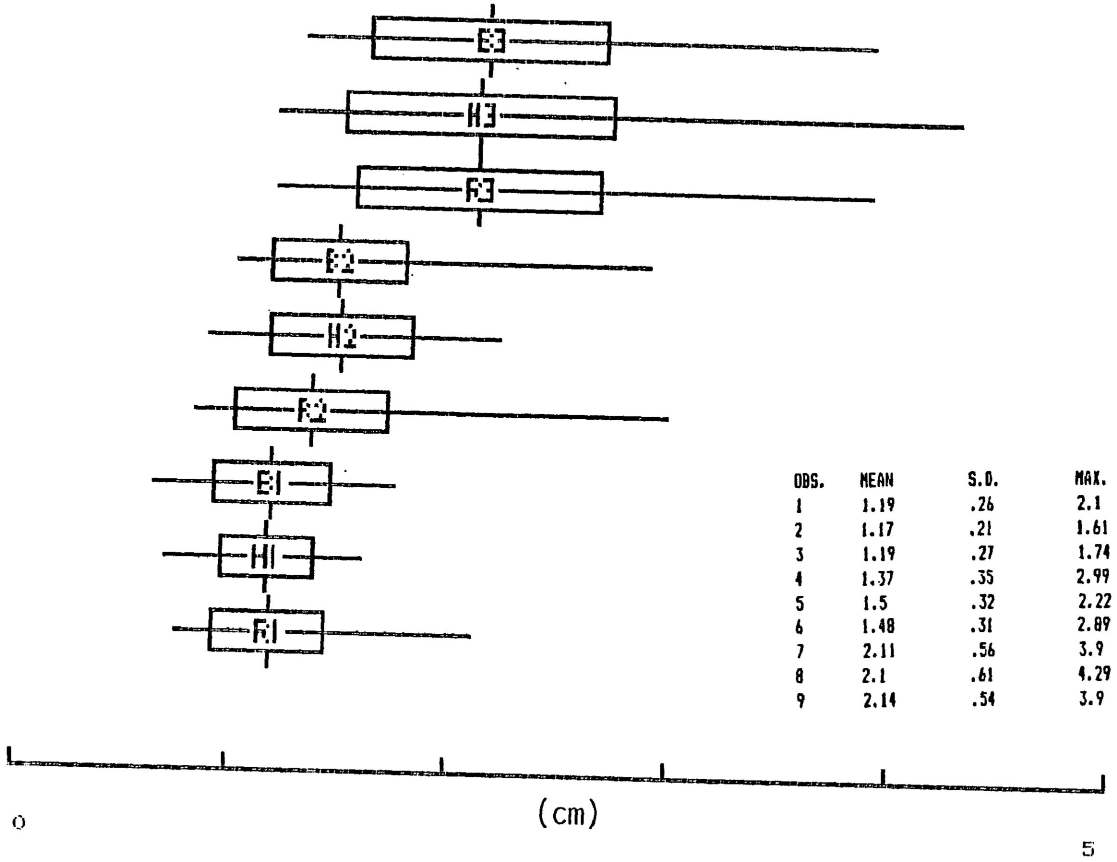
OBS.	MEAN	S.D.	MAX.	MIN.
1	8.28	2.72	14.67	3.68
2	7.16	2.35	12.01	1.83
3	7.33	2.78	14.92	2.14
4	8.52	2.5	15.18	2.94
5	9.21	2.54	16.48	4.98
6	8.9	2.4	13.67	3.99
7	10.16	2.55	16.89	5.04
8	10.21	2.17	16.06	5.63
9	9.67	1.97	13.95	6.08

Fig. 16d Hubbs' diagram of foliated length of progeny grown in 33% light intensity (R1, H1, B1), 56% light intensity (R2, H2, B2), and 100% light intensity (R3, H3, B3) where R = random selection, H = height vs. age selection, and B = b.a.i. vs. c.a. selection.



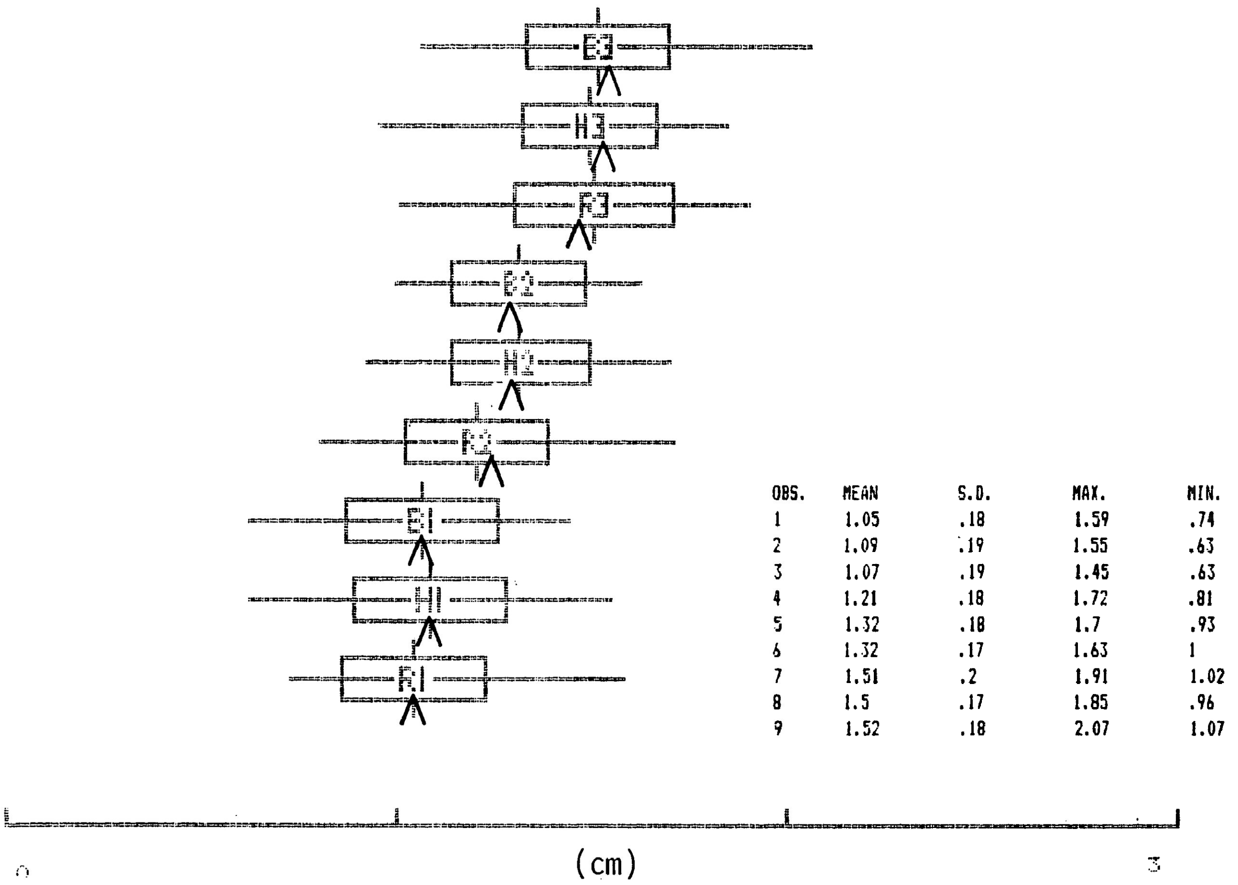
OBS.	MEAN	S.D.	MAX.	MIN.
1	9.57	2.7	16.01	4.86
2	8.45	2.43	13.27	2.78
3	8.53	2.86	16.08	2.92
4	9.8	2.52	16.05	4.36
5	10.56	2.56	18.04	5.79
6	10.14	2.46	15.08	5.22
7	11.64	2.66	18.78	6.1
8	11.62	2.17	17.56	6.89
9	10.97	2.1	15.56	7.21

Fig. 16e Hubbs' diagram of height of progeny grown in 33% light intensity (R1, H1, B1), 56% light intensity (R2, H2, B2), and 100% light intensity (R3, H3, B3) where R = random selection, H = height vs. age selection, and B = b.a.i. vs. c.a. selection.



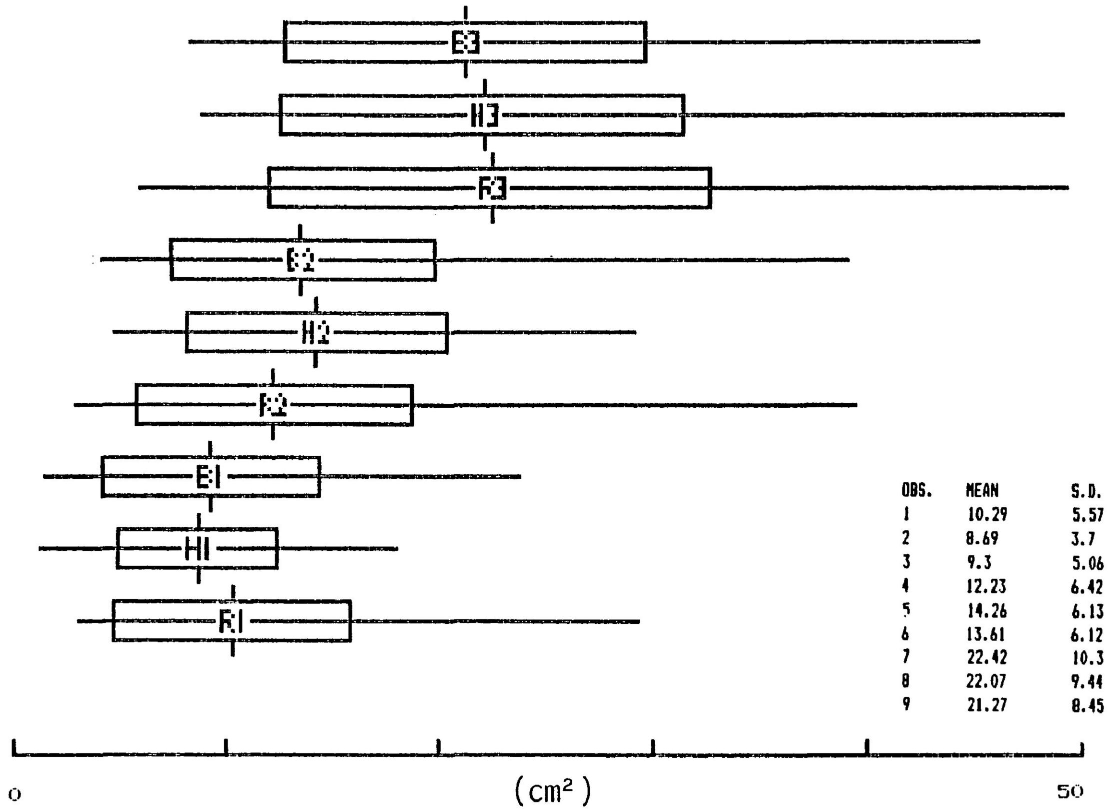
OBS.	MEAN	S.D.	MAX.	MIN.
1	1.19	.26	2.1	.76
2	1.17	.21	1.61	.7
3	1.19	.27	1.74	.66
4	1.37	.35	2.99	.83
5	1.5	.32	2.22	.89
6	1.48	.31	2.89	1.02
7	2.11	.56	3.9	1.19
8	2.1	.61	4.29	1.2
9	2.14	.54	3.9	1.32

Fig. 16f Hubbs' diagram of foliated width of progeny grown in 33% light intensity (R1, H1, B1), 56% light intensity (R2, H2, B2), and 100% light intensity (R3, H3, B3) where R = random selection, H = height vs. age selection, and B = b.a.i. vs. c.a. selection.



OBS.	MEAN	S.D.	MAX.	MIN.
1	1.05	.18	1.59	.74
2	1.09	.19	1.55	.63
3	1.07	.19	1.45	.63
4	1.21	.18	1.72	.81
5	1.32	.18	1.7	.93
6	1.32	.17	1.63	1
7	1.51	.2	1.91	1.02
8	1.5	.17	1.85	.96
9	1.52	.18	2.07	1.07

Fig. 16g Hubbs' diagram of needle length of progeny grown in 33% light intensity (R1, H1, B1), 56% light intensity (R2, H2, B2), and 100% light intensity (R3, H3, B3) where R = random selection, H = height vs. age selection, and B = b.a.i. vs. c.a. selection. (/\) indicates means adjusted for seed weight effects.



OBS.	MEAN	S.D.	MAX.	MIN.
1	10.29	5.57	29.23	3.08
2	8.69	3.7	17.96	1.29
3	9.3	5.06	23.83	1.47
4	12.23	6.42	39.44	2.89
5	14.26	6.13	29.12	4.73
6	13.61	6.12	39.23	4.19
7	22.42	10.3	49.36	5.98
8	22.07	9.44	49.12	8.89
9	21.27	8.45	45.17	9.3

Fig. 16h Hubbs' diagram of foliated area (fw x fl) of progeny grown in 33% light intensity (R1, H1, B1), 56% light intensity (R2, H2, B2), and 100% light intensity (R3, H3, B3), where R = random selection, H = height vs. age selection, and B = b.a.i. vs. c.a. selection.

The results from the nested ANOVA are presented for balance (Table 10) and unbalanced data sets (Table 11). The balanced data were artifically organized to follow a randomized complete block design to compare with work published by Stanton and Canavera (1983) (Table 12).

The balanced and unbalanced data sets produced similar trends, but analysis of the balanced data set seemed less sensitive, probably because the degrees of freedom for the error was reduced from 348 to 162 when the data was balanced in the nested factorial analysis. Nonetheless, both data sets showed family differences to be very strong for all characters in the nested factorial design, which supports our observations at harvest time.

The ANOVAs for the 4 month-old progeny showed selection method progeny differences were not significant for any character we measured regardless of the data set or the ANOVA approach (Tables 10-12). Plus-tree selection methods would appear to offer no advantage over random selection. Progeny from parents expressing superior growing space efficiency do not show superior growth when grown in an environment of equal growing space. Characters responsible for the parents' expression of superior growing space efficiency either show low heritability or have not yet been expressed in this juvenile stage of the progeny's development.

There was no selection method by light interaction. If greater growth under shade in mature stands is responsible for a tree's expression of superior growing space efficiency, then this trait either is not transmitted to progeny or is not manifested at the seedling stage. The ANOVAs (Tables 10 and 11a) do show a strong light by family interaction for total oven-dry weight which suggests tolerance is under some form of genetic

TABLE 10

NESTED FACTORIAL ANOVA (UNIQUE SUM OF SQUARES) FOR MARKS LAKE PROGENY

Source of Variation	Degrees of Freedom	Root O.D.W.	Top O.D.W.	Total O.D.W.	Foliated Length	Foliated Width	Foliated Area	Height	Needle Length
Light Blocks	2	No test due to restriction error							
Selection	2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
B x S	4	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Family/S	27	**	**	**	**	**	**	**	**
B x F/S	54	**	**	**	n.s.	*	n.s.	n.s.	n.s.
Error	348								
Total	437								
Selection with Seed weight removed as a covariant	2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*
Regression term in covariant	1	**	**	**	**	**	**	**	**

n.s. = not significant * = significant at $\alpha = 0.05$ ** = significant at $\alpha = 0.01$

TABLE 11a

NESTED FACTORIAL ANOVA (BALANCED DATA, SEQUENTIAL SUM OF SQUARES) FOR MARKS LAKE PROGENY

Source of Variation	Degrees of Freedom	CHARACTER F-RATIO TEST RESULTS							
		Root O.D.W.	Top O.D.W.	Total O.D.W.	Foliated Length	Foliated Width	Foliated Area	Height	Needle Length
Light Blocks	2	No test due to restriction error							
Selection	2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
B x S	4	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Family/S	24	**	**	**	**	*	*	**	**
B x F/S	48	*	**	*	n.s.	n.s.	n.s.	n.s.	n.s.
Error	162								
Total	242								
Selection with Seed Weight Removed as a Covariant	2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Regression term in covariant	1	*	*	*	*	*	*	*	*

n.s. = not significant   * = significant at $\alpha = 0.05$ ** = significant at $\alpha = 0.01$

TABLE 11b

ANOVA (BALANCED DATA) FOR MARKS LAKE PROGENY

TOTAL OVEN-DRY WEIGHT

Source of Variation	Degrees of Freedom	M.S.E.	Sig. of F.	Component of Total Variance
Light Blocks	2	949950.06		35%
Restriction Error	0			unknown
Selection	2	23.45	n.s.	0%
Light x Selection	4	2108.39	n.s.	0%
Families within Selection	24	14483.53	**	10%
Light x Families	48	8429.74	*	10%
Error	162	5109.03		45%
TOTAL	242			

n.s. = not significant

* = significant at $\alpha = 0.05$

** = significant at $\alpha = 0.01$

TABLE 11c

TOTAL OVEN-DRY WEIGHT (MG) FOR MARKS LAKE PROGENY

Family	Total Oven-Dry Weight (mg) for Marks Lake Progeny Grown Under Full Light Intensity	
10-6	459.1	A
9-127	416.3	A
9-116	397.3	AB
7-44	380.8	AB
5-32	376.6	AB
9-5	362.3	AB
9-11	317.5	AB
3-15	299.2	AB
3-19	296.3	AB
5-8	285.1	AB
1-4	283.5	AB
10-13	280.1	AB
9-105	278.5	AB
4-19	269.7	AB
3-7	265.7	AB
9-114	255.4	AB
6-23	252.0	AB
6-28	245.7	AB
9-100	239.5	AB
9-7	192.1	AB
4-21	181.2	AB
8-51	170.5	AB
8-6	139.1	AB
6-19	137.4	AB
6-38	134.5	AB
9-105	79.6	B

Note: Families with the same letter are not significantly different from one another ($\alpha = 0.05$ SNK test).

TABLE 12

COMPLETELY RANDOMIZED BLOCK DESIGN FOR MARKS LAKE PROGENY WITH FAMILIES AS EXPERIMENTAL UNITS (FROM BALANCED DATA)

Source of Variation	Degrees of Freedom	Root O.D.W.	Top O.D.W.	Total O.D.W.	Foliated Length	Foliated Width	Foliated Area	Height	Needle Length
Eight Blocks	2	No test due to restriction error							
Selection	2	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Error	85								
Total	89								

n.s. = not significant

* = significant at $\alpha = 0.05$

** = significant at $\alpha = 0.01$

control. Figure 17 graphically shows oven-dry weight by light interaction for three families. Families that grow best in the open do not grow best, relative to others, in the shade. I carefully examined the photocopies of the Marks Lake progeny. Family 5-8 exhibited superior growth in the shade while Family 9-11 showed superior growth in the full sun. I could not see distinctive features in needle shape or needle angle that could separate the two genotypes.

Table 11b shows the M.S.E. values for total oven-dry weights of the progeny and their components of variance. Oven-dry weight was one of the most important measures of growth, and its analysis is shown in detail. Other characters showed similar patterns. Selection method and selection by light interaction are not responsible for any measurable variance. Family and family x light effects contribute 10% to the total variance each. Light (blocks) and sampling variance (three trees per family) contribute 35% and 45% of the total variance, respectively. The high sampling variance (within-family variance) is a result of the high mortality. High sample variance may explain why light x family interactions were not detected for some characters but was detected for oven-dry weight. Fortunately, sample variance is not used to test for selection method differences. Selection differences are tested by family-within-selection method variance. The ratio of selection method variance to family variance is so small that it is unlikely that increased family number would sufficiently increase the power of the ANOVA test, hence increasing the chance of detecting differences between selection methods.

When families were considered the main effect, no significant differences between families could be detected within light treatment blocks

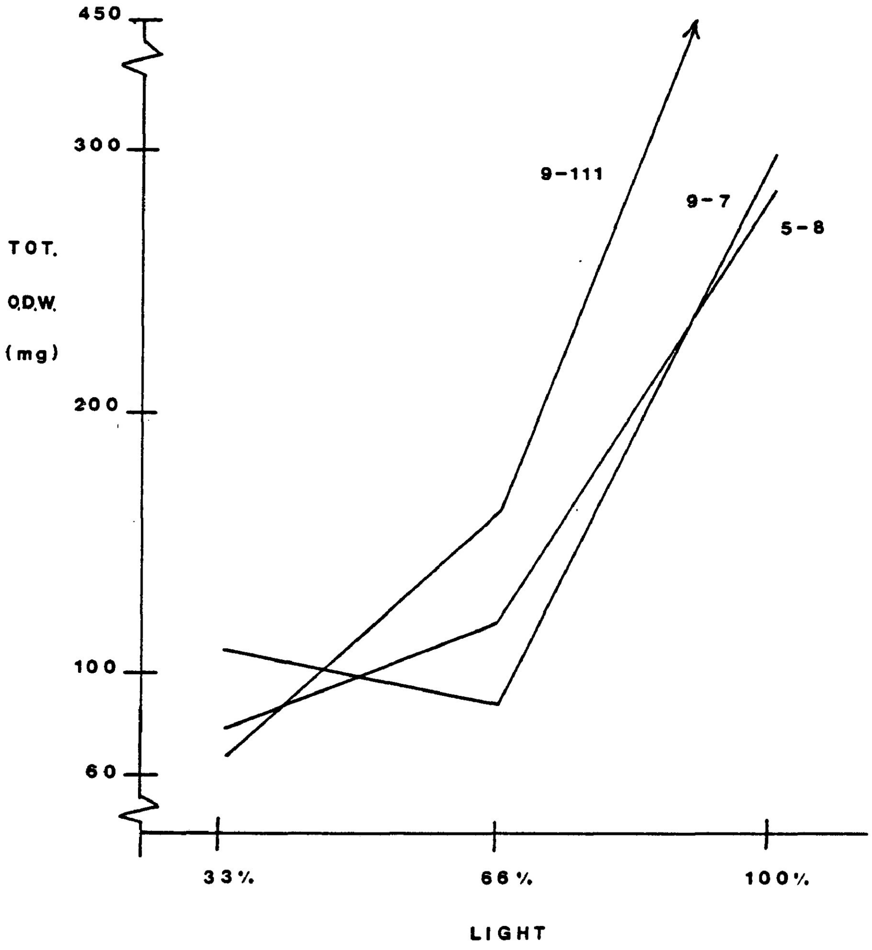


Fig. 17 Graph of total oven-dry weight (mg) x light interaction for 3 families (9-111, 9-7, 5-8)

except for the block with no shade. This is a direct result of the high sample variance. Table 11c shows total oven-dry weight of families ranked largest to smallest for the block with no shade. Letters indicate which families are not significantly different from one another (S.N.K. test).

The analysis of covariance that removed the effect of seed weight as a covariate did not detect a significant difference between selection methods with the exception of needle length data (Table 10). The regression term for seed weight was highly significant in the analysis of covariance (Tables 10 and 11a), but an examination of the effects of seed weight upon progeny performance within each block found the linear relationship to be quite weak. Table 13 shows the r^2 values for each regression. Light x seed weight interaction was found to be non-significant for total oven-dry weight. This pattern was assumed to hold for the other characters. For these reasons, seed weight effects may have contributed slightly to family differences but likely did not influence results concerning selection methods.

PARENT PROGENY CORRELATION

Table 14 shows parent character to progeny character correlations. The large number of negative progeny-versus-parent correlations and the erratic patterns of the correlation coefficients between light blocks suggests that the progeny are too young and the families too few to provide any trends or allow any generalizations concerning heritabilities. The hypothetical parent/progeny character parallels may be more fanciful than real.

TABLE 13

COEFFICIENT OF DETERMINATION (r^2) FOR SEEDLING CHARACTERS DEPENDENT UPON FAMILY MEAN SEED WEIGHT

Seedling Character	No Shade	55% Light Intensity	33% Light Intensity
Total Dry Weight (g)	0.13*	0.08	0.11
Foliated Length (cm)	0.10	0.05	0.09
Seedling Height (cm)	0.11	0.07	0.10
Foliated Width (cm)	0.12	0.05	0.10
Needle Length (cm)	0.24**	0.05	0.04
Foliated Area (1 x w) (cm^2)	0.15*	0.05	0.09

* = significance at $\alpha = 0.05$

** = significance at $\alpha = 0.01$

All others were not significant.

TABLE 14

PARENT VS. PROGENY CORRELATION COEFFICIENT (r) FOR VARIOUS CHARACTERS BY SELECTION METHOD AND BLOCK

	Progeny Height To Parent Height	Progeny Foliated Length to Parent Crown Length	Progeny Foliated Width to Parent Crown Radius	Progeny Foliated Area to Parent Crown Area	Progeny Total Oven-Dry Weight Per Unit Foliated Area to Parent BAI per unit CA
All Blocks					
Random	-.18	-.07	-.07	-.13	-.07
Ht vs Age	+.04	-.22	-.21	-.14	-.10
BAI vs CA	-.18	+.20	+.02	.08	-.25
Block 1 (Full Shade)					
Random	-.34	+.15	-.25	-.21	-.21
Ht vs Age	+.04	-.23	-.11	-.14	-.10
BAI vs CA	-.19	+.21	+.03	+.08	-.25
Block 2 (Medium Shade)					
Random	-.32	+.15	-.25	-.17	-.26
Ht vs Age	+.04	-.23	-.11	-.14	-.11
BAI vs CA	-.16	+2.0	+.02	-.08	-.25
Block 3 (No Shade)					
Random	-.16	-.42	-.11	-.12	.04
Ht vs Age	+.05	+.23	-.11	-.14	-.10
BAI vs CA	-.19	+.21	+.03	+.08	-.25

Note: All correlated coefficients were non-significant ($\alpha = 0.05$).

DISCRIMINANT ANALYSIS

Discriminant analysis was explored as a technique for developing new plus-tree selection criteria and methodology. The technique of discriminant analysis attempts to statistically distinguish between two or more groups by forming one or more linear combinations of the discriminating variables. Prior to analysis, three artificial progeny performance groups were identified including the tallest 10, median 9 and shortest 10. The discriminating variables were all the respective parent characters listed in Table 15. The analysis was done with an S.P.S.S. program (Norman, 1975) (see Appendix 8) which eliminated variables in a step-wise fashion if they did not contribute significantly (Wilkes Lambda test) to the discriminating function.

Two variables, crown length and the volume:c.r. ratio had the principal coefficients (canonical covariates) in both discriminant functions. The first function explained 69% of the group variance and the second function explained the remainer. These functions successfully classified progeny into the three height performance groups 60% of the time. Chi-square tests indicated that the predictive value of the two functions was low. Figure 18 is a scattergram of the standardized observations. The overlap of groups and the number of outliers supports the results of the chi-square test indicating that the functions and coefficients had low discriminating power for progeny performance.

The most important discriminating variable was crown length. Observations of the raw data show a weak trend where the shorter crowned parents tend to have the taller progeny (Table 15). Although the discriminant analysis results did not produce a strong progeny performance classification

TABLE 15

PROGENY HEIGHT GROWTH PERFORMANCE GROUPS AND ASSOCIATED PARENT CHARACTERS

Progeny Performance Group	Family	Mean Progeny Height (cm)	DBH (cm)	Height (m)	Parent Characters				Volume (m^3)	BAI/CA (cm^2/m^2)	Volume/CR (m^3/m^2)
					Crown Length (m)	Crown Radius (m)	Crown Area (m^2)	B.A.I. (cm^2)			
1	10-6	13.67	18.6	20.5	7.5	1.50	11.25	42.60	0.23	3.79	0.16
1	9-5	13.51	17.1	18.1	5.0	0.68	3.37	22.52	0.18	6.67	0.26
1	9-7	13.43	19.4	20.1	7.3	0.85	6.20	29.11	0.25	4.69	0.29
1	9-114	13.27	19.2	17.8	7.5	1.33	9.94	54.33	0.22	5.47	0.17
1	9-11	13.18	22.0	19.6	9.5	1.40	13.30	53.44	0.31	4.02	0.22
1	7-44	13.06	19.2	18.6	5.5	1.02	5.64	29.09	0.23	5.16	0.22
1	1-4	13.01	23.4	15.6	12.2	1.75	21.35	115.58	0.30	5.41	0.17
1	9-127	12.72	18.8	15.6	7.8	1.10	8.58	37.34	0.19	4.35	0.17
1	9-111	12.71	16.6	17.5	5.0	0.85	4.25	25.29	0.16	5.95	0.19
2	6-38	12.69	20.3	20.6	7.5	1.15	8.63	28.98	0.28	3.36	0.24
2	4-19	12.66	20.5	17.5	12.5	1.23	15.31	69.91	0.25	4.57	0.20
2	5-8	12.38	18.3	18.6	5.8	0.65	3.77	44.24	0.21	11.74	0.32
2	4-21	12.22	27.6	20.5	11.5	2.03	23.29	82.36	0.51	3.54	0.25
2	10-13	12.10	23.5	21.1	7.0	1.38	9.62	78.08	0.38	8.11	0.28
2	9-116	11.34	21.9	21.6	12.3	1.30	15.99	36.40	0.33	2.28	0.26
2	5-32	11.18	18.6	20.1	8.3	0.95	7.88	42.60	0.23	5.40	0.24
2	6-23	11.00	17.0	16.3	5.8	0.93	5.37	28.05	0.16	5.23	0.17
3	3-15	10.87	15.7	14.8	7.5	1.13	8.44	52.99	0.13	6.28	0.11
3	9-100	10.59	24.3	19.5	10.7	1.65	17.65	70.57	0.38	4.00	0.23
3	3-7	10.49	27.0	20.2	11.7	1.93	22.52	82.47	0.48	3.66	0.25
3	8-51	10.27	17.2	16.8	5.5	1.05	5.78	46.33	0.17	8.02	0.16
3	3-19	10.05	24.2	20.6	12.5	1.0	20.00	41.59	0.39	2.08	0.25
3	6-19	9.60	17.8	18.6	12.3	1.43	17.53	32.94	0.20	1.88	0.14
3	8-6	9.47	22.3	20.0	8.0	1.30	10.40	65.00	0.33	6.25	0.25
3	6-28	8.85	22.8	20.1	10.0	1.53	15.25	58.95	0.34	3.87	0.22
3	9-105	8.35	20.0	20.1	7.5	0.90	6.75	40.69	0.26	6.03	0.29

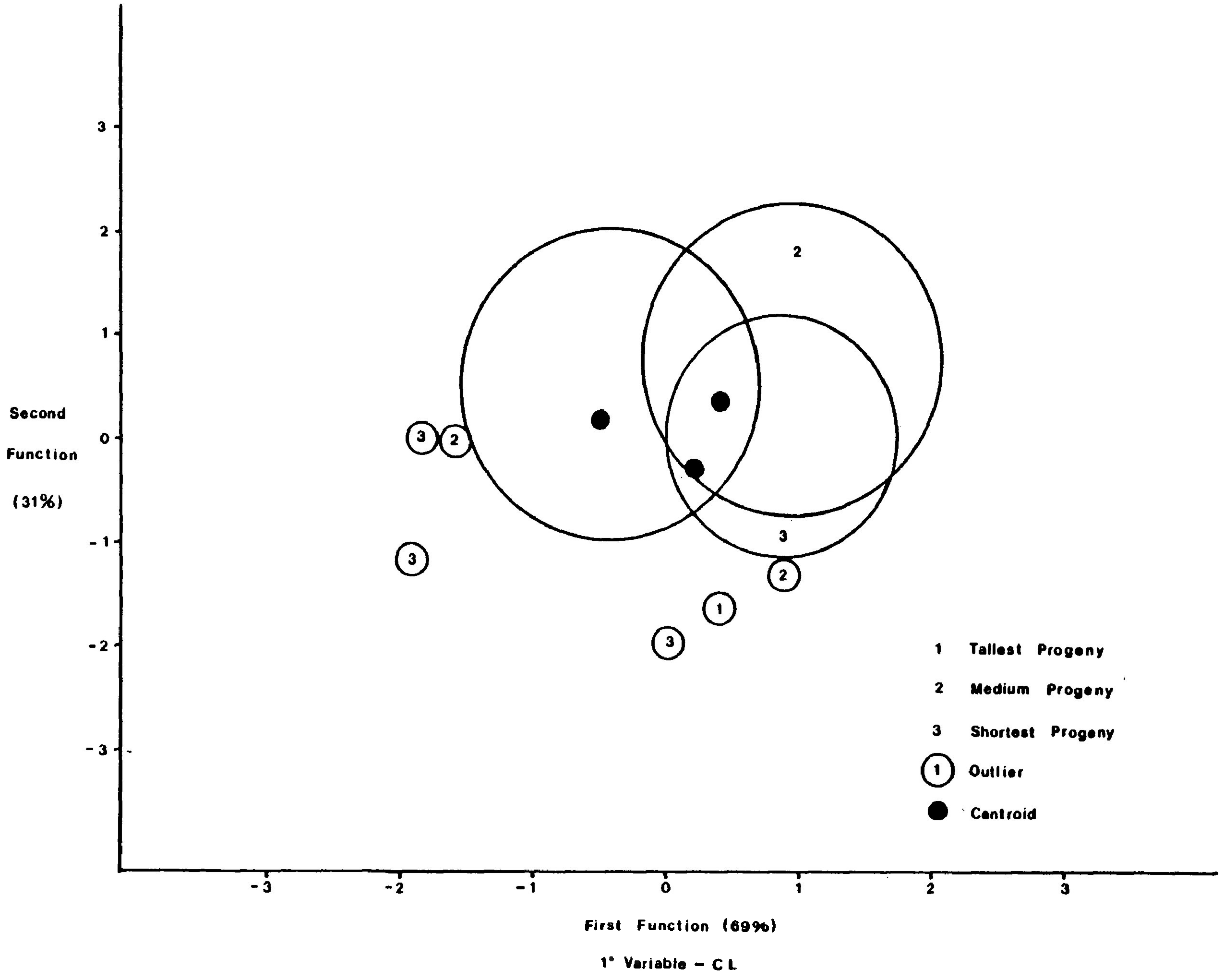


Fig. 18 Scattergram of discriminated functions with parent characters as variables for classifying 3 progeny height performance groups

function, they did help identify the weak trend of the parent crown length relationship to progeny performance.

DISCUSSION

THE RELATIONSHIP OF B.A.I. VS. C.A. AND THE IMPLICATIONS FOR PLUS-TREE SELECTION

The operational implication of plus-tree selection for growing space efficiency has relevance if progeny tests show the technique to be worthwhile. The functions that serve as the baseline for plus-tree selection influences the nature and extent of the field work. The strong relationship seen between b.a.i. and c.a. in this study (r^2 = 0.45 or 0.52) is expected because the crown produces the photosynthate necessary for cambial growth of the stem. Brown and Goddard (1961) and Thomas (1980) report a similar goodness-of-fit for b.a.i. vs. c.a. regression with an r^2 of 0.69 for 50 loblolly pine from a single stand and r^2 of .47 to .67 for approximately 100 western hemlock trees for each of 12 sites, respectively. The different r^2 values may reflect different sites, different sample numbers and/or different tree form that varies with shade tolerance and age. The three species have different adaptive features which will also influence the baseline function. Of the three species, western hemlock is the most tolerant, followed by black spruce and then loblolly pine (Harlow and Harrar, 1969).

The inequality of the b.a.i. vs. c.a. regression slopes calculated for the Matawin River and Marks Lake study areas is disappointing because a common regression line across sites would improve the efficiency of plus-tree selection field procedures. One set of tables showing the minimum b.a.i. for each crown size class could be used for identifying plus-trees regardless of stand structure, age, or site if the relationship between b.a.i. and c.a. was stable.

Thomas (1980) found similar b.a.i. vs. c.a. regression lines to exhibit different slopes across his 12 plots; however, he suspected this difference was due to age rather than edaphic differences. Trees from our two study areas were about the same age, but the soils and stand structures were quite different which suggests that edaphic and biotic factors influence the b.a.i. vs. c.a. relationship.

Thomas (1980) corrected each plot regression line by substracting the grand mean from plot adjusted means and adding this value to each observation. The adjusted values were pooled and a new regression was run. This common baseline selected essentially the same plus-trees that were obtained by separate plot regressions. Even if the relationship of b.a.i. vs. c.a. does change across sites, Thomas' work suggests the construction of harmonized lines would be possible for black spruce from a large enough sample.

The most difficult and most subjective crown measure was crown radius, but the strong correlation between crown area and crown length ($r^2 = 0.75$ in Matawin River area and $r^2 = 0.83$ in Marks Lake area) suggests that a baseline of b.a.i. upon crown length may be adequate for plus-tree selection for growing space efficiency. Crown radius is also highly correlated with crown area ($r^2 = 0.69$ and 0.78) and could serve as a criterion for plus-tree selection as well. The strong correlation of d.b.h. upon b.a.i. suggests further simplification of field measurements is possible. For example, a regression of d.b.h. upon crown length might prove adequate as a baseline for plus-tree selection providing that long-term progeny trials find plus-tree selection for growing space efficiency to be practical.

Low level aerial photographs could be used to improve estimates of crown area. Thomas (1980) found this technique to be quite effective with the tall (30m+) western hemlock, but the application of this technique in black spruce stands would be limited because identifying the subject tree in the typically dense canopy would be very difficult. Our strong r^2 values indicate ground estimates of crown parameters are adequate.

Crown configuration can be expressed in terms other than the crown length x radius value. Both crown volume and crown surface area can be determined from the crown length and radius. Volumes or surface areas of the crowns can be calculated if the crowns are considered as cones, cylinders or parabolae, whichever shape best describes the shape of the crowns. The formulae for describing the surface area of cones and parabolae involve the multiplication of a constant applied to the crown length:radius ratio, if that ratio is greater than 1 (Dale, 1962). Since black spruce nearly always has a crown length:radius ratio greater than 1, the constant applied to the crown length radius would not significantly alter the relationship between crown area index and b.a.i. because only the scale would be changed. If crown volumes are estimated, one crown parameter would be squared and this exponential increase may turn a linear relationship into a curvilinear one. Brown and Goddard (1961) found that exponential increases in the crown parameters reduced the coefficient of determination ($r^2 = 0.59$) by 10% compared with the regression of crown length x radius on b.a.i. ($r^2 = 0.69$).

THE IDENTIFICATION OF CROP IDEOTYPES

The candidate plus-tree crown parameters from the Marks Lake area were examined to see if a crop ideotype could be generalized for trees with superior growing space efficiency. Student-Newman-Kuel (S.N.K.) tests (Steel and Torrie, 1981), Hubbs' diagrams and the scaled diagrams did not help identify crop ideotypes associated with a plus-tree selection method. Trees selected for growing space efficiency typically did not have the long narrow crown recommended by Farmer (1978) and Cannell (1978).

Harper (1977) suggests that crown structure may explain observed interspecific differences in growing space efficiency. When the log (10) mean tree volume was plotted against log (10) stand density for commercial western conifers and hardwoods from yield table data, the linear functions showed similar slopes yet different y-intercepts for each species (Fig. 1). The homogeneous slopes ranged from -1.7 to -1.8, somewhat steeper than the -1.5 slope described by many authors for log (10) mean plant weight vs. log (10) plant density. The consistency with which all species in pure stands conform to the -1.5 slope of the log weight vs. log density function has resulted in the function being called to the law of final constant yield or the 3/2 law. Species, such as noble fir, with superior growing space efficiency or higher mean tree volume at any given density than other species, have larger y-intercepts than other species (Fig. 19). Harper (1977) suggested that the distinctly pyramidal shape of the Noble fir crowns might be responsible for superior growing space efficiency when compared to the broadly pyramidal crown of the western hemblock or the round crowns of the hardwoods. Perhaps a pyramidal crown would be a black spruce crop ideotype. Could some crown shapes have less light extinction within the canopies than other shapes allowing more available energy for tree growth? Harper (1977) points out that the measurement of light extinction within the crown is technically difficult and nearly impossible to relate to crown shape because foliage morphology, density, orientations, and the tree's position in the stand will contribute to light extinction.

Yield table data for the major boreal species were compared with Harper's observations of western species. Figure 20 is a plot on log paper of mean tree volume vs. density for the major boreal species for site class 1 from Plonski's (1974) normal yield tables. The resultant linear functions are nearly identical to the ones described by Harper (Fig. 19). The larger volumes/ha achieved by jack pine and poplar are explained by the length of the line defined by the 3/2 law. At maturity the less tolerant jack pine and poplar hold a high volume in a few stems while black spruce stands remain quite dense with lower volumes/tree. Black spruce shows the greatest y-intercept and hence expresses superior growing space efficiency. Black spruce has a long narrow crown while jack pine has a broadly pyramidal crown and poplar has a large round crown. This observation supports the long narrow crown pulpwood crop ideotype theory described by Farmer (1978), but one may not be able to detect intraspecific variation in spruce crown shape.

The dashed line in Figure 20 shows the hypothetical gains possible if black spruce tree improvement efforts were aimed at increasing growing space efficiency. The selection differential required to achieve this hypothetical gain of 0.013 m^3 of wood volume per m crown radius with an assumed heritability of 0.20 would be 0.045 m^3 volume per m crown radius.

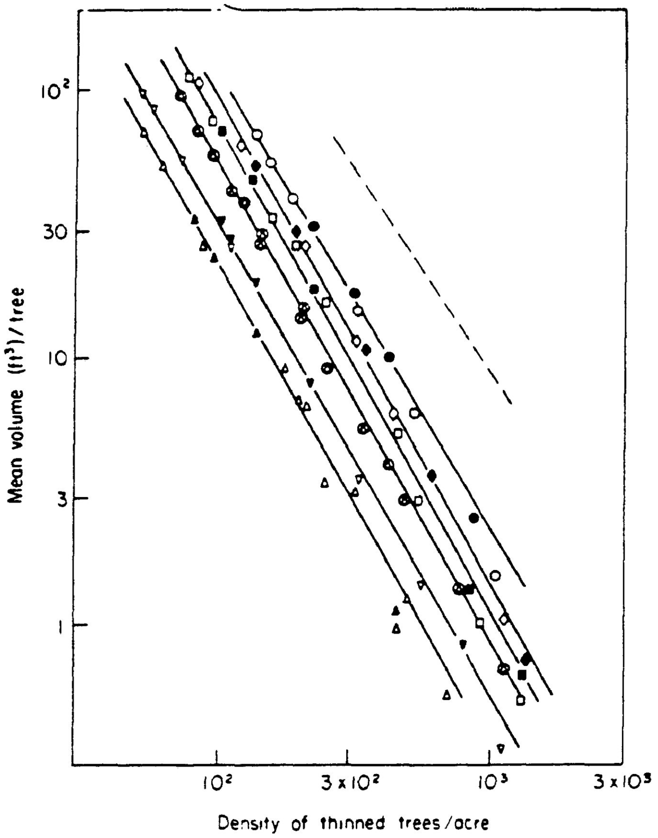


Fig. 19 The relationship between the density of trees and their mean volume in fully stocked stands up to 100 years after planting. Calculated from data in Forest Management Tables (Bradley et al., 1966). For each species two or three sets of yield class data (Y.C.) are given - these represent sites of different yielding ability. Noble fir, Y.C.240(○); Y.C.160(●); western hemlock, Y.C.260(◇); Y.C.180(◆): Sitka spruce, Y.C.260(□), Y.C.200(■): Scots pine, Y.C.160(△), Y.C.100(▲): European larch, Y.C.140(▽), Y.C.80(▼): sycamore/ash/birch (joint tables), Y.C.120(▽), Y.C.80(▼). The data for the separate yield classes lie along common thinning lines, whose gradients range from -1.72 to -1.82. A slope gradient -1.5 is shown at right for comparison. (From White and Harper, 1970)

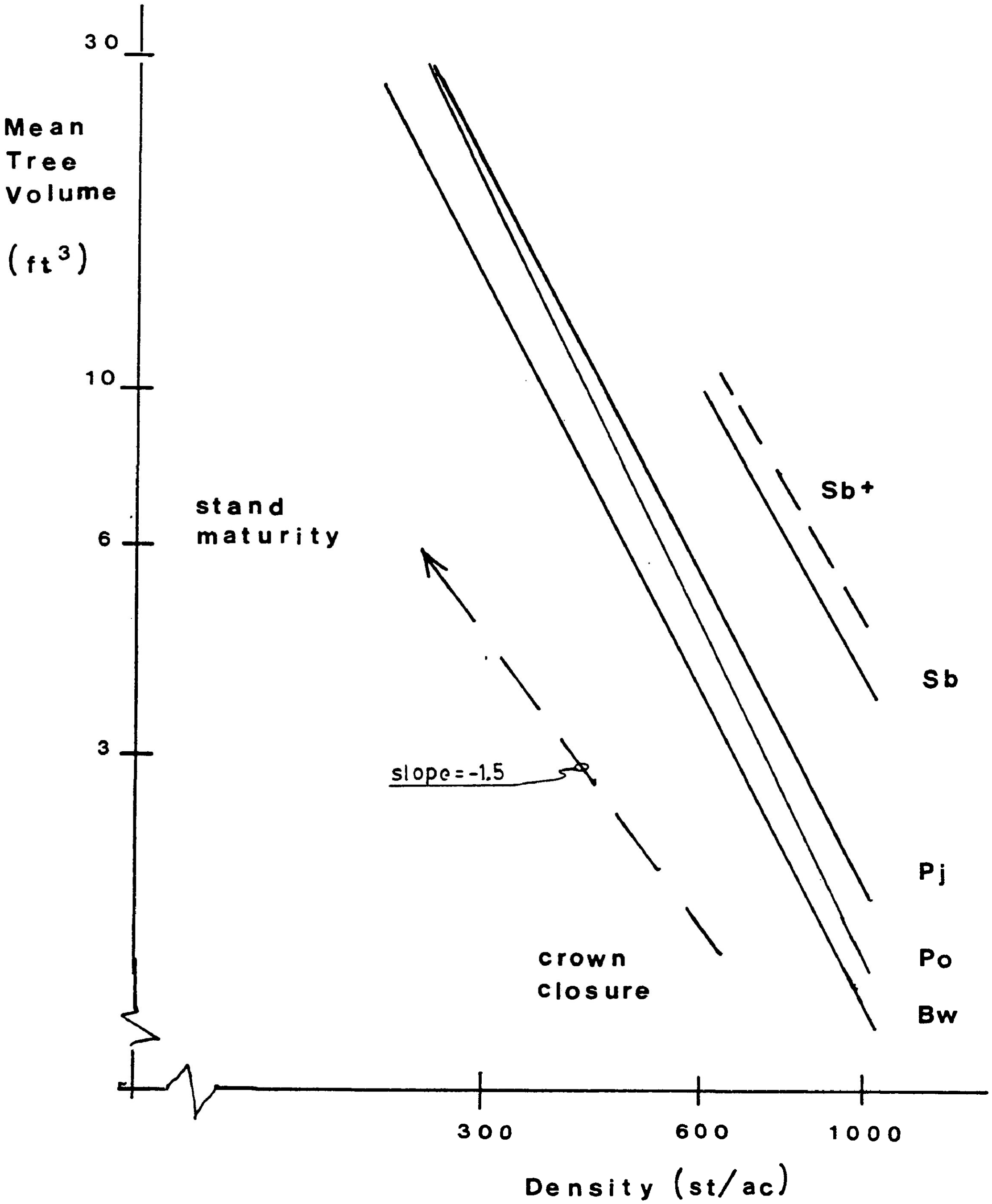


Fig. 20 The relationship between density of boreal tree species and their mean volume. Calculated from Plonski's (1974) yield class tables for site class 1 for black spruce (Sb.), jack pine (Pj.), poplar (Po.) and white birch (Bw.) The dashed line marked Sb.+ shows the possible results from plus-tree selection efforts toward improving growing space efficiency.

The hypothetical superior trees within a normal stand of mean tree volumes of 0.11 m^3 and 1 m crown radii would have average volumes of 0.18 m^3 for the same crown sizes.

Baskerville (1965) sampled 101 trees of *Abies balsamea*, 14 of *Picea glauca* and 24 of *Betula papyrifera* across six plots within a forty year-old natural stand. The density ranged from 1,700 stems/ha to 12,000 stems/ha across the six plots. Stem, branch and foliage analysis showed the smaller crowned trees were more efficient in producing wood/foliage dry weight than the larger crowns. Dense stands of small crowned trees had the greatest volume yield/ha for *Abies balsamea*. Although the less tolerant *Betula papyrifera* shows the same pattern of greater efficiency with smaller crowns, it fails to stock itself adequately to give high yields per hectare. *Picea glauca*, intermediate in tolerance, expressed intermediate characters. The *Abies balsamea* crop ideotype would appear to have a small compact crown. Baskerville (1965) proposed that the efficiency of smaller crowns could be related to tree forms with small crown areas that have more numerous shade-needles than the larger crowned trees. Shade-needles are best adapted to low light intensities by virtue of physiology (Tucker and Emmingham, 1977; Dengler, 1980; McClendon and McMillan, 1982). Perhaps conifer crop ideotypes will have small crowns or will have morphologically distinct needles.

Identification of a crop ideotype is complicated by genotype x environment interactions. Cannell (1978) recommends that plus-trees that show optimum crown form plasticity with ontogeny may result in increased yield/ha. A genotype that can develop a tall broad crown to capture the site (isolation ideotype) and with age develop a long slender crown after the plantation achieves crown closure (crop ideotype) should be developed through tree breeding programs. If breeding a plastic isolation/crop ideotype (Cannell, 1978) is not possible, genotypic mixes of crop and isolation ideotypes may be an alternative.

Cannell (1982) found significant family (genotype) x spacing interaction for ten open-pollinated *Picea sitchensis* (Bong.) Carr. progeny and two provenances that were assessed for height and volume across two spacing intervals (0.14 m and 1.40 m) after 4-6 years growth. He suggested that if family selection occurred too early in the plantation's development, crop ideotypes would be rogued out and productivity losses would result after crown closure. Franklin's (1979) work on juvenile-mature correlations also supported this conclusion.

The selection of crop ideotypes with distinctive crown shapes from wild stands will be confounded by the variation in growing space which at least influences crown size and probably influences crown shape. The irregular growing space in wild stands may explain why distinctive crown shapes were not found that corresponded to superior growing space efficiency. It is possible that identification of crop ideotypes is most efficient in spruce plantations with fixed spacing.

THE USE OF MULTIVARIATE STATISTICS IN TREE IMPROVEMENT

Discriminant analysis of the Marks Lake population showed that the taller black spruce progeny came from short-crowned parents. Perhaps short, compact crowns are a black spruce crop ideotype. This would agree with Baskerville's (1965) observations on the relative efficiency of balsam fir with small, compact crowns.

When the entire Marks Lake sample of subject trees was ranked from the largest to the smallest ratio of b.a.i./c.a. and similarly ranked for vol./c.r., the trees with the smaller crowns had the largest ratios although the volume or b.a.i. was not very high for these trees. Many of the trees ranked in the top 20 for both ratios were included in the parent groups with the highest positive residuals for ln (b.a.i.) vs. ln (c.a.) and ln (vol.) vs. ln (c.v.) regressions, respectively. It appeared that the untransformed regressions were biased somewhat toward larger crowned trees because of heteroscedasticity. Larger crowned trees tended to have lower b.a.i. to c.a. ratios.

Multivariate statistical technique could find broad applications in tree improvement, especially with indirect selection. Progeny of proven performance could be used to "back-track" with multivariate statistics to identify parent characters that showed a relationship to progeny success.

MARKS LAKE PROGENY TRIAL: SELECTION METHOD DIFFERENCES

A fundamental problem with plus-tree selection is isolating environmental from genetic effects that contribute to superior phenotypic expression. The b.a.i. vs. c.a. method of selection was expected to reduce the chances of selecting inferior genotypes with superior phenotypic expression because of chance competitive advantages such as luxurious space. Competitive advantage was felt to be a major disadvantage of the height vs. age selection method. Progeny test results indicate that b.a.i. vs. c.a. selection is no more effective in this regard than the height vs. age selection method.

The ANOVAs of progeny growth data showed no significant differences between selection methods. Open-pollinated progeny from parents that expressed superior growing space efficiency did not express superior growth traits when grown in uniform spacing.

Selection methods contributed 0% to the total variation for total oven-dry weight. Families contributed 10% as did family vs. light interaction. The most significant variance components were within-family variance and between light block variance, 45% and 35%, respectively (Table 11b). An adequate family number was present to test for the selection method differences. The high mortality from damping-off reduced the within family sample from 10 to 3 individuals which may help explain the high within-family variance. Other characters showed the same patterns as total oven-dry weight.

Similar to this work, Stanton and Canavera (1983) tested four plus-tree selection methods across two stands that included the b.a.i. vs. c.a. method along with a random control for their effectiveness on improving white birch (*Betula papyrifera*) volume growth. Although ANOVA of 1 year heights of progeny growth under greenhouse conditions showed significant differences between the selection methods, none of the progeny means associated with the selection methods were significantly different from the control. They also found significant differences in progeny height associated with stand origin; however, variation among families was not significant by their methodology.

The significance of Stanton and Canavera's (1983) results are difficult to interpret due to experimental design limitations. Stanton and Canavera's randomized complete block design with subsampling probably will not properly evaluate family differences. Perhaps they used multiple range tests to detect the lack of difference in height between families.

The family x selection interaction source of variation in Stanton and Canavera's (1983) design is invalid since families are necessarily considered nested within selection method (Table 1).

To allow direct comparison to Stanton and Canavera's (1983) work and to explore the impact of their experimental design upon the results, the Marks Lake progeny were analyzed as a simple randomized complete block design. Experimental units were represented by family means from the Marks Lake balanced data set. No significant differences between selection methods were found in the modified ANOVAs for any of the Marks Lake progeny characters. Thus, Stanton and Canavera's indication of differences between selection methods, although not significantly different from random selection, were stronger than those I found for black spruce.

The Marks Lake progeny results imply that characters responsible for growing space efficiency are not heritable or have not yet expressed themselves. If the trend of progeny growth continues then the results may also be interpreted to show that the b.a.i. versus c.a. method is insufficient for identifying parents that express superior growing space efficiency. It must be emphasized that one year progeny growth results do not carry much weight.

Differences between selection method groups of progeny may have been reduced because of the small selection differential of the parent population. The selection differential was reduced because many of the plus-trees selected by the b.a.i. vs. c.a. and random methods did not have enough cones for the progeny test. Although a T-test could not detect differences between the theoretically superior and random trees and the trees actually used in the experiment, the lower selection differential may have compromised the progeny trial's ability to detect differences between selection method groups.

Variation in Marks Lake parent tree growth is likely influenced by microsite differences within the study area. Figure 2 and the detailed soil pit descriptions in Appendix 1 indicate substantial variation in soil features are present across the study area. The confounding effects of soil quality on phenotypic expression severely limits the application of plus-tree selection on this site and many other boreal sites where soil heterogeneity is a problem. It is unfortunate that the seed from the Matawin population was destroyed because the soils were homogeneous within most of the study area and were less likely to confound the experimental results.

Few workable alternatives for mass-selection for growing space efficiency exist if the long-term progeny trials show that b.a.i. vs. c.a. method is an insufficient measure of growing space efficiency. Competition indices have not yet been developed which predict subject tree growth with consistency. Thus, the difficulties associated with the definition and measurement of growing space may render the concept of selection for growing space efficiency impractical from wild stands.

LIGHT EFFECTS ON MARKS LAKE PROGENY GROWTH

Most black spruce reforestation efforts with improved growing stock will be on productive upland sites in Northwestern Ontario. Thus, nutrients and moisture should not be limiting factors. Tree improvement should be toward growing space efficiency because light probably is the important limiting resource on these sites (Harper, 1977; Johnston et al., 1969;

Stiell, 1970; Eriksen & Whitney, 1981; Eriksen & Nilsen, 1982). Progeny were grown under different light intensities to explore its influence on selection for growing space efficiency.

Differences in progeny growth associated with light level were easy to observe. Best overall growth was in the unshaded block. In contrast, seedlings of some tree species such as Douglas Fir (*Pseudotsuga menziesii* (Mirb.) Franco.) grow best in medium shade levels (Drew and Ferrell, 1977).

If superior growing space efficiency is linked to shade tolerance within a mature forest canopy, then the progeny selected by b.a.i. vs. c.a. method might outperform the other two groups under shaded conditions. The ANOVAs of progeny growth data did not detect significant light by selection method interaction. Thus, progeny from parents expressing superior growing space efficiency do not perform better under shaded conditions than progeny from trees selected by other methods.

The first year Marks Lake progeny dry weights show a strong light x family interaction but this is not the case for progeny height or foliar measurements. If growing space efficiency is linked to tolerance mechanisms the b.a.i. vs. c.a. method fails to select the appropriate superior genotype, although the four-month growth period in this study is not adequate to be conclusive. Genotype x environment interactions are common and many report genotype x light interactions (Bourdaue, 1963; Townsend et al., 1972; Johnston, 1969).

The family x light interaction on the Marks Lake progeny does provide an opportunity for research into improving yield with plantation mixtures of genotypes that show competitive ability. Family 5-8 grows better in the shade relative to other families while 9-111 grows much better than

5-8 in a shade-free environment. Perhaps mixtures of these families planted at a variety of spacing intervals will show positive competitive ability because they can exploit different light intensities.

Adams' et al. (1973) review of agricultural literature showed that impressive gains in yield are possible when crops are grown in genotypic mixtures that express high levels of positive competitive ability (see Sakai, 1955; Shutz and Brim, 1967; Weibe et al., 1963; Khan et al., 1975; Trenbath, 1974). Competitive ability is similar to genotype x genotype interaction and is usually expressed as the difference in performance between mixed and pure plantations. The response can be negative (see Lee, 1960), positive or neutral. Positive competitive ability implies that plantation mixtures exceed monoculture yields, neutral competitive ability results in mixtures showing intermediate yields compared to monocultures, and negative competitive ability results in mixtures giving less yield than monocultures.

Tauer (1975) reports positive competitive ability for a pair of *Populus trichocaipa* Torr. and Gray clones. Adams et al. (1973) found positive competitive ability among four loblolly pine family combinations and negative competitive ability among two different family combinations.

The magnitude and direction of competitive ability changes with the character measured and across sites. Shutz and Brim (1971) and Trenbath (1974) indicate that plantations of genotype mixtures express greater stability across sites than plantations of pure lines. It is not known whether or not these genotypic mixtures were comprised of crop and isolation ideotypes with distinctive morphological features such as the broad and narrow tree crown forms described by Cannell (1978).

Isebrands (1984) has shown that poplar clones showed distinct differences in crown architecture when planted under various spacings in pure and mixed plantations. Preliminary field studies have shown that poplars can be selected for optimum spacing regimes on the basis of crown architecture. Two clones, NE-1 (*P. nigra x P. latifolia*), and NE-387 (*R. Condicars x P. CV. berolinensis*) were chosen to represent two distinct crown types. NE-1 has a narrow crown with acute branch angles and NE-387 has a wide crown with horizontal branch angles. Average yield for 1:1 clone moistures were halfway between the higher yielding NE-387 or the lower yielding NE-1 pure plantation yields. In other words, the clones express neutral competitive ability. The ratio of mixed to pure plantation yields decreased with smaller spacing intervals, indicating that spacing may be an important factor in designing plantations of clonal mixtures.

It is unlikely that genotypic mixtures of black spruce expressing positive competitive ability can be designed based on crown shape. Black spruce phenotypes express little variation in form and branch angle (Morgenstern, 1975). As discussed previously, the large variation in black spruce crown length and radius seen in this study is probably a reflection of the variation in tree growing space within the natural stand.

The family versus light interaction found in this study might imply that crop and isolation ideotypes are distinguishing themselves independent of selection method. If the b.a.i. vs. c.a. selection method identifies both crop and isolation ideotypes, and if these traits are heritable, the progeny variance will be large, and the ability to detect selection method differences will be weakened. Examination of the variation within the selection methods (Table 15 and Figures 16a-h) does not support this hypothesis. The patterns of variation do not show progeny of b.a.i. vs. c.a. and random selected trees to be more variable than the progeny selected by height vs. age. The height vs. age progeny would be least variable if only isolation ideotypes were chosen by this method. To see differences between the random and b.a.i. vs. c.a. selected parent's progeny may require a larger number of replicates than the three progeny for the balanced design and the five progeny for the unbalanced design used in this experiment. Family number might have to be substantially increased as well.

FAMILY DIFFERENCES AND THE INFLUENCE OF SEED WEIGHT

Family differences among Marks Lake progeny for all characters within light treatments were found by the nested ANOVA. This is contrary to Stanton and Canavera's (1983) findings for white birch (*Betula papyrifera*). The large sample variance from seedling mortality reduced the ability to detect differences between families when they were examined as main effects within each light treatment. The family means shown in Table 11c do not warrant a high level of confidence because the sample variance is so large. Strong family differences in seed weight were apparent (Tables 7 and 8). Perhaps the family differences in progeny growth may be a result of the maternal effects of seed weight. Analysis of covariance shows the regression term for seed weight across all blocks to be highly significant for all characters (Tables 10 and 11) but progeny vs. seed weight regressions within each block were non-significant or very weak (Table 13). The insignificant regression may also be a reflection of the large sample variance.

Most literature indicates that early progeny performance is strongly influenced by seed weight (Burgor, 1964; Lavender, 1958; Youngberg, 1952;

Harif, 1977; Wang, 1969; Musalem, 1975; Logan and Pollard, 1981). But Dorman (1976) found no correlation between seed weight and seedling performance for loblolly pine. For these reasons seed from the Matawin and Marks Lake area was weighed and analyzed. Many researchers report large intraspecific differences in seed weight between provenances, stands, and individual trees (Birot, 1978; Rubanik and Parshina, 1978; Paci, 1978; and Wang, 1979). Seed from the Matawin study area was significantly heavier than seed from the Marks Lake study area, but both areas expressed strong family differences (Tables 12 and 13).

Sorensen (1977) found significant differences in seed weight between *Abies procera* seed collection years as well as year by source and year by tree within source interaction. Perhaps different season effects may result in some seed crops being heavier in the Marks Lake area than in the Matawin River area from year to year, but seed used in this study was from the same cone crop year.

Youngberg (1952) found seed weight to be significantly affected by soil fertility. The higher cation exchange capacity of the Matawin River area clay soils will have more available nutrients than the fine sands of the Marks Lake area (Pritchett, 1979). The different stocking between the two sites probably has less impact on the seed weight than soil fertility (see Barnes, 1969). Perhaps the family seed weight differences indicated substantial microsite fertility differences from tree to tree. The Marks Lake soil pit observations support this possibility, but more detailed soil surveys and analyses are required. If soil fertility differences between trees in a stand are high, plus-tree selections will be confounded by soil fertility advantages, and single-tree selections of superior genotypes is made much more difficult.

The lack of correlation between parent tree size and vigour with seed weight in this study (Table 14) suggests that seed weight may be under independent genetic control. Nogaev (1977) did not find correlations between *Larix siberica* seed weight and gross tree morphology except for d.b.h. Seed weight and number of *Larix sukaczewii* seed were positively correlated to parent tree height and diameter (Voichal and Barabin, 1980), but seed weight was not correlated to parent growth for white spruce (*Picea glauca* (Moench) Voss.) (Khalil, 1981). Agricultural researchers found wheat grain size to be under strong genetic control. The wheat grain was found to act as a strong photosynthate sink which always led to a corresponding gain in vegetative mass when the ears were cut in half or pruned (Martinez, Serrasco and Thorne, 1979; Bingham, 1967; Austin et al., 1977).

Salisbury (1942) and Baker (1972) have examined the adaptive value of seed size. They suggest that moisture and competition are strong selection pressures across successional stages which will lead to genetic variation of plant seed weight. Levin points out that compromises between greater seed dispersal and different energy storage capacities will lead to the evolution of seeds with different lipid contents. Lipids are the primary energy source for the germinating seed. Levin (1974) also found seed weight to be an independent character from lipid content unless taxa were grouped by plant type. For example, trees have both large seeds and high lipid contents compared to annual plants. The work of the ecologists and the success of tree nut and fruit cultivation suggest that strong genetic control of seed weight independent of tree growth is quite probable.

The weak correlation found between progeny performance and seed weight may be a result of an inadequate sample number and high variances within each block. Seed weight effects might have been confounded with germination capacity and germination energy caused by differences in Spencer-Lamier cavity microenvironment or other environmental differences. If seeds had been stratified or received other pre-germination treatments, germination variation might have been reduced. Perhaps lipid content variation (Levin, 1974) is more important than seed weight for black spruce seedling development. Large variances may have resulted from using 10 seeds per weighted seed lot. The seed is very light and perhaps 10 seeds per seed lot is too small or five seed lots/family may be inadequate. Khalil (1981) found seed weight was strongly correlated to white spruce seedling performance when he used 1,000 seeds per lot for weight measurements.

Needle length and seed weight were highly correlated. When the variance resulting from seed weight was removed in the covariance analysis the only progeny character that showed a significant difference between selection methods (unbalanced data) was needle length. Generally, plus-tree progeny have longer needles than the random progeny when needle length is adjusted for seed weight; this is a very weak trend (Fig. 16d). This effect was very weak since no differences between selection methods for any progeny characters were detected in the covariance analysis of the balanced data set and only one needle was measured per seedling. Plus-tree progeny with longer needles may express superior growth over many growing seasons because of the increase in leaf area.

PARENT AND PROGENY CORRELATIONS

Correlation of parent and progeny characters was examined in this study, and relationships were found to be weak and often negative. The hypothetical parent/progeny character parallels in Table 14 may be more fanciful than real. Table 14 shows positive correlations exist between parent and progeny height across all blocks for the height vs. age selection method group. Positive correlations also exist between parent crown length and radius across all blocks for the b.a.i. vs. c.a. selection method group. While heritability can be estimated as twice the correlation coefficient of parent/progeny performance data, the weak and often negative correlations for some characters found in the study supports the contention that the seedling progeny were too young to provide realistic heritability estimates. As well, the experiment may have too few families to get meaningful heritability estimates even at a much later point in time. None of the parent/progeny correlations were statistically significant.

The second, long-term variably spaced progeny trial established from the Marks Lake seed source should provide heritability estimates in five to ten years. It will be interesting to see how the heritability of black spruce crown dimensions will compare with Bailey's et al. (1974) published heritabilities for 6-7 year old crown features of *Pinus virginiana* Mitl. estimated to be between 29 and 72 percent. More importantly, the long-term progeny trial will provide heritability estimates for b.a.i. per unit crown area from which estimates of genetic gain can be made for the measure of growing space efficiency. The value of plus-tree selection for growing space efficiency as a tree improvement method can only be determined from long-term trials. These preliminary findings suggest that the theory is attractive, but the methodology is still elusive. Perhaps research into family selection to develop methods that capitalize on superior growing space efficiency should be seriously considered as an alternative to single tree plus-tree selection.

CONCLUSIONS

The four month-old greenhouse grown progeny results imply that if trees selected for superior growing space efficiency by the b.a.i. vs. c.a. baseline have inherent advantages in the lower light intensities within mature stands, their juvenile progeny do not express these qualities. Characters responsible for growing space efficiency are not heritable or have not yet expressed themselves. The results may also be interpreted to show that the b.a.i. vs. c.a. method is not a good measure of parent growing space efficiency and is no less biased than the height vs. age selection method.

Parent and progeny correlations for height and crown features were weak and often negative. This indicates heritability estimates for characters related to growing space efficiency are likely to be as low as estimates related to growth in general. The progeny were too young and poorly developed to provide conclusive results and realistic heritability estimates. A long-term progeny trial has been established to further test for differences between selection methods and will provide reasonable heritability estimates in 10 years.

Few workable alternatives for plus-tree selection for growing space efficiency exist if the Marks Lake progeny trial is interpreted to show that b.a.i. vs. c.a. is an insufficient measure of growing space efficiency. Trees selected by transformed regressions of b.a.i. vs. c.a. and volume vs. crown radius were not much different than those selected for the b.a.i. vs. c.a. method. Independent measures of growing space and competition indices have not yet been developed which can predict subject tree growth with the consistency required to make plus-tree selection.

Even if long-term trials find the b.a.i. vs. c.a. selection method to be effective, problems remain. I found the b.a.i. vs. c.a. regression slope changed between the Marks Lake and Matawin River sites. Thomas (1980) found that the same function was influenced by age; hence, new regressions would be required for each stand unless harmonized curves were developed. Crown area and b.a.i. measurements are tedious but highly correlated to crown length and d.b.h., respectively. These latter measurements may provide an easier to use substitute in the construction of baselines for plus-tree selection.

The attempt to relate crown shape as a crop ideotype to growing space efficiency, defined by the b.a.i. vs. c.a. regression, was unsuccessful. Morphological variation is limited genetically for black spruce and is subject to environmental influence. It is unlikely that crown shape can be integrated as a measure of growing space efficiency in plus-tree selection but it might be useful in selection from plantations with fixed spacing.

Discriminant analysis of Marks Lake progeny helped identify a weak crown shape trend. Taller progeny came from a group of parents with short crowns. Discriminant analysis techniques can be useful tools in tree improvement. Parent characters that discriminate groups of progeny with desirable features can be identified using discriminant techniques of multivariate statistics.

The light x family interaction found in this study might be exploited in future research work. Plantations of genotype mixtures composed of individuals that grow well in the shade and others that excel in shade-free environments may increase yields compared to monocultures. This expression of "positive competitive ability" has been documented in agricultural and forestry experiments. Some design mixtures are based on crown form but this may not be possible with black spruce.

The preliminary results of this thesis suggest that plus-tree selection by the b.a.i. vs. c.a. method is not effective. The difficulties associated with the definition and measurement of growing space in wild stands may render the concept of plus-tree selection for growing space efficiency impractical. It must be emphasized, however, that the concept of growing space efficiency can be applied to family selection methods and is not limited to single-tree plus-tree selections. Successful applications of family selection for growing space efficiency would add to current tree improvement efforts by emphasizing the role of stand improvement to increase yield. Improved stands will probably not consist of individuals with the greatest height growth potential; rather, they will consist of individual trees with complimentary growth habits and are efficient users of their available growing space.

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