

THE APPLICATION OF MASS SELECTION IN TREE IMPROVEMENT

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ABSTRACT

Six choices are discussed in relation to the practice of mass selection: 1) should any effort be devoted to phenotypic selection or should selections be based only on progeny tests; 2) should the comparison-tree or individual-tree method of selection be used; 3) should selections be made in wild stands or in plantations; 4) should selections be made on good, average, or poor sites; 5) what criteria should be stressed in selection; and 6) should selections be made in mature, immature, or juvenile growth stages. Tentative answers, based on assumulating experience in tree improvement, frequently run counter to current practice.

Forest tree improvement is faced with a unique situation in modern breeding; the selection of organisms in their wild state, often unbenefitted by any cultural practice. *Mass* selection is the most frequently applied method of forest tree improvement. In mass selection, individuals are chosen on the basis of their phenotype and selected individuals are allowed to interbreed. The term mass selection comes from the French *en masse* and refers specifically to the bulking "in mass" of selected individuals. The definition has nothing to do with the number of individuals selected (Brewbaker, 1964; Falconer, 1960; Knight, 1948). Seed collected from selected trees that were pollinated by average or unselected trees is not the result of mass selection, although it has been misinterpreted as such in the forestry literature. Seed produced in unrogued seed orchards by the interpollination of selected clones or trees is an example of seed produced by mass selection.

Because of the importance of mass selection in forest tree improvement, one would expect the techniques and criteria for choosing plus trees to have been subjected to critical analysis. Such is not the case. Little concerted effort has been directed to collecting data necessary to evaluate selection alternatives.

Undoubtedly, mistakes have been made in phenotypic selection. In fact, the mean of select-tree progenies is frequently little different than that of commercial checks, indicating that genetic gain from phenotypic selection has been small. The average superiority in height of all crosses among select pines in 67 progeny tests of the North Carolina State-Industry Cooperative Tree Improvement Program (1972) was only 5 percent, and one-tenth of the select-tree progenies averaged 19 percent poorer than the commercial checks. Close to half of the "plus tree" selections produce progeny that are no better than commercial lots.

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Wright has frequently suggested that phenotypic selection in wild stands was futile and designed an improvement program for red pine (Pinus resinosa Ait.) in which selections would be made on the basis of progeny tests alone (Wright and Bull 1963). Therefore, the first question to consider in a selection program is whether any effort at all should be devoted to phenotypic selection or whether selections should be based entirely on the results of progeny tests, measures of a parent's breeding value as judged by the superiority of its progeny.

If phenotypic selection is used, other choices must be made. In this paper, various alternatives are considered: 1) should the comparison-tree or individual-tree selection method be used, 2) should selections be made in wild stands or in plantations, 3) should selections be made on good, average, or poor sites, 4) what criteria should be stressed, 5) should selections be made in mature, immature, or juvenile growth stages. The implications of each alternative will be discussed, although definitive answers cannot be provided.

Phenotypic Selection vs Progeny Testing

The first decision in a selection program is whether effort should be devoted to phenotypic selection or whether selection should be made only after progeny testing. The less than spectacular results of phenotypic selection suggest that it may be of little value. However, costs of this portion of a tree improvement program are probably the lowest of any phase, and phenotypic selection could to some degree be woven into normal woods operations.

It would make no sense to completely ignore phenotypic differences in trees. Even if reliance were to be placed on progeny testing, the testing should be restricted to the one or two best trees per stand, for they have shown that in at least one environment they have the potential to produce a superior phenotype. Secondly, as progeny testing is currently practiced, results are long forthcoming. It has frequently been shown that even small gains of less than one percent can pay for a tree improvement program (Perry and Wang 1958, Lundgren and King 1966). Even a small profit accumulated while awaiting the results of progeny testing can quickly add up to millions of dollars if enough acres are planted. Establishment of clonal seed orchards in the south prior to progeny testing has been justified on this basis (Zobel and McElwee 1964). The validity of the economic argument can perhaps be judged by the fact that it has convinced progressive industries, and as mentioned above, profitable gains of 5 percent in height growth are realized from unrogued orchards (North Carolina State University Cooperative Tree Improvement and Hardwood Research Programs 1972).

In addition, progeny tests cannot be justified on the basis of genetic gain alone (Namkoong 1970). Analysis shows that phenotypic selection is favored over progeny testing even when heritability is very low, because of the longer selection cycle and higher cost involved in progeny testing (Namkoong 1970, Toda 1970).

The conclusion is that as long as costs of phenotypic selection remain low, it constitutes a wise first step to tree improvement. However, probable gains from this phase are also low and might not justify use of very rigorous searches or evaluation procedures.

Comparison-Tree vs Individual-Tree Selection

There are basically two methods applied during the initial phase of selection of superior trees from wild populations. One method is comparison-tree selection and the other is individual-tree or base-line selection (van Buijtenen 1969).

The comparison- or check-tree method is most in vogue and preferred for species growing in relatively uniform, even-aged stands of a single dominant species or at most, only a few species. Such conditions are most commonly met in species of early successional or pioneer status like the southern pines. In practice, after a superior tree candidate is located, it is scored for traits of interest in relation to a number of surrounding trees, the "comparison trees" (Cech 1959, Pitcher and Dorn 1967). If the candidate exceeds the comparison trees by a certain arbitrary amount, it is selected for incorporation into the weeding program, often by grafting scion into a seed orchard. The object of using comparison trees is to adjust or correct the phenotypic value of the candidate tree for distinguishing

it from other stands. It is feared that environmental differences between stands or areas that vary in soil, climate, or stand history would make it difficult to evaluate breeding value on the basis of phenotype. The environmental check through the use of comparison trees is believed to result in an improvement in the accuracy of recognizing individuals with good genotypes as contrasted to merely good phenotypes.

Individual-tree selection must be used when stands are uneven-aged and when high species diversity makes it impossible to find comparison trees adjacent to the select-tree candidate (Beineke and Lowe 1969). Mixed hardwood forests are an example. In its most simply-applied form, individuals are located and their value for traits of interest is compared to the average for the region in which the selections are made. The average is a "base-line," giving the system its other name, base-line selection. If the candidate exceeds the base-line by an arbitrary amount, it is selected and incorporated into the breeding population. The base-line may take the form of a regression equation relating height or diameter to age but it could even be a multiple regression equation that takes into account physical factors of the site such as soil texture and drainage. The candidate tree is not compared directly to surrounding trees of the same species.

In either comparison-tree or individual-tree selection, it should be common practice to accept only one tree per stand into a breeding orchard in order to avoid the chance of including relatives, and thus unknowingly leading to inbreeding in future generations. While individual-tree selection could be applied to any species, the comparison-tree method requires relatively homogeneous and nearly pure stands.

The possible familial relationship of the comparison trees to the candidate trees has never been considered, although some relationship must occur within a stand. For example, for each of two trees to be unrelated, four different parents, eight different grandparents, sixteen different great grandparents, etc. are required. For each of six trees to be unrelated, twelve parents, twenty-four grandparents, and forty-eight great grandparents are required. Unless a population has been constantly shrinking, comparison and candidate trees must be related. Therefore,

comparison-tree selection can be analyzed as within-family selection. In a recent paper, Ledig² has shown that the efficiency ($E_{c/i}$) of comparison-tree selection relative to individual-tree selection is:

$$E_{c/i} = (1-r) [(n-1)/n(1-t)]^{1/2} \quad (1)$$

where r is a relationship coefficient expressing the average relationship among comparison and candidate trees, n is the number of comparison trees plus the candidate tree, and t is the intraclass correlation or the ratio of the variance among comparison- and candidate-tree groups to the total phenotypic variance. r may vary from 0 to 1; i.e., from no relationship to complete clonal identity. The intraclass correlation is composed as:

$$t = rh^2 + c^2, \quad (2)$$

where h^2 is heritability and c^2 is the proportion of the total variance accounted for by environmental variation among stands.

Comparison-tree selection will be the more effective method of selection for situations in which c^2 is large and r is small (Figs. 1, 2). Heritability will also have a small effect. Comparison-tree selection will be less effective than individual-tree selection when heritabilities are low because of low additive genetic variance and high tree-to-tree environmental variance, assuming variance among stands is the same in the two situations.

Strictly speaking, equation (1) and Figures 1, 2 apply only when there is no prior selection of stands. In practice, only the better stands are screened for superior trees. However, preliminary selection of stands does not change the points at which comparison-tree and individual-tree selection are equally effective (i.e., $E_{c/i} = 1.0$). The relative superiority or inferiority of comparison-tree selection does change. That is, with prior stand selection, the advantage of comparison-tree selection will not be as great as shown in Figures 1, 2 for low r and high c^2 and the disadvantages will not be as great for high r and low c^2 .

A review of commonly observed values of c^2 and h^2 and circumstantial evidence on probable values of r suggests that comparison-tree selection will often be less effective than individual-tree selection². In fact, genetic gain achieved by selection of longleaf pine (*Pinus palustris* Mill.) using the comparison-tree method was much less than gain achieved by ignoring the comparison trees entirely (Snyder 1969). It would seem wise to avoid selection of trees by direct comparison with surrounding dominants unless the population structure and appropriate variances are known to justify the comparison-tree method.

Selection in Wild Stands vs Plantations

In some cases, plantations have been avoided in the search for superior trees. The reason has been fear of selecting locally non-adapted trees, because the seed origin of older plantations is frequently unknown. However, there is probably little fear of obtaining maladapted trees from selection in mature plantations. Experience with exotics throughout the world suggests that one generation of environmental selection goes a long way towards the creation of acclimated land races. For example, progeny of both European larch (*Larix decidua* Mill.) and Douglas-fir (*Pseudotsuga menziessi* Mirb.) Franco of unknown source grown from seed introduced in the 19th Century outperformed all recently-imported provenances tested in New Zealand (Miller and Thulin 1967, Thulin 1967).

² Ledig, F. T. 1972. An analysis of methods for the selection of superior trees from wild stands. Forest Science; in submission.

Nevertheless, experience also suggests that selections should not be made in plantations of non-local or unknown provenances younger than rotation age. Frost damage to the most rapidly growing sources of ponderosa pine (Pinus ponderosa Laws.) in some Oregon-Washington provenance tests did not occur until 29 years after establishment, while local sources were relatively free of injury (Squillace and Silen 1962). The same unusual frost killed the largest trees of non-local sources in the classic Douglas-fir seed source study, even though they had grown without injury for 42 years (Pacific Northwest Forest and Range Experiment Station 1964). Thus, care must be exercised in selecting within plantations of unknown or non-local source and the trees should be of rotation age or older.

There are conceivable advantages to selection in plantations rather than in wild stands. Plantation trees have been grown under uniform spacing and are all of the same age. Therefore, phenotypic differences are more likely reflections of inherent potential and not the result of special advantage or handicap in competition. In natural stands, basal area and height growth throughout the rotation are greatly affected by differences of only 2 or 3 years in establishment (Krueger 1967, Brown and Goddard 1961). Secondly, compared to wildings, plantation trees have been subjected to cultural practices more typical of those that the progeny of select trees will experience. The ability to withstand transplanting shock is one trait that may be required of select-tree progeny and growth under reduced competition is another. Genetic variation in the ability to withstand transplanting shock has been suggested by Beineke and Perry (1966) and variation in competitive ability by Huhn (1970). Plantation trees have already been subjected to selection for recovery from transplanting shock by nature of their method of establishment. In addition, adjacent trees in plantations are less likely to be related than they are in natural stands. Thus, if c^2 is greater than 0.17, the comparison-tree method of selection could be safely applied, resulting in a better evaluation of breeding value than could be obtained by individual selection. Selection of plantation-grown slash pine by the comparison-tree method resulted in substantial gain relative to commercial lots (Webb and Barber 1966).

Selection on Good vs Poor Sites

The best phenotypes are found on the best sites. But should selection be restricted to the best sites or should trees from average and poorer sites also be selected? The conservative answer is to select trees from sites similar in type to those on which their progeny will be planted. An organization that held predominantly land of site II would be conservative if it selected its plus trees from stands of site II or I. Selection from sites a little better in index than those which will be regenerated may compensate for the better cultural conditions the select-tree progeny will enjoy. However, Brown and Goddard (1961) felt that good phenotypes from poor sites would react more favorably on better sites than the reverse, and warned against confining selections to better sites. In Texas, differences among loblolly pine (Pinus taeda L.) progenies were more pronounced on poor, droughty sites than on better ones (Texas Forest Service 1971). Generally, differences among progenies or provenances are accentuated on the best sites (Bey and Funk 1970, Kitzmiller 1972, Morgenstern and Teich 1969, Snyder and Allen 1971). Superior trees may be the individuals most capable of responding to improved site conditions.

Selection Criteria

Many criteria have been proposed for superior tree selection. These depend primarily on the species and the product. Desirable wood properties, determined by product requirements, have been important items in some tree improvement programs. It is necessary that tree breeders not lose sight of the product for which they are breeding their trees. Many of the important economic gains in the breeding of agronomic crops have come not from increasing yield but from changing processing characteristics (Allard 1964). On the other hand, forestry is uniquely different from agriculture in the long time that is required to develop a line through breeding and to mature it into a crop. Even if the wood characteristics desired 50 years from now were known, it would be only barely possible to select the desired trees, incorporate them into a seed orchard, harvest seed in commercial quantities, and grow a crop to rotation age. Mill technology can change much more rapidly. For example, in 1919 pine composed barely 5 percent of the pulp and paper produced in the United States, but in only 20 years it surpassed spruce, thanks to a technological shift from the sulphite to the sulphate process (Panshin et al., 1950). The best the tree breeder might do is to maintain the present wood properties and perhaps increase the uniformity of the furnish. In this regard, the breeding of trees with more uniform properties from core-to-outer-wood or from base-to-top would always be desirable. Namkoong et al., (1969) came to the conclusion that gain in growth rate should not be sacrificed by selection for wood properties which have relatively ephemeral value.

Volume (or perhaps weight) production is the most universally desired characteristic in silviculture and will be the only trait considered in detail here. The simplest criterion would be to select trees which exceeded the mean height or diameter for a given age by a certain arbitrary amount, determined, in part, by the number of trees to be ultimately retained. Frequency distributions of diameter growth rates and clear stem lengths such as that of Trimble and Seegrift (1970) for red oak (Quercus rubra L.) or Hocker (1972) for white pine (Pinus strobus L.) would be useful in setting the selection differential. Such a system would result in most selected trees originating on the very best sites. While genetic differences might in fact be most pronounced on such sites, it is doubtful whether this system is desirable. An improvement would be the incorporation of site evaluation in the selection process (see Squillace 1967, Robinson and van Buijtenen 1971). Trees that exceeded the mean height or diameter for a given age on a given site class would then be selected. Preferably, sites would be classified by physical and edaphic features and not by tree height, because there is genetic variation among stands and site index defined by tree height is genetically influenced. Site index correction based on tree height is subject to the same criticisms as the comparison-tree method of selection.

In determining the age of the tree to compute rate of increment, it may be desirable to determine the tree's actual age at the base and not at breast height. S. A. M. Manley (pers. comm.) has suggested that tolerant trees, such as red spruce (Picea rubens Sarg.) may be adapted for relatively slow growth for a period of many years. Selection on the

basis of breast height alone could result in the inclusion of many slow starters. Other breeders suggest using recent periodic increment rather than height or diameter accumulated over the tree's entire age. Which method is used depends in part on the desired product. Selection based on current increment might result in the choice of a tree that starts slowly and grows more rapidly later while one that grew rapidly in the juvenile stages and slowed down as it reached rotation age might be rejected (Fig. 3). If different growth curves do occur and are genetically controlled, it would be very desirable to determine actual tree age, as suggested by Manley, and not just breast-height age. On the other hand, the effects of environment in the form of competition and suppression may be so important that attempts to reconstruct influences upon a tree's growth and development would be largely futile, and recent increment would then be the most favored criteria for indicating a tree's true potential. In fact, correlations of parent-progeny performance are usually better when based on recent periodic increment than on mean increment of parent trees over their entire age, suggesting that periodic increment, say the last ten years, is preferable to mean increment for selection of superior individuals (Steinhoff and Hoff 1971).

Several breeders have recognized that the growing space available to a tree has a profound influence on its increment and they proposed ways of accounting for the effects of competition. One way is to relate diameter or height growth to the basal area of competing trees within a given radius (Krueger 1967). However, a tree's own crown size is a better measure of the competition that it received (Brown and Goddard 1961). Volume or growth increment has been related to crown size as either crown volume or crown surface (Rudolf 1956, Brown and Goddard 1961). Crown surface seems a priori the better measure because it is a more appropriate reflection of the light intercepting surface of the tree than crown volume. Trees with a high increment relative to their crown surface would be considered efficient in wood production, and if their superiority met an arbitrary standard, would qualify as plus trees (Fig. 4).

Crown surface is an estimate of leaf surface area or leaf mass. Leaf mass could be measured more directly. One method is the harvest and weighing of all leaves, perhaps by collection of leaf litter in the fall. However, the technique would probably prove more costly than is justified by the expected gains from phenotypic selection.

Volume growth per unit area not volume growth per tree is of ultimate interest to silviculturists. The smaller the projected crown area, the more stems that can be accommodated per hectare. Interestingly, the dbh-crown area relationship is not affected by site or by stand density; the dbh of open-grown trees can be predicted from the same regression used for trees in a closed stand (Stout³, Minckler and Gingrich 1970). Trees whose dbh exceeded that predicted for their crown diameter would be preferred, because they would maximize volume production per hectare.

³ Stout, B. B. 1962. Crown-stem relationships in forest trees. Unpublished manuscript. Forestry Department, Rutgers University, New Brunswick, New Jersey.

The relationships of Stout³ between dbh and crown area and Brown and Goddard (1961) for growth increment and crown surface both result from similar causal factors and both focus on the relationship of growth increment to the growing space of a tree, but both ignore age except as it is correlated with crown size. The relationship of Brown and Goddard (1961) was meant to be applied within a single stand in which age would be relatively constant. Stout's³ relationship would indicate which trees were most efficient in bole production unit per unit area but not how long it took to achieve this production. A regression equation predicting volume ha⁻¹ from crown surface (or crown radius x crown depth which is proportional to surface) and age would be the ideal, and not difficult to construct. It may be that the addition of age to crown surface would lend little to the predictive ability of the regressions, but the combination seems theoretically satisfying. Volume of a tree (V) to a four-inch top could be represented by the volume of a truncated cone:

$$V_T = (\pi D^2/8 - 6.2832)H, \quad (3)$$

where D is basal diameter and H is height. More generally:

$$V_T = (k_1 D^2 + k_2)H, \quad (4)$$

where k_1 , k_2 stand for the constants. Then volume ha⁻¹ (V_A) is:

$$V_A = V_T/C, \quad (5)$$

where C is area of the crown projected on the ground. To relate V, an indication of the competition received by an individual tree, to crown area, and age (A), the following relationships can be used:

$$D^2 = k_3 + k_4 C \quad (6)$$

$$H = k_5 A^{k_6}, \quad (7)$$

where k_3, \dots, k_6 are empiric constants. Many foresters (see Stout³) have shown a linear relationship between basal area and crown area, resulting in an expression such as (6). The log-log relationship is frequently a satisfactory description of height growth with age and (7) is the form of the relationship before logarithmic conversion. Substituting (6) and (7) into (5):

$$V_A = \beta_1 A^{k_6} + \beta_2 A^{k_6} C$$

$$V_A = (\beta_1 + \beta_2 C^{-1}) A^{k_6}, \quad (8)$$

where β_1 and β_2 are appropriate combinations of k_1, \dots, k_5 . A regression can be fitted with putative least squares estimates of β_1 , β_2 and k_6 found by iterative techniques. Multiple linear regression, though not based on expected relations among the variables, might yield

³ Stout, B. B. 1962. Crown-stem relationships in forest trees. Unpublished manuscript. Forestry Department, Rutgers University, New Brunswick, New Jersey.

just as suitable prediction equations for VA. Trees would be selected that exceeded the predicted volume ha^{-1} for their crown size and age by a predetermined amount.

If volume increment for the most recent 10-year period rather than volume production is to be the basis for selection, then the first derivative or a difference equation of (8) would be used. If weight, not volume, growth is of primary interest, then V_A would be replaced by the product of volume times specific gravity.

Mature Tree vs Early Selection

Some silviculturists prefer to select in older, mature stands⁴, while others advocate selection in immature stands (Isaac 1955). The rationale for selecting among young trees is that defects, such as a tendency to crook, to fork, or to produce steeply-angled branches, are easily seen. Through the formation of reaction wood, older trees cover up such imperfections. On the other hand, trees superior at a young age may be unable to retain their growth rate until rotation age and in the long run produce only average trees. The conservative decision would be to select trees of an age sufficient to produce a bole of the size required for the desired product. A tree with a growth curve of type 1 (see Fig. 3), a "stayer," will be of little value to a pulpwood producer, although it would be preferable to type 2, a "sprinter," for a sawtimber operator.

If phenotypic selection is relatively ineffective, there is a very good argument for selecting in younger stands. Such selection will result in rapid starters, but from among this group, progeny testing could identify those that also maintain the early lead (type 3, Fig. 3). The place to start in raising the growth curve is most likely the early age classes.

Selection at a very early age, the juvenile stage, is a third possibility. However, most foresters disdain "super-seedling" selection and similar practices. Wakely (1971) argued that his data on height and diameter growth of thousands of trees repeated over a 30-year period showed that early selection was not feasible. It is true that many mistakes would be made in early selection judged by performance at rotation age. In spite of the inaccuracy of early selection, economic gain would be maximized as judged even from Wakeley's data.

Genetic gain for volume production at rotation age can be treated as a correlated response to selection for height, diameter, or any other predictor of growth rate in the juvenile stage (Nanson 1965, 1970). The response to selection for juvenile traits (G_j) is:

$$G_j = h_j^2 i \sigma_{p_j}$$

where h_j^2 is the heritability of the juvenile trait (even an index or composite trait), i is the selection intensity, and σ_{p_j} is the phenotypic standard deviation for the trait. Then the correlated gain for the mature trait based on selection for the juvenile trait (G_{mj}) is:

⁴ Little, S. 1964. Master plan for breeding and testing pitch-loblolly pine hybrids, selected loblolly pines, and selected pitch pines. U.S. Forest Service, Northeast. Forest Expt. Sta., unpublished file report 4110-NE-1106-28. 26 pp.

$$G_{mj} = b_{mj}G_j$$

$$G_{mj} = b_{mj}h_j^2 i\sigma_{pj},$$

where b_{mj} is the regression between breeding value for volume production at rotation age and the juvenile trait. Gain for the mature trait based on selection for the mature trait itself (G_m) is:

$$G_m = h_m^2 i\sigma_{pm},$$

where h_m^2 is the heritability of the mature trait and σ_{pm} is the phenotypic standard deviation of the trait. To simplify, assume that by suitable transformations σ_{pm} is roughly equal to σ_{pj} then the efficiency of juvenile selection relative to mature selection ($E_{j/m}$) is:

$$E_{j/m} = G_{mj}/G_m = b_{mj}h_j^2/h_m^2$$

Juvenile selection will be more effective than mature selection if $b_{mj}h_j^2 > h_m^2$. While this may not be true for mass selection in wild stands it is certainly likely for progeny tests as explained below. Under more restrictive assumptions it can be shown that juvenile selection will be more effective than mature selection if $r_p > h_m^2$, where r_p is the phenotypic correlation between mature and juvenile traits (see Nanson 1970). Juvenile testing might change the conclusions of Namkoong (1970) that progeny testing was not justified by expected genetic gain. In fact, the balance might be tipped in favor of progeny testing after a single initial cycle of mass selection.

Juvenile tests could occupy smaller, more homogeneous areas than mature tests and would even be conducted under highly controlled conditions. Therefore, heritability for juvenile traits would be higher than that for mature traits because heritability increases as environmental variation decreases. For example, Stonecypher (1966) found heritabilities of 0.06 to 0.10 for height growth of loblolly pine after one growing season in the field in the North Carolina State - International Paper Company Heritability Study, while in a pot experiment that utilized some of the same crosses, Ledig and Perry (1967) found heritabilities of 0.86 to 0.92 for dry weight of seedlings. Therefore, even weak correlations of juvenile with mature traits (e.g. $r = 0.1$ to 0.2) might result in greater gain from juvenile than mature selection. But in fact, correlations may not be weak. Many reports of weak correlations between nursery and field performance may be partly the result of differences among progenies in the ability to recover from transplanting shock, because such correlations generally improve with age after transplanting (e.g. Steinhoff and Hoff 1971, Squillace and Silen 1962). Wakeley's (1971) correlations of 0.40 to 0.69 for 30-year on 3-year height in slash (*Pinus elliottii* Engelm.) and loblolly pine are heartening. Rather than illustrating the futility of early selection as concluded by Wakeley, these correlations indicate that great gains are likely from early selection. In addition, Wakeley's correlations were based on individual trees; juvenile-mature correlations of mean progeny heights will be higher.

There are additional advantages favoring early or seedling selection. Selection intensity under seedling selection schemes can undoubtedly be

higher than those under ordinary progeny test schemes. Increasing selection intensity would increase genetic gain, favoring seedling selection over later selection. It is simpler to establish and maintain a uniform test of seedling-sized materials kept for only one or two years than of large trees at 6 x 6 or greater spacing maintained for one or two scores of years. Thus, more progenies can be evaluated as seedlings than could be evaluated as mature trees and perhaps for lower costs. As mentioned above, Namkoong's (1970) analysis indicates that progeny tests cannot be justified in terms of their genetic gain alone, but juvenile testing would change those conclusions drastically by shortening the evaluation period and lowering costs.

Another advantage of seedling selection is that more cycles of selection can be accomplished in a given time period. Because gains from each cycle are additive, total gain in a 20-year period would have to be four times as effective as selection at 5-years to justify the extra delay. In the pines, production of ovulate strobili occurred at 5 years on the average, so that the time required for progeny evaluation may delay genetic improvement more than the time required for trees to attain reproductive maturity (Righter 1939).

As final consideration, seedling height or diameter are not the only criteria that can be utilized in superior-tree selection by early progeny evaluation. Flushing date and growth period were used by Nanson (1965) to predict mature-tree value. Recent work indicates that photosynthetic rate and the distribution of growth in seedlings has great promise in comparing progenies to assess growth potential (Ledig 1969). Growth of altitudinal provenances of balsam fir (Abies balsamea (L.) Mill.; Fryer and Ledig 1972) and different crosses between black (Picea mariana (Mill.) B.S.P.) and red spruce and their hybrids (Ledig and Manley, in preparation) was related very closely to photosynthetic rate.

Conclusions

Obviously, the success of phenotypic selection will depend both on the species and the product for which it is to be bred. Making the correct decisions depends on knowledge of growth patterns, of variation due to both genetic and environmental causes, and most importantly of the genetic system and the relationship structure of the population. Although such information should and could be gathered to increase the effectiveness of tree improvement programs, critical study of selection procedures has been strangely neglected. Tree breeders cannot yet quantitatively analyze selection alternatives.

The following guidelines are suggested by the accumulating experience:

1. It seems ridiculous to abandon phenotypic selection in favor of random choice of parents even if orchard establishment will be based on the results of a progeny test, primarily because the cost of phenotypic selection is a relatively minor part of the total cost of tree improvement. On the other hand, it seems unwise to devote a great deal of the total financial resource to field selection because improvements in selection technique are likely to result in only marginal returns.

2. Selection programs should utilize plantations when possible, with due consideration to the risks of obtaining not-fully-adapted parents.
3. When selection is practiced in wild stands, the comparison-tree method should be avoided, in the absence of knowledge to the contrary, because in many cases it will result in less gain than individual selection.
4. Candidates for selection should be no older or larger than necessary for the product of interest, and preferably younger when form characteristics are considered.
5. For volume growth, trees should be selected to maximize volume production per unit area, not just per tree. Sampling should be employed to determine the relationship of volume hectare⁻¹ to age and crown area. The value of a tree will be measured by the degree it deviates from the regression in a positive direction. Best results will probably be attained by selecting for volume increment during a recent period, say 10 years, rather than during the total life of the tree, because of the difficulty in reconstructing past influences on a tree's growth.
6. A large number of trees should be included in initial phenotypic selections and final selection should be based on progeny tests. Though controversial, I would suggest short-duration tests with evaluation to be made in 5 years or earlier. It seems probable that within a few years, seedling evaluation by measurements of photosynthetic rate will be proven and juvenile selection will result in greater gain through increased selection intensity, shorter selection cycles, and higher heritabilities.

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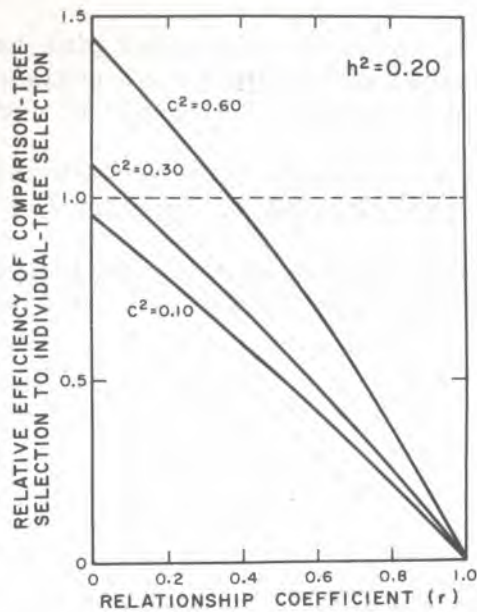


Figure 1.--Relative efficiency of comparison-tree selection, considered as within family selection, to individual-tree selection as related to the relationship among comparison and candidate trees (r) for a heritability (h^2) of 0.2 and various values of c^2 , the proportion of the phenotypic variance due to environmental variation among stands. The lower the c^2 and the higher the relationship coefficient, the less effective is comparison-tree selection.

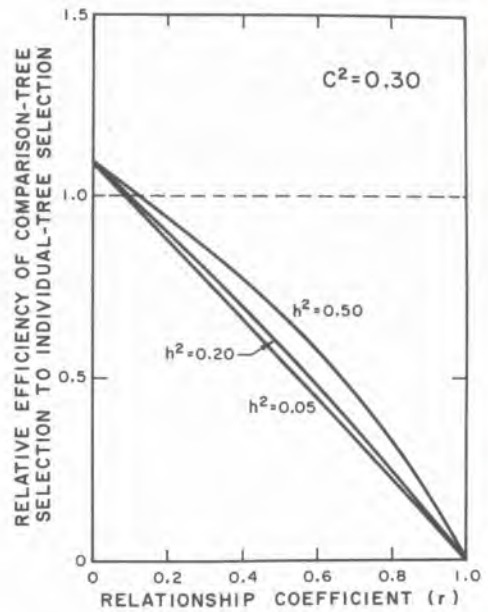


Figure 2.--Relative efficiency of comparison-tree selection, considered as within family selection, to individual-tree selection as related to the relationship among comparison and candidate trees (r) for $c^2 = 0.3$ and various values of heritability (h^2). The lower the heritability and the higher the relationship-coefficients, the less effective is comparison-tree selection.

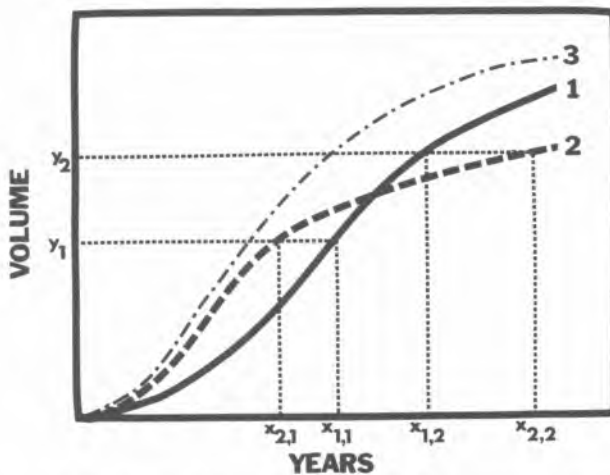


Figure 3.--Hypothetical volume-growth curves. For pulpwood production where bolts of small size (e.g. y_1) can be utilized, trees with curves such as type 2 would maximize production relative to type 1 by shortening rotation age ($x_{2,1} < x_{1,1}$). For sawtimber production where logs of large size (e.g. y_2) are preferred, trees with growth curves of type 1 would be preferred to those with type 2 because for this product, rotation age of type 2 is longer ($x_{2,2} > x_{1,2}$). The age at which selection is practiced depends, therefore, on the product desired. Selection of the tree with greatest volume production at age $x_{1,2}$ might result in the wrong choice for pulpwood producer while selection at age $x_{2,1}$ would be undesirable for a sawtimber operator. A growth curve like type 3 would be desirable in either situation.

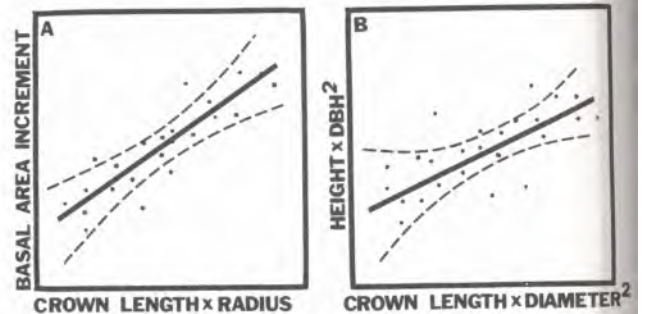


Figure 4.--Previously suggested relationships for the selection of superior trees. A. Trees whose basal area increment exceeds the arbitrary confidence interval for the product of their crown length x radius, which is proportional to crown surface area, are selected (after Brown and Goddard 1961). B. Trees whose height x dbh^2 , which is roughly proportional to volume, exceeds the arbitrary confidence interval for the product of their crown length x diameter², which is proportional to crown volume, are selected (after Rudolf 1956). Both methods compensate for the effects of competition.