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Abstract. The commonly applied comparison-tree method of selection is analyzed as a form of within-family selection. If environmental variation among comparison- and select-tree groups, c^2, is a relatively small proportion (17 percent or less with 5 comparison trees) of the total variation, comparison-tree selection will result in less genetic improvement than individual-tree selection. Even if c^2 is large, individual-tree selection may be more effective than comparison-tree selection if comparison and candidate trees are related. Estimates of c^2 and of relationships among trees in wild stands derived mainly from published reports suggest that comparison-tree selection may in fact result in less genetic gain than individual-tree selection in many tree species. In any case, comparison-tree selection will seldom be much more effective than individual-tree selection. Development of alternate techniques for applying site corrections in the selection of superior trees is suggested. ***Forest Sci. 20:2–16.***

Additional key words. *Pinus rigida*, base-line selection, phenotypic selection.

TREE IMPROVEMENT has become an almost universal part of intensive forest management. The first phase in a tree improvement program for indigenous species is usually the selection of superior phenotypes from wild populations. There are basically two methods applied during the initial selection phase, comparison-tree selection and individual-tree or base-line selection.

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 breeding 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 environmental effects common to that stand but 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

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TABLE 1. Observational and causal components of variance for families of size n. Explanation in text.

Observed variance	Expected mean squares	Causal components	
		additive genetic	phenotypic
Among family means	$\sigma_b^2 + \frac{1}{n}\sigma_w^2$	$\frac{1+(n-1)r}{n}\sigma_g^2$	$\frac{1+(n-1)t}{n}\sigma_p^2$
Among individuals within families	$\sigma_w^2 - \frac{1}{n}\sigma_w^2$	$\frac{(n-1)(1-r)}{n}\sigma_g^2$	$\frac{(n-1)(1-t)}{n}\sigma_p^2$

are made. The average is a "base-line," giving the system its more common 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, only one tree per stand should be accepted into a breeding orchard to avoid the chance of including relatives, and thus unknowingly lead 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.

Genetic Gain

Where a choice between methods exists, relative genetic gain or improvement should be a prime consideration. Genetic gain from phenotypic selection is the increase in mean of progeny of the selected parents over the mean of the parental population prior to selection:

$$G = ih^2\sigma_p. \qquad (1)$$

Gain (G) depends on the intensity of selection (i), heritability (h^2), and the phenotypic standard deviation (σ_p). It seems intuitively reasonable that the use of comparison trees as a correction for environmental effects will increase genetic gain. However, there is a danger that the comparison trees will be related to the candidate tree and under that condition, comparison-tree selection becomes within-family selection (Falconer 1960).

Within-Family Selection

Both the additive genetic variance (σ_g^2, variance due to additive effects of the genes and utilizable in a program of mass selection) and the phenotypic variance can be partitioned into between-family (σ_b^2) and within-family (σ_w^2) components as in Table 1. With families of any finite size, the between-family variance is augmented by the standard error [2] of family means, σ_w^2/n, where n is the number of individuals in the family. Thus, the residual variance within families is reduced by σ_w^2/n.

For families of infinite size, the additive genetic variance between families is $r\sigma_g^2$, where r is the relationship coefficient; for example, $r = .25$ for half-sib families (one parent in common) and $r = .5$ for full-sib families (both parents in common) under the usual assumptions of Mendelian, diploid inheritance, and no linkage (Falconer 1960). The remainder, $(1 - r)\sigma_g^2$ is the additive genetic variance within families. But for randomly located families of finite size, the additive genetic variance between families is augmented by $1/n$ of the additive genetic variance within families so that the within family genetic variance is correspondingly reduced.

The phenotypic variance among families can be written as $t\sigma_p^2$, where t is the so-called intraclass correlation coefficient, σ_b^2/σ_p^2, a measure of the similarity within

groups or the differences between. The remainder of the variance within families is $(1 - t)\sigma_p^2$. Again, for randomly located families of finite size, the variance among families is augmented by $1/n$ of the variance within families and the within family variance is correspondingly reduced (Table 1).

For individual selection, heritability is the total additive genetic variance divided by the phenotypic variance:

$$h^2 = \sigma_g^2/\sigma_p^2. \quad (2)$$

Within-family heritability is the additive genetic variance within families divided by the phenotypic variance within families:

$$\begin{aligned} h_w^2 &= \frac{(n-1)(1-r)\sigma_g^2/n}{(n-1)(1-t)\sigma_p^2/n} \\ &= [(1-r)/(1-t)]\,(\sigma_g^2/\sigma_p^2) \\ &= [(1-r)/(1-t)]h^2. \end{aligned} \quad (3)$$

The phenotypic standard deviation for individual selection is σ_p while the standard deviation applicable to within-family selection is:

$$\sigma_{p_w} = \sigma_p[(n-1)(1-t)/n]^{\frac{1}{2}}. \quad (4)$$

So that gain from within-family selection is:

$$\begin{aligned} G_w &= ih_w^2\sigma_{p_w} \\ &= ih^2\sigma_p\,[(1-r)/(1-t)]\times \\ &\quad [(n-1)(1-t)/n]^{\frac{1}{2}} \\ &= ih^2\sigma_p\,(1-r)\,[(n-1)/(1-t)n]^{\frac{1}{2}}. \end{aligned} \quad (5)$$

An analysis of equation (5) makes it obvious that genetic gain decreases as the degree of relationship, r, within the family increases. In the extreme, when $r = 1$ (that is, the "family" is a clone or a completely homozygous line), no gain is possible.

Also, gain is inversely related to $(1 - t)$ where t measures the variation between groups relative to the total phenotypic variation and can never be greater than 1. Variation between groups or similarity within groups (either check- and candidate-tree groups or families), depends on (1) the relationship among individuals within the group, (2) the additive genetic variance, and (3) the effects of a common environment. Therefore, the intraclass correlation can be expanded as:

$$\begin{aligned} t &= [r\sigma_g^2 + \sigma_c^2]/\sigma_p^2 \\ &= r(\sigma_g^2/\sigma_p^2) + \sigma_c^2/\sigma_p^2 \\ &= rh^2 + c^2, \end{aligned} \quad (6)$$

where c^2 is the proportion of the total variance accounted for by environmental variation among check- and candidate-tree groups. The formulation for genetic gain from within-family selection (eq. 5) was used to calculate the gain from selection by the comparison-tree method.

Efficiency of Comparison-Tree Selection

The efficiency (E) of comparison-tree selection relative to individual-tree selection is given by the ratio of G_w to G for the same selection intensity, i:

$$\begin{aligned} E &= G_w/G \\ &= (1-r)\,[(n-1)/n(1-t)]^{\frac{1}{2}}. \end{aligned} \quad (7)$$

When $E > 1$, the comparison-tree method results in greater expected gain than individual-tree selection and when $E < 1$, the expected gain from individual-tree selection is the greater. The situation in which comparison-tree selection will be most effective is when (1) r is very low or zero and (2) t is very large either because of high heritability (h^2) or a high proportion of variance due to common environment (c^2). The latter possibility is the reason that comparison-tree methods are usually adopted. Note that c^2 and h^2 are not independent. For a given h^2, c^2 can increase only if the environmental variance among groups increases at the expense of the environmental variance within groups while the additive genetic variance and total environmental variance remain unchanged.

In some tree improvement programs, candidate and check trees are chosen only from the best stands.[1] Initial selection of stands is not universally practiced because natural stands, not high-graded, are too rare in some areas to allow any freedom of choice. Nevertheless, the foregoing anal-

[1] Personal communication from J. P. van Buijtenen, 1973.

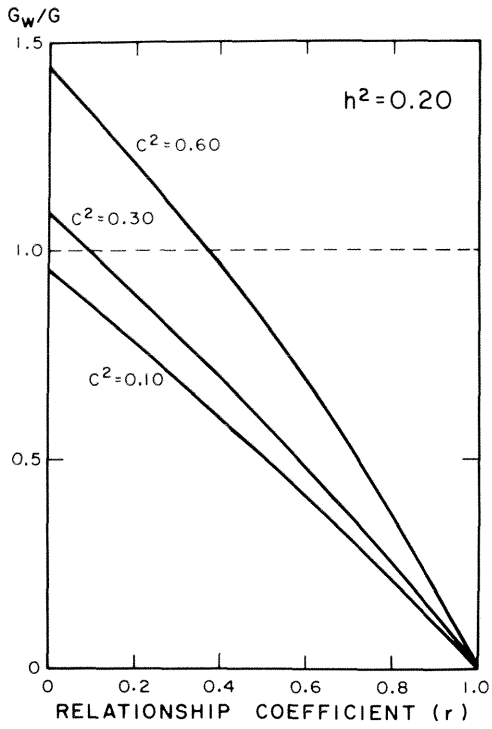

FIGURE 1. *Relative efficiency (G_w/G) of comparison-tree selection, considered as within-family selection, to individual-tree selection as related to the relationship among comparison and candidate trees (r) for a heritability (h^2) of 0.2 and various values of c^2, the proportion of the phenotypic variance due to environmental variation among comparison- and candidate-tree groups. The lower the c^2 and the higher the relationship coefficient, the less effective is comparison-tree selection. Values of G_w/G apply to the case of no prior selection of stands but shape of the curves and the x-intercept are unchanged even if stand selection precedes tree selection.*

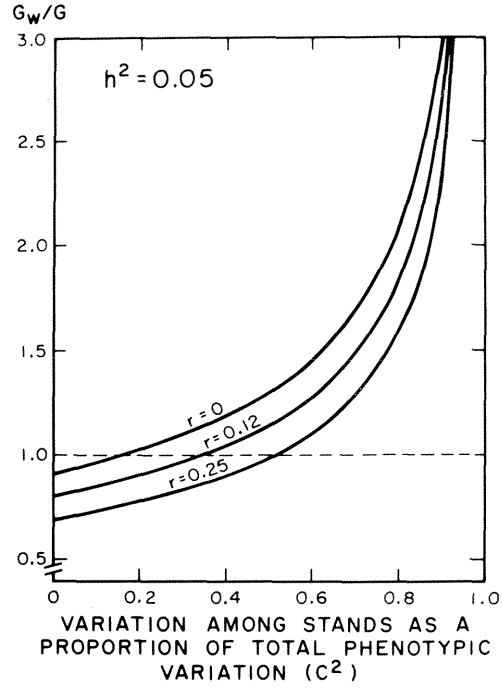

FIGURE 2. *Relative efficiency (G_w/G) of comparison-tree selection, considered as within-family selection, to individual-tree selection as related to c^2, the proportion of the phenotypic variance due to environmental variation among comparison and candidate-tree groups for a heritability (h^2) of 0.05 and various values of the relationship coefficient (r). Values of G_w/G apply to the case of no prior selection of stands but shape of the curves and the x-intercept are unchanged even if stand selection precedes tree selection.*

ysis can be criticized because it omits consideration of gain due to stand selection where such selection occurs.

Stand selection can be accounted for in the following way. Assume that stand selection precedes both comparison-tree and individual-tree selection and is practiced with equal intensity in both cases, resulting in a gain G_s. The assumption is trivial because the best trees in individual-tree selection will certainly occur in the best stands. If prior selection of stands has occurred, the ratio of gain by comparison-tree selection to gain by individual-tree selection is:

$$(G_s + G_{w|s})/(G_s + G_{i|s}) = 1 + (G_{w|s}/G_{i|s} - 1)/(G_s/G_{i|s} + 1), \quad (8)$$

where $G_{i|s}$ is gain from individual-tree selection and $G_{w|s}$ from comparison-tree selection following stand selection. Now, $G_{w|s}/G_{i|s}$ in equation (8) is of the same form as G_w/G in equation (7). And just as above, if $G_{w|s}/G_{i|s} < 1$, then individual-tree selection is more effective than comparison-tree selection, while if $G_{w|s}/G_{i|s} > 1$, the reverse is true. The balance point in equations (7) and (8) is the same but

the relative superiority of one method of selection over the other may not be as great in (8) as in (7), depending on the gain from stand selection. It is important to note that the parameters σ_p^2, h^2, and c^2 for the total population considered in equation (7) will not be the same as those for the population of selected stands appropriate to equation (8) which are impossible to estimate from the literature. It seems likely that σ_p^2 and c^2 for the population of the selected stands will decrease because the environmental range has been narrowed. The effect on h^2 is less obvious because it depends on the genetic as well as the environmental variance.

Note that if additive genetic variance among stands was zero, which might occur with respect to characters of little value to fitness in a species with a wide dispersal potential, then equation (8) reduces to equation (7). For the evaluation that follows, estimates of the population parameters will apply most closely to equation (7) and for convenience, results will be reported with regard to the situation in which prior selection of stands has not occurred.

E was evaluated for the range of arithmetically possible values of h^2,c^2, and r, assuming five comparison trees; that is, $n = 6$ (Fig. 1–3). According to van Buijtenen (1969), five comparison trees is the usual number in southern pine selection and the comparison trees are within 100 feet of the candidate tree, but as close as possible. Many tree improvement programs utilize fewer comparison trees and preferably trees that are within 66 feet of the candidate tree (Cech 1959, Pitcher and Dorn 1967, Walters *et al.* 1960). The effectiveness of comparison-tree selection increases as the number of comparison trees increases. The increase is rapid at first and then becomes infinitesimal (Fig. 4). Note that in some situations, comparison-tree selection will never be more effective than individual-tree selection no matter how many comparison trees are used. Increasing the number of comparison trees defeats the purpose of the method, however, because it becomes increasingly difficult to assume that the comparison trees occupy the same microsite as the candidate tree.

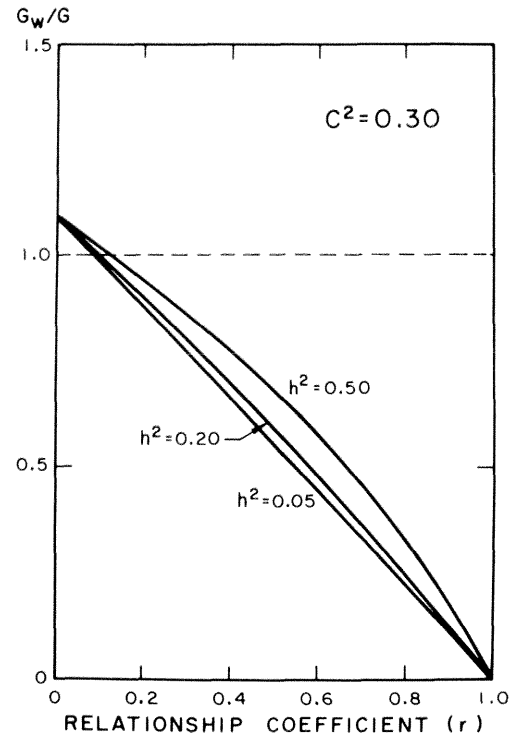

FIGURE 3. *Relative efficiency (G_w/G) of comparison-tree selection, considered as within-family selection, to individual-tree selection as related to the relationship among comparison and candidate trees (r) for $c^2 = 0.3$ and various values of heritability (h^2). The lower the heritability and the higher the relationship-coefficient, the less effective is comparison-tree selection. Values of G_w/G apply to the case of no prior selection of stands but shape of the curves and the x-intercept are unchanged even if stand selection precedes tree selection.*

The curves in Fig. 1–3 do not represent trends that can be achieved by modifying variance components; they merely indicate possible combinations of h^2,c^2, and r. For a real population occupying a specified range, variances are presumably fixed. For low values of c^2 (less than 0.17) comparison-tree selection is never as effective as individual-tree selection even when there is no relationship ($r = 0$) among comparison and candidate trees (Fig. 1). Under the same situation but with $c^2 = 0.3$,

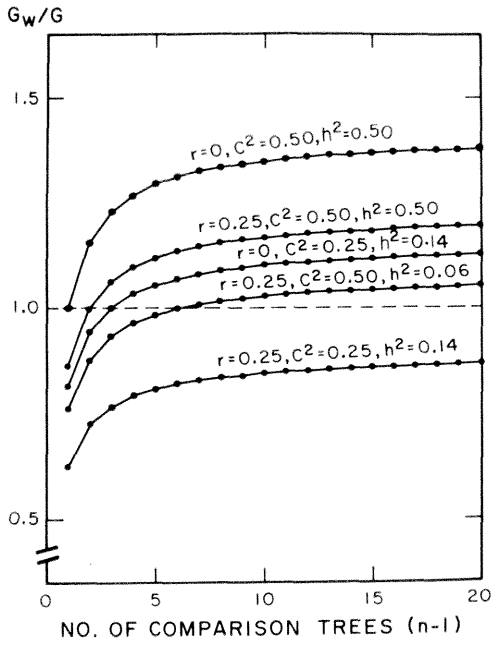

FIGURE 4. *Relative efficiency (G_w/G) of comparison-tree selection, considered as within-family selection, to individual-tree selection as related to the number of comparison trees ($n - 1$), for various values of the relationship coefficient among comparison and candidate trees (r), heritability (h^2), and the proportion of the phenotypic variance due to environmental variation among comparison- and candidate-tree groups (c^2). Values of G_w/G apply to the case of no prior selection of stands but shape of the curves and the x-intercept are unchanged even if stand selection precedes tree selection.*

comparison-tree selection is never more than nine percent more effective than individual tree selection for the case with no prior selection of stands; and if r exceeds 0.1, it is less effective. In general, the effectiveness of comparison-tree selection increases sharply in situations for which c^2 is 0.7 or larger (Fig. 2), but its efficiency depends to a great extent on r. It is not usually realized that for constant c^2, r, and n the lower the heritability, the less effective is the comparison-tree method (Fig. 3). Expressed in another way, when the proportion of the environmental variance attributable to differences within groups is large at the expense of a decrease in genetic variation, the less effective is comparison-tree selection relative to individual-tree selection.

It is now necessary to determine reasonable values of h^2 and c^2 for populations of forest trees corresponding to a region over which selection would be practiced and to estimate r for groups of trees within stands. With values of h^2, c^2, and r we can decide what part of the curves (Fig. 1–3) are applicable to the problem of selection from wild stands.

Environmental Variation Among Stands, c^2

Estimates of c^2 can be obtained from experiments replicated in different environments or from studies of phenotypic variation in natural populations. The ideal estimate of c^2 would be:

$$\hat{c}^2 = \frac{\sigma_l^2 + \sigma_{gl}^2 + \sigma_r^2}{\sigma_l^2 + \sigma_{gl}^2 + \sigma_r^2 + \sigma_g^2 + \sigma_w^2}, \qquad (9)$$

where σ_l^2 is the variance among locations, σ_{gl}^2 is the genotype × environment interaction variance, σ_g^2 is the total genetic variance, σ_r^2 is the plot-to-plot variance, and σ_w^2 is the within plot variance, assuming plots are as large as the area occupied by candidate and comparison trees. The inclusion of plot-to-plot variance in the numerator could be questioned, but the error will be on the conservative side; *i.e.* result in overestimation of c^2. For plots of small size, σ_r^2 should not appear in the numerator.

Experiments that allow the partition of location, genotype × location, and within plot variances are rare. First, few genetic experiments have been replicated in two or more locations. For example, Namkoong *et al.* (1966) tabulated heritability estimates and found no case in which variances among locations or locations × genotypes were estimated. Investigators who do include plantings at different locations frequently fail to report variance components within plot and sometimes not even among locations. Both components are required for estimation of c^2.

Table 2 lists estimates from an exten-

TABLE 2. Environmental variation among sites, c^2, as a proportion of the total phenotypic variance based on experiments replicated on different sites.

Species, author, and trait	Construction[1]	$\hat{c}^2$	Comments
Pinus taeda (Pederick 1970)			
Double bark thickness adjusted for diameter inside bark	$\frac{(\sigma_l^2 + \sigma_{r/l}^2 + \sigma_{gl}^2 + \sigma_r^2)}{(\sigma_l^2 + \sigma_{r/l}^2 + \sigma_{gl}^2 + \sigma_r^2 + \sigma_g^2 + \sigma_w^2)}$	.08 .29	Variance calculated among 6 full-sib families grown on two sites several miles apart in south Georgia. Genetic variance may be less than that between wild stands, so c^2 is overestimated. Genetic variance includes variance among North Carolina seed sources of Piedmont, Fall Line, and Coastal Plain origin. Planting locations were widely separated, one in each of the 3 physiographic provinces.
Pinus taeda (Stonecypher 1966)			
First year height Second year height	$\frac{(\sigma_l^2 + \sigma_{r/ls}^2 + \sigma_{gl}^2 + \sigma_r^2)}{(\sigma_l^2 + \sigma_{r/ls}^2 + \sigma_{gl}^2 + \sigma_r^2 + \sigma_g^2 + \sigma_w^2)}$	.34 .30	Based on 280 open-pollinated families divided into 10 sets of 28 each and grown on 2 sites several miles apart in south Georgia.
First year height First year height (log transformation)		.34 .47	Based on 191 full-sib families from parents mated in N.C. Design I divided into 10 sets and grown on 2 sites several miles apart in south Georgia.
Pinus sylvestris (Schrum 1969)			
Sixth year height Number of branches Needle length, six years	$\frac{(\sigma_l^2 + \sigma_{r/l}^2 + \sigma_{gl}^2)}{(\sigma_l^2 + \sigma_{r/l}^2 + \sigma_{gl}^2 + \sigma_g^2 + \sigma_r^2)}$	.42 .24 .28	Based on 27 open-pollinated families grown at 6 locations in New York, New Jersey, and Pennsylvania. Within plot variance not available because single-tree plots were used. Because the area of a single replicate was quite small, plot-to-plot (error) variance was included only in the denominator, to partly compensate for environmental variation among trees within plots for natural stands. c^2 probably overestimated.

[1] σ_l^2 = variance among locations
$\sigma_{r/l}^2$ = variance among replications within location
$\sigma_{r/ls}^2$ = variance among replications within location x set combinations
σ_{gl}^2 = genotype x locations plus genotype x replication interaction variance
σ_r^2 = plot-to-plot variance
σ_g^2 = variance among families
σ_w^2 = within plot variance

sive, although not an exhaustive, search of the literature. Only traits of general interest in tree selection are included. Needle length is included because it is considered an environmentally sensitive trait but is often highly correlated with volume growth (Schreiner *et al.* 1962, Squillace and Silen 1962, King and Nienstaedt 1969). In many cases c^2 was probably overestimated but it was nevertheless always below 0.5.

Phenotypic variation studies utilizing a nested sampling scheme can also be used to estimate c^2 as:

$$\hat{c}^2 = \sigma_s^2/(\sigma_s^2 + \sigma_t^2), \qquad (10)$$

where σ_s^2 is the variance among sites, and σ_t^2 is the variance among trees within sites. The difficulty with this approach is that σ_s^2 may contain genetic variance as well as environmental variance and therefore, c^2 would be overestimated. Ideally, the numerator should reflect only environmental and genotype $\times$ environmental variance.

Unfortunately, most investigators present results of phenotypic variation studies only in terms of means and do not publish variance components. Nevertheless, there are some helpful estimates of these components in the literature (Table 3). For some traits, c^2 is large, about 0.5, but for most traits it is much lower. All of the values cited are probably overestimated substantially because genetic variation is confounded with environmental variation in the area and stand components of variance.

A phenotypic variation study in pitch pine (*Pinus rigida* Mill.) was made by the author. Components of variance among 26 areas (from Quebec to Georgia), among stands in areas (2 each in 23 areas, 1 each in 2 areas, and 3 in one area), and trees in stands (6) are presented in Table 4 for various characteristics. Components were calculated for height and dbh both adjusted by regression on age, for double bark thickness adjusted for diameter inside bark, for extracted specific gravity, and for tracheid length. For height, c^2 is slightly higher than in studies cited in Tables 2 and 3. The higher estimate might be attributed to the large region over which c^2 is estimated in this case or simply to a difference among species.

In general, those traits commonly found to have the highest heritabilities, such as specific gravity and fiber or tracheid length, have the highest values of c^2. A probable reason is that the within-plot variance is greater for the more environmentally sensitive characteristics. A small difference in age or competition due to spacing may have large effects on growth traits (Krueger 1967), resulting in high environmental variation among trees within stands, and therefore, proportionally less variation among stands.

For diameter increment, a conservative value for c^2 might be 0.25 while for height increment, 0.45 is about average although generalization is dangerous. For double bark thickness in loblolly pine, c^2 varied from 0.08 to 0.29 (Pederick 1970). Pederick considered double bark thickness an important trait because it was highly correlated with dbh but had a higher heritability. In general, c^2 will lie between 0.2 and 0.5 for most situations and characteristics if the estimates cited are typical.

Relationship Among Comparison and Candidate Trees

Because the greatest proportion of seed from a single tree falls within a short distance, many of the individuals in any small group could be half-sibs of each other and the relationship coefficient of half-sibs is 0.25. If their pollen parent was also identical, the individuals would be full-sibs with a relationship coefficient of 0.5. Therefore, in some situations, the regeneration of a stand by a relatively few seed trees could lead to rather close relationships within the resulting stand although no inbreeding was involved. Even two grandparents in common would lead to a relationship of 0.12.

Some possible ways in which a comparison tree could be related to a candidate tree are diagrammed in Fig. 5. The relationship among the comparison trees themselves is not important; the key is the average of the relationships each bears to the candidate tree. For evaluating the comparison-tree method, r is the average of

TABLE 3. Environmental variance among sites, c^2, as a proportion of the total variance based on phenotypic variation studies.

Species, author, and trait	Construction[1]	$\hat{c}^2$	Comments
Populus deltoides (Farmer and Wilcox 1966)			
Specific gravity	$\frac{(\sigma_a^2 + \sigma_s^2)}{(\sigma_a^2 + \sigma_s^2 + \sigma_t^2)}$	.42	Based on 10 trees in each of 2 areas 150 miles apart in Mississippi. c^2 overestimated because genetic variance among provenances is included in the numerator.
Quercus falcata var. *pagodaefolia* (Farmer and Nance 1969)			
Specific gravity	$\frac{(\sigma_a^2 + \sigma_s^2)}{(\sigma_a^2 + \sigma_s^2 + \sigma_t^2)}$	.29	Based on 10 trees in each of 3 stands in each of 2 areas in west Tennessee and central Mississippi. $\hat{c}^2$ is the average of estimates for 4 10-year segments for specific gravity and 2 rings for fiber length. c^2 overestimated because genetic variance among provenances included in the numerator.
Fiber length		.51	
Platanus occidentalis (Schmitt and Wilcox 1969)			
Height	$\frac{\sigma_s^2}{(\sigma_s^2 + \sigma_t^2)}$	.53	Based on 30 trees in each of 3 stands over 160 miles apart in Mississippi and Louisiana. Stands varied from 20- to 30-years-old and no correction was made for age so that c^2 for height and dbh are definitely overestimated. All values should be considered overestimates because genetic variance among provenances is included in the numerator.
DBH		.33	
Straightness		.47	
Specific gravity		.33	
Fiber length		.41	
Pinus elliottii var. *elliottii* (Squillace 1966)			
Needle length	$\frac{(\sigma_a^2 + \sigma_s^2)}{(\sigma_a^2 + \sigma_s^2 + \sigma_t^2)}$	.46	Based on 5 trees in each of 55 stands throughout the variety range. Estimates for cone and other needle characteristics run from .08 to .54. c^2 certainly overestimated because nursery tests demonstrated that 50 percent of the total genetic variation was among areas and stands and this variance is included in numerator here.

[1] σ_a^2 = variance among areas
σ_s^2 = variance among stands within areas
σ_t^2 = variance among trees within stands

TABLE 4. Phenotypic components of variance (percent) and c^2 for pitch pine over its entire range. c^2 is overestimated because genetic variation among provenances is included in the numerator.

Characteristics	Areas	Stands	Trees	$\hat{c}^2$
Height adjusted for age	27.6	36.4	36.0	.64
DBH adjusted for age	13.5	12.3	74.2	.26
Epicormic sprouting	3.6	16.5	79.9	.20
Bark thickness adjusted for diameter inside bark	13.3	13.3	73.4	.27
Extracted specific gravity[1]/adjusted for age	28.3	6.7	65.0	.35
Tracheid length[1]/adjusted for age	28.3	19.7	52.1	.48

[1] Based on two 12 mm increment cores per tree.

the relationships of each of the comparison trees with the candidate. For five comparison trees, three of which are half-sibs of the candidate tree (though not necessarily of each other) and two of which are unrelated, $r = 0.15$. As the number of comparison trees was increased, it is likely that r would decrease.

While published data permitting the estimation of c^2 are rare, estimates of the relationship among trees within a stand are virtually non-existent. However, such relationships could be very high. From an analysis of the cone serotiny trait in jack pine (*Pinus banksiana* Lamb.), Sittman and Tyson (1971) estimated the inbreeding coefficient, F, among trees as 0.05. The relationship coefficient is twice the inbreeding coefficient so that for jack pine, r would be at least 0.1. This estimate does not take into account relationship among adjacent trees due to common parentage resulting from non-random seed and pollen dispersal. On the other hand, an estimate of F for loblolly pine (*Pinus taeda* L.) was negligible (Franklin 1971).

Distinct differences in isozymes among plots of cryptomeria (*Cryptomeria japonica* Don.) and Japanese arbor-vitae (*Thujopsis dolobrata* Sieb. *et* Zucc.) growing on similar sites within the same forest have been found by Sakai and Park (1971) and Sakai *et al.* (1971). Variation among plots or similarity within suggests genetic drift or relationship because of common ancestry within groups of trees. A similar conclusion could be reached from Wright's (1962) calculations of neighborhood sizes (groups in which mating is essentially at random and beyond which crossing is restricted) based on pollen dispersion studies. Neighborhood size for many tree species ranged from 2.2 to 365 trees. Most estimates were near the lower extreme. Neighborhoods of such small size would be conducive to a high degree of inbreeding and

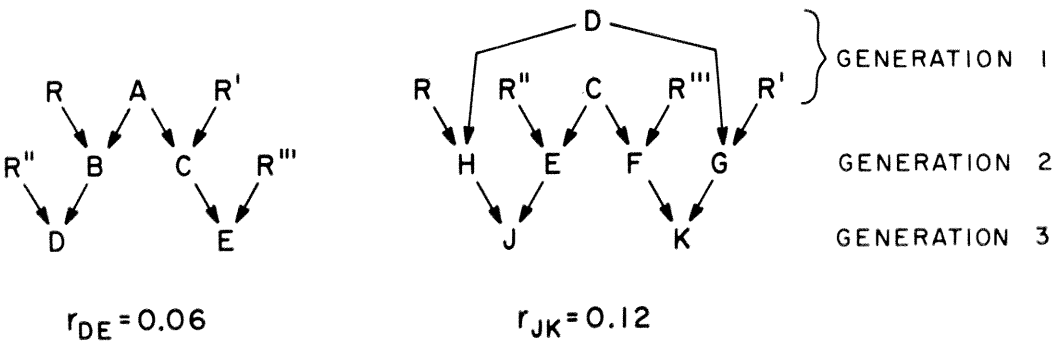

FIGURE 5. *Two of many possible pedigrees leading to relationship among comparison and candidate trees D and E or J and K.*

Wright's calculations suggest a strong possibility of common ancestry among adjacent trees. American elm (*Ulmus americana* L.) was an exception with calculated neighborhoods of 317 to 1,400 trees.

In the International Paper Company–North Carolina State Heritability Study, several reports suggested that trees within naturally occurring groups may be related to each other (Kinloch and Stonecypher 1969, Stonecypher 1966, Ledig and Perry 1967). Within each of 65 arbitrarily delimited groups of loblolly pine, one was chosen as male parent and crossed to several other trees in the group as female parents. The mating pattern was Design I of Comstock and Robinson (1948, 1952). Analysis for several characteristics revealed that the component of variance for males was larger than that for females within males, although the reverse should theoretically be true if the males were unrelated to the females or the females unrelated to each other. The results are evidence of coancestry within naturally-occurring groups (Kinloch and Stonecypher 1969).

E. B. Snyder[2] reported that intercrossing loblolly pine with neighboring trees (trees within 300 ft) resulted in considerable depression of seed yield and of nursery weight and height growth of progeny. The depression was 14, 9 and 2 percent for the three traits respectively. Depression in crossbred progeny indicates that the neighboring trees were related. For slash pine (*Pinus elliottii* Engelm.), inbreeding results in approximately 5 percent reduction in seed yield and 4 percent reduction in height growth for every increase of 0.2 in the relationship coefficient between mated trees (Squillace and Kraus 1963, Gansel 1971), so that the reduction found by Snyder from crossing neighboring trees suggests a relationship coefficient of 0.1 to 0.6.

In practice, the comparison trees are more likely to be related to the candidate tree than would be expected by chance. The comparisons are the best adjacent trees; in other words, trees that have the closest resemblance to the candidate tree are chosen as comparisons, certainly increasing the probability of relationship. Particularly in pioneer species such as pines, aspens, and tulip-poplar (*Liriodendron tulipifera* L.) relationships within small groups of trees seem quite possible, especially in view of the fact that trees with similar, good attributes are chosen as comparison trees. The evidence cited suggests that high values of r are likely.

[2] Personal communication, 1973.

Heritability

The proper estimate of heritability to apply to phenotypic selection is an estimate based on parent-offspring regression or correlation (Falconer 1960). For specific gravity, published estimates for pines run from 0.30 to 0.72 (Illy 1966, Polge and Illy 1968, van Buijtenen 1962, Squillace *et al.* 1962). For height of young trees or seedlings correlated with parental height, estimates have been 0.06 to 0.07 in conifers (Holst and Teich 1969, Squillace *et al.* 1967). For Namkoong's (1970) analysis of the allocation of selection intensity, 0.05 was assumed a reasonable heritability for growth traits in trees. Higher estimates (0.14–0.57) have been obtained when progeny height has been regressed on their parent's mean annual elongation for a 10-year period rather than for the entire rotation (Squillace and Bingham 1954, Steinhoff and Hoff 1971, Snyder 1969). In general, comparison-tree selection will be less effective for growth traits such as height and diameter than for specific gravity. The lower the heritability for a given c^2 and r, the less effective comparison-tree selection is relative to individual selection.

Discussion and Suggestions

It seems quite likely on the basis of published information that parent-offspring heritabilities are less than 0.5 for most characteristics and probably below 0.2 for growth traits. The proportion of variance due to common environment, c^2, is between 0.2 and 0.5 for most traits, being nearer the high value for height and wood properties and nearer the low value for diameter. It is nearly impossible to quantify

the relationship, r, within natural groups of trees, but evidence suggests that such relationships exist and are high, although they should vary substantially among species, depending upon their population structure.

It seems reasonable, therefore, to expect that tree breeders are operating in a range of values in which comparison-tree selection is little more effective than individual selection and for certain traits (for example, diameter growth) most probably results in less genetic gain. Basically, this is because comparison-tree selection may be correcting for family mean values (that is, the additive genotype) rather than for environmental effects. Some empirical results suggest that this is actually the case. Snyder (1969) randomly chose 100 longleaf pine (*Pinus palustris* Mill.) over a three-county area in Mississippi. Gain that would have been obtained by selection of the best 25 percent was calculated based on the correlation of 8-year progeny height with parental height adjusted for age. Alternately, gain could be calculated for selection based on the parental height adjusted for both age plus the mean of 3 comparison trees or on the comparison-tree mean alone. Gain after adjustment for comparison trees was only 50 percent of that for individual-tree selection (that is, adjustment for age only) or 71 percent when adjusted for comparison trees plus age. Thus, use of comparison trees reduced gain relative to individual-tree selection. Relationships among trees in groups probably accounts for the inefficiency of comparison-tree selection in longleaf pine.

The fault with comparison-tree selection is not that bad trees would be chosen, but that good trees would be discarded. The result is that less than the maximum genetic gain will be achieved per unit effort. Further, the comparison-tree method is thought to be a rigorous procedure which in fact is not the case. Gain might be as great from the relaxed procedure of choosing the best tree in a good stand without the expense of scoring it against comparison trees.

Increasing the number of comparison-trees (Fig. 4) will improve the effectiveness of the method. Not only does a larger number of checks increase effectiveness but it would probably reduce the average relationship among trees by utilizing comparison trees not immediately adjacent to the candidate tree. However, comparison trees distant from the candidate will not occupy the same microsite and therefore fail in their primary purpose of correcting for local environment.

The procedure suggested by Brown and Goddard (1961) is a likely one for reducing if not eliminating the defects of within-stand selection. In their scheme, regressions between crown size and basal area increment are determined for the entire stand. Trees are chosen that lie above a given confidence interval for the regression. The regression takes into account the competitive influence to which a tree has been subjected and is theoretically a sound approach, considering the allometric relationship between crown and bole[3] (Stout 1964, Minckler and Gingrich 1970). The method, however, is hardly the usual comparison-tree method and approaches individual-tree selection using a base-line. A disadvantage is that the method would involve a great deal of work to develop a new base for each stand screened for superior trees.

Base-lines could be developed from accumulated comparison-tree data in those programs that have utilized that method. Estimates of c^2 suggest that such base-lines could apply over wide areas. Alternately, multiple regression equations relating volume to age, crown diameter, and other factors could be developed especially for plus-tree selection as advised by Robinson and van Buijtenen (1971). It would seem desirable to make adjustments for all environmental factors possible (as suggested by Squillace 1967) if the cost was not too high. Environmental correction should take the form of site evaluations based on

[3] Stout, Benjamin Boreman. 1967. Allometric constant variation between and within forest tree species. Unpublished Ph.D. dissertation. Department of Botany, Rutgers University, New Brunswick, New Jersey. 82 p.

soil and climatic factors and secondary vegetation rather than evaluations based on a number of nearby check trees. Frequency distributions of traits in natural populations, such as that for diameter growth rate developed for red oak (*Quercus rubra* L.) by Trimble and Seegrist (1970), would be especially helpful in phenotypic selection and might be acquired from presently existing CFI data and other unpublished sources. All such adjustments and corrections as well as the comparison-tree and base-line methods of selection themselves should be evaluated on the basis of realized gains in the progeny.

Conclusions

Comparison-tree selection attempts to correct phenotypic values for environmental effects by scoring plus-tree candidates against the best, adjacent check trees. Individual selection is selection on the basis of an individual's own phenotype without consideration of check trees. Because there is likely to be some relationship among adjacent trees within a stand, the comparison-tree method can be treated as within-family selection. Within-family selection will result in greater gain than individual selection only if the family relationship is very low and if environmental variation (c^2) among groups is very large relative to genetic and within-group environmental variation.

Studies specifically designed to estimate the relationship among trees in groups (such as comparison and candidate trees) is totally lacking. There is a pressing need for basic research on population structure, including estimates of inbreeding, and for more complete reporting of environmental variances in addition to genetic variance in field experiments in order to correctly evaluate selection procedures. A logical choice between comparison-tree selection and individual-tree selection is not possible unless estimates of the variance among groups and knowledge of the population structure (that is, relationship among trees in groups) are known to favor one or the other approach. However, in most pioneer species, comparison-tree selection is suspect. It is likely the worst method advisable for species in which inbreeding is believed to occur, such as tulip-poplar. Though most established tree improvement programs, industrial and governmental, have used comparison-tree selection to establish breeding populations, those contemplating new programs would do well to reexamine the procedure with respect to their species.

Literature Cited

BEINEKE, WALTER F., and WILLIAM J. LOWE. 1969. A selection system for superior black walnut trees and other hardwoods, p. 27–33. *In* Proceedings of the Tenth Southern Conference on Forest Tree Improvement. Houston, Texas.

BROWN, CLAUD L., and RAY E. GODDARD. 1961. Silvical considerations in the selection of plus phenotypes. J Forest 59:420–426.

BUIJTENEN, J. P. VAN. 1962. Heritability estimates of wood density in loblolly pines. Tappi 45:602–605.

———. 1969. Progress and problems in forest tree selection, p. 17–26. *In* Proceedings of the Tenth Southern Conference on Forest Tree Improvement. Houston, Texas.

CECH, FRANKLIN C. 1959. Superior tree selection—a comparison of grading systems, p. 49–52. *In* Proceedings of the Fifth Southern Conference on Forest Tree Improvement. Raleigh, North Carolina.

COMSTOCK, R. E., and H. F. ROBINSON. 1948. The components of genetic variance in populations. Biometrics 4:254–266.

———. 1952. Estimation of average dominance of genes, p. 494–516. *In* Heterosis. Iowa State College Press, Ames.

FALCONER, D. S. 1960. Introduction to quantitative genetics. Ronald Press, New York. 365 p.

FARMER, R. E., JR., and J. R. WILCOX. 1966. Specific gravity variation in a lower Mississippi Valley cottonwood population. Tappi 49:210–211.

———, and W. L. NANCE. 1969. Phenotypic variation in specific gravity and fiber length of cherrybark oak. Tappi 52:317–319.

FRANKLIN, E. C. 1971. Estimates of frequency of natural selfing and inbreeding coefficients in loblolly pine. Silv Genet 20:194–195.

GANSEL, CHARLES R. 1971. Effects of several levels of inbreeding on growth and oleoresin yield in slash pine, p. 173–177. *In* Proceedings of the Eleventh Conference on Southern Forest Tree Improvement. Atlanta, Georgia.

HOLST, M. J., and A. H. TEICH. 1969. Heritability estimates in Ontario white spruce. Silv Genet 18:23–27.

ILLY, GEORGES. 1966. Recherches sur l'amélioration genetique du pin maritime [in French, English summary]. Ann Sci Forest 23:757–948.

KING, JAMES P., and HANS NIENSTAEDT. 1969. Variation in eastern white pine seed sources planted in the Lake States. Silv Genet 18:83–86.

KINLOCH, BOHUN B., JR., and ROY W. STONECYPHER. 1969. Genetic variation in susceptibility to fusiform rust in seedlings from a wild population of loblolly pine. Phytopathology 59:1246–1255.

KRUEGER, KENNETH W. 1967. Investigating dominance in Douglas-fir stands. U S For Ser Res Pap PNW-43. Pacific Northwest Forest and Range Exp Sta, Portland, Ore. 10 p.

LEDIG, F. THOMAS, and THOMAS O. PERRY. 1967. Variation in photosynthesis and respiration among loblolly pine progenies, p. 120–128. *In* Proceedings of the Ninth Southern Conference on Forest Tree Improvement. Knoxville, Tennessee.

MINCKLER, LEON S., and SAMUEL F. GINGRICH. 1970. Relation of crown width to tree diameter in some upland hardwood stands of southern Illinois. U S For Serv Res Note NC-99. North Central Forest Exp Sta, St. Paul, Minn. 4 p.

NAMKOONG, GENE. 1970. Optimum allocation of selection intensity in two stages of truncation selection. Biometrics 26:465–476.

———, E. B. SNYDER, and R. W. STONECYPHER. 1966. Heritability and gain concepts for evaluating breeding systems such as seedling orchards. Silv Genet 15:76–84.

PEDERICK, LEON A. 1970. Variation and inheritance of stem form and bark thickness in young loblolly pine. Technical Report No. 41, School of Forest Resources, North Carolina State University, Raleigh, N. C. 44 p.

PITCHER, JOHN A., and DONALD E. DORN. 1967. A new form for reporting hardwood superior tree candidates, p. 7–12. *In* Proceedings of the Fifth Central States Forest Tree Improvement Conference. Wooster, Ohio.

POLGE, H., and G. ILLY. 1968. Héritabilité de la densité du bois et corrélations avec la croissance étudiées à l'aide de tests non destructifs sur plants de pins maritimes de quatre ans [in French, English summary]. Silv Genet 17: 173–181.

ROBINSON, J. F., and J. P. VAN BUIJTENEN. 1971. Tree grading without the use of check trees, p. 206–211. *In* Proceedings of the Eleventh Conference on Southern Forest Tree Improvement. Atlanta, Georgia.

SAKAI, KAN-ICHI, YASUSADA MIYAZAKI, and TAKASHI MATSUURA. 1971. Genetic studies in natural populations of forest trees. I. Genetic variability on the enzymatic level in natural forests of *Thujopsis dolabrata*. Silv Genet 20: 168–173.

SAKAI, KAN-ICHI, and YOUNG-GOO PARK. 1971. Genetic studies in natural populations of forest trees. III. Genetic differentiation within a forest of *Cryptomeria japonica*. Theor Appl Genet 41:13–17.

SCHMITT, DAN, and JAMES R. WILCOX. 1969. Sycamore variation in the lower Mississippi valley. U S Forest Serv Res Note SO-91. Southern Forest Exp Sta, New Orleans, La. 6 p.

SCHREINER, ERNST J., E. W. LITTLEFIELD, and E. J. ELIASON. 1962. Results of 1938 IUFRO Scotch pine provenance test in New York. U S Forest Serv, Northeastern Forest Exp Sta Pap No 166. Upper Darby, Pa. 23 p.

SCHRUM, GREGORY MICHAEL. 1969. Genetic variance and heritability estimates for Scotch pine: environment and age effects. Publication No. 132–69, Center for Air Environment Studies, Pennsylvania State University, University Park, Pa. 59 p.

SITTMANN, K., and H. TYSON. 1971. Estimates of inbreeding in *Pinus banksiana*. Can J Bot 49:1241–1245.

SNYDER, E. BAYNE. 1969. Parental selection versus half-sib family selection of longleaf pine, p. 84–88. *In* Proceedings of the Tenth Southern Conference on Forest Tree Improvement. Houston, Texas.

SQUILLACE, A. E. 1966. Geographic variation in slash pine. Forest Sci Monogr 10. 56 p.

———. 1967. Selection of superior trees, p. 7–9. *In* Proceedings of the Ninth Southern Conference on Forest Tree Improvement. Knoxville, Tennessee.

———, and R. T. BINGHAM. 1954. Breeding for improved growth rate and timber quality in western white pine. J Forest 52:656–661.

———, R. T. BINGHAM, GENE NAMKOONG, and H. F. ROBINSON. 1967. Heritability of juvenile growth rate and expected gain from selection in western white pine. Silv Genet 16:1–6.

———, R. M. ECHOLS, and KEITH W. DORMAN. 1962. Heritability of specific gravity and summerwood per cent and relation to other factors in slash pine. Tappi 45:599–601.

———, and J. F. KRAUS. 1963. Effects of inbreeding on seed yield, germination, rate

of germination, and seedling growth in slash pine, p. 59–63. *In* Proceedings of a Forest Genetics Workshop. Macon, Georgia.

———, and ROY R. SILEN. 1962. Racial variation in ponderosa pine. Forest Sci Monogr 2. 27 p.

STEINHOFF, R. J., and R. J. HOFF. 1971. Estimates of heritability of height growth in western white pine based on parent-progeny relationships. Silv Genet 20:141–143.

STONECYPHER, ROY W. 1966. The loblolly pine heritability study. Technical Bulletin No. 5, Southlands Experiment Forest. Woodlands Department, Southern Kraft Division, International Paper Co., Bainbridge, Georgia. 167 p.

STOUT, B. B. 1964. Stem-crown relationships in Scotch pine, p. 31–35. *In* Proceedings of the Eleventh Northeastern Forest Tree Improvement Conference. New Brunswick, New Jersey.

TRIMBLE, GEORGE R., JR., and DONALD W. SEEGRIST. 1970. Distribution of diameter growth rates and clear stem lengths as a basis for selecting superior phenotypes. U S Forest Serv Res Pap NE-160. Northeastern Forest Exp Sta, Upper Darby, Pa. 11 p.

WALTERS, J., J. SOOS, and P. G. HADDOCK. 1960. The selection of plus trees on the University of British Columbia Research Forest, Haney, B C. Faculty of Forestry Res Pap No 33, University of British Columbia, Vancouver, Canada. 11 p.

WRIGHT, JONATHAN W. 1962. Genetics of forest tree improvement. Food and Agricultural Organization of the United Nations, Rome. 399 p.