

FAMILY INDICES FOR SEED-ORCHARD SELECTION

by Gene Namkoong¹

Many seed orchard programs include a stage at which clones or seedlings are culled on the basis of progeny tests. Though breeding systems which involve progeny testing differ in efficiency, they all provide information on an individual's breeding value through its own performance and that of parental or seedling relatives. A combined index on any one trait, using information from a set of relatives, is desirable. However, tree breeders appear to be planning only limited use of indices on data from relatives. In so doing, they may be foregoing a considerable advantage, for the increased gain by index selection might often be substantial.

If the phenotypic mean value of an individual is measured by its own performance and that of his relatives, and these values are listed as x_1, x_2, \dots, x_n , then a single total evaluation (y) of these phenotypic means can be used to measure the individual's genetic value (g) where:

$$y = b_1x_1 + b_2x_2 + \dots + b_nx_n = \sum_1^n b_jx_j \quad (1)$$

and where b_1, b_2, \dots, b_n are unknown coefficients which weight the various phenotypic means. The problem is to choose the b_j values so that culling in the seed orchard (on the basis of (y)) will provide maximum gain in (g).

The equation for genetic gain by simple selection in a normally distributed population is:

$$\Delta G = i \sigma_y h^2 = i \sigma_y \frac{\text{Cov}(g, y)}{\sigma_y^2} = i \frac{\text{Cov}(g, y)}{\sigma_y} \quad (2)$$

Where i = the selection intensity (Z/p)
 Z = the ordinate of the normal distribution at the truncation point
 p = the proportion selected
 $\text{Cov}(g, y)$ = the covariance of the individual's true genetic value (g) and the index measurement of that value (y)
 σ_y = the standard error of (y)

Since the value of (i), which depends on the number of genotypes selected, will usually be predetermined, only the righthand ratio of (2) is maximized. This is done by the appropriate selection of weights (b) which in turn requires maximizing the correlation between (g) and (y) or minimizing the error in estimating (g) by the value of (y) (Smith 1936). In a manner analogous to regression theory, least-squares equations can be derived from $g_i = y_i$

$$g_i = y_i + e_i \\ = \sum_j b_j x_{ij} + e_i$$

The least-squares solution for (b) is:

$$\underline{b} = (\sigma_{x_j x_j'})^{-1} (\sigma_{yx_j})$$

Where b = the column vector of weights

$(\sigma_{x_j x_j'})$ = the phenotypic covariance matrix

(σ_{yx_j}) = the column vector of covariances between (y) and the x_j 's

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Indices of this type were developed by Hazel (1943) for use with information on several traits and on several relatives. If the assumptions are approximately fulfilled, the index method will always be at least as efficient, and usually more efficient, than the tandem method (Hazel and Lush 1942, Young 1961).

Clonal Seed Orchards

In clonal orchards each ortet's performance in the woods (as judged by its deviation from local averages or controls), together with the relative mean score of its progeny family, will usually be available. For brevity, ramet data are ignored. To maximize gain, the weighting coefficients are computed from:

$$\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} = \begin{bmatrix} \sigma_{x_1}^2 & \sigma_{x_1 x_2} \\ \sigma_{x_1 x_2} & \sigma_{x_2}^2 \end{bmatrix}^{-1} \begin{bmatrix} \sigma_{gx_1} \\ \sigma_{gx_2} \end{bmatrix}$$

where, b_1 = weight given to wild tree performance
 b_2 = weight given to progeny test performance

$\sigma_{x_1}^2$ = phenotypic variance among wild trees

$\sigma_{x_2}^2$ = phenotypic variance among progeny means

$\sigma_{x_1 x_2}$ = phenotypic covariance of wild tree with progeny test performance (i.e., $\frac{1}{2} \sigma_{A'}^2$)

σ_{gx_1} = covariance of additive genetic value with ortet performance (i.e., σ_A)

σ_{gx_2} = covariance of additive genetic value with progeny performance (i.e., $\frac{1}{2} \sigma_A$)

Since environments generally will be uncorrelated, $\sigma_{x_1 x_2}$ will usually be equivalent to the genetic covariance between parent and progeny mean. The covariance of the clone's additive genetic value and parental (ortet) performance (σ_{gx_1}) will be the total

additive genetic variance of the wild population, and the covariance of clonal value and relative progeny performance (σ_{gx_2}) generally will be one-half of the additive genetic variance in the population of the clones.

When selection in the woods has truncated the population, and this reduced population is brought into the progeny test, a reduction in additive variance will usually have occurred. The selected clonal genotypes are the same as they were in the wild, and no new genotypes are created and no genetic recombination effected between the initial and clonal selection stages. The reduced additive variance ($\sigma_{A'}$), in relation to the wild woods population's σ_A is:

$$\sigma_{A'}^2 = \sigma_A^2 \left[1 - \frac{\sigma_A^2}{\sigma_{x_1}^2} i(i-t) \right]$$

where (t) is the first-stage selection truncation point on a standardized basis (Finney 1956). Though this reduction is often ignored, it may be sufficient to change the index coefficients significantly. Therefore, instances of high and low reductions will be examined.

As an example of a simple situation, assume the following values for a low intensity of wild tree selection and low heritability, and the highly effective reduction of phenotypic variance from 100 in the wild population to 16 in the population of progeny means:

$$\sigma_{A'}^2 = \sigma_A^2, \quad \sigma_{x_1}^2 = 100, \quad \sigma_{x_2}^2 = 16$$

These values give a ratio of $b_1 : b_2$ as 0.3 : 1.0, and maximum selection gain on culling orchard clones will be obtained by evaluating the data with these weights. For example, if the wild-tree and progeny-test scores for two clones are 100 and 150 vs. 120 and 140, respectively, their total scores would be 180 vs. 176.

The joint effects of the size of genetic variance and the relative size of $\sigma_{x_1}^2$ to $\sigma_{x_2}^2$ can be more readily visualized if the ratio of $b_1 : b_2$ is written as:

$$2 - \frac{\frac{1}{2} \sigma_A^2}{\sigma_{x_2}^2} : \frac{\sigma_{x_1}^2}{\sigma_{x_2}^2} - \frac{\sigma_A^2}{\sigma_{x_2}^2}$$

when we assume $\sigma_{A'}^2 = \sigma_A^2$.

Highly effective progeny testing at low heritabilities produces high ratios of $\sigma_{x_1}^2 / \sigma_{x_2}^2$ and a heavier weighting of b_2 relative to b_1 . Figure 1 shows a family of curves based on different levels of σ_A at a standardized $\sigma_{x_1}^2 = 100$. Two cases are presented.

In the left-hand chart, no selection in the woods is assumed and hence $\sigma_{A'}^2 = \sigma_A^2$. In the other chart, a selection of 1 : 10,000 in the woods is assumed and hence:

$$\sigma_{A'}^2 = \sigma_A^2 \left[1 - \frac{\sigma_A^2}{\sigma_{x_1}^2} \right] (.95)$$

Relative weights may be estimated by picking the curve closest to expected genetic variance and finding the point on it closest to the expected ratio of

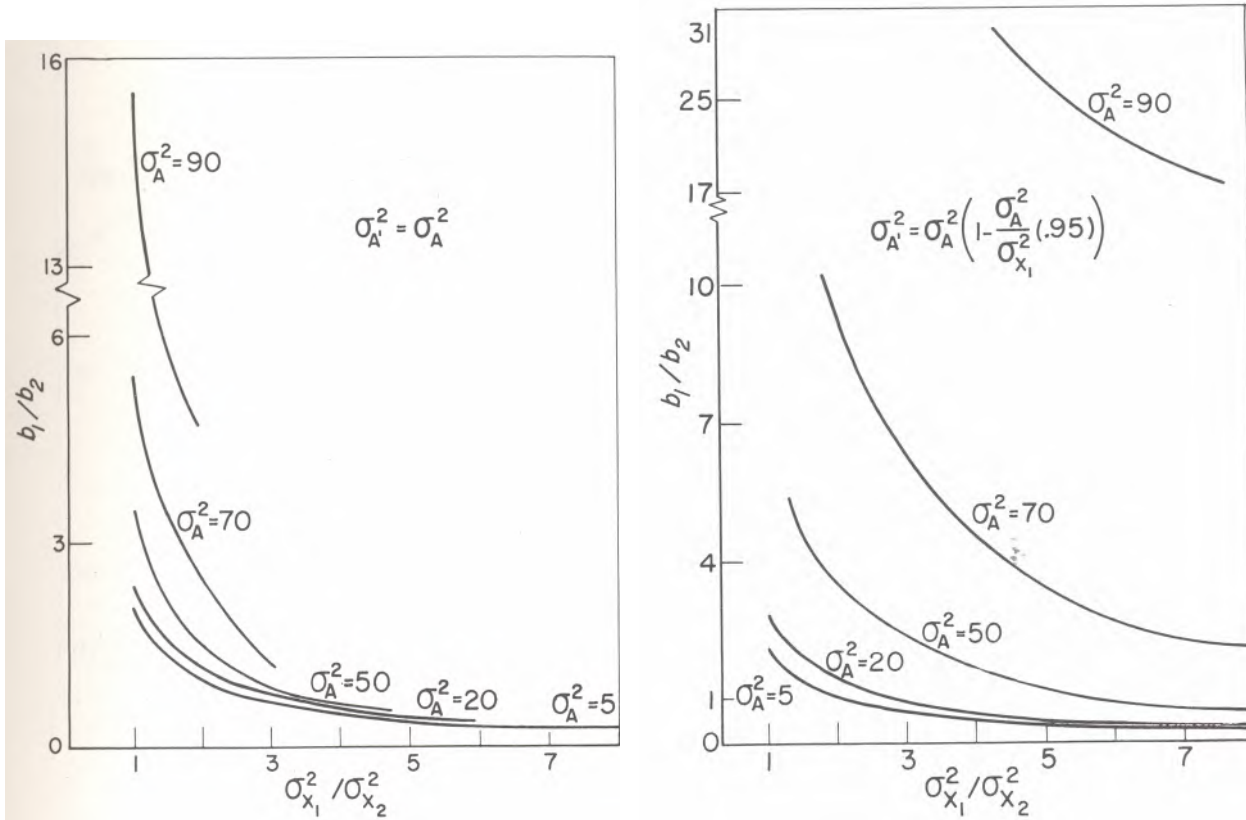


FIGURE 1. — Ratio of optimum weights for wild-tree data (b_1) and progeny mean data (b_2).

$\sigma_{x_1}^2/\sigma_{x_2}^2$. For example, at $\sigma_A^2 = 5$ and $\sigma_{x_1}^2/\sigma_{x_2}^2 = 5$,

the ratio of b_1/b_2 is approximately 0.5. By interpolating between the curves for intermediate levels of σ_A^2 and "woods" selection intensities, one can estimate the relative weights to be assigned for a wide range of heritabilities $\sigma_A^2/100$, phenotypic variance ratios $\sigma_{x_1}^2/\sigma_{x_2}^2$, and selection intensities (i).

For higher σ_A^2 and lower $\sigma_{x_1}^2/\sigma_{x_2}^2$, the weight placed on progeny mean performance decreases.

Expected gains must be compared to evaluate index selection. The gain from selection based on progeny test data only is $i_2 (\frac{1}{2}) \sigma_A'/\sigma_{x_2}$, where i_2 is the selection intensity of the orchard culling. The gain from index selection is:

$$i_2 \frac{\text{Cov}(g, y)}{\sigma_y}$$

where $\text{Cov}(g, y) = (b_1 \ b_2) \begin{bmatrix} \sigma_{gx_1} \\ \sigma_{gx_2} \end{bmatrix}$

$$= (b_1 \ b_2) \begin{bmatrix} b_1 \sigma_{x_1}^2 + b_2 \sigma_{x_1 x_2} \\ b_1 \sigma_{x_1 x_2} + b_2 \sigma_{x_2}^2 \end{bmatrix} \\ = (b_1 \ b_2) \begin{bmatrix} \sigma_{x_1}^2 & \sigma_{x_1 x_2} \\ \sigma_{x_1 x_2} & \sigma_{x_2}^2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} \\ = \sigma_y^2$$

Thus, index selection gain is $i_2 \sigma_y$.

The ratio $(\sigma_y) : (\frac{1}{2} \sigma_A'/\sigma_{x_2})$ is traced for several values of σ_A^2 and $\sigma_{x_1}^2/\sigma_{x_2}^2$ in Figure 2 assuming $\sigma_A^2 = \sigma_A'^2$, and alternatively assuming an initial selection of 1 : 10,000. The superiority of index selection is obvious. The effect of initial selection is to make index selection dramatically more advantageous, since genetic variance in the clonal

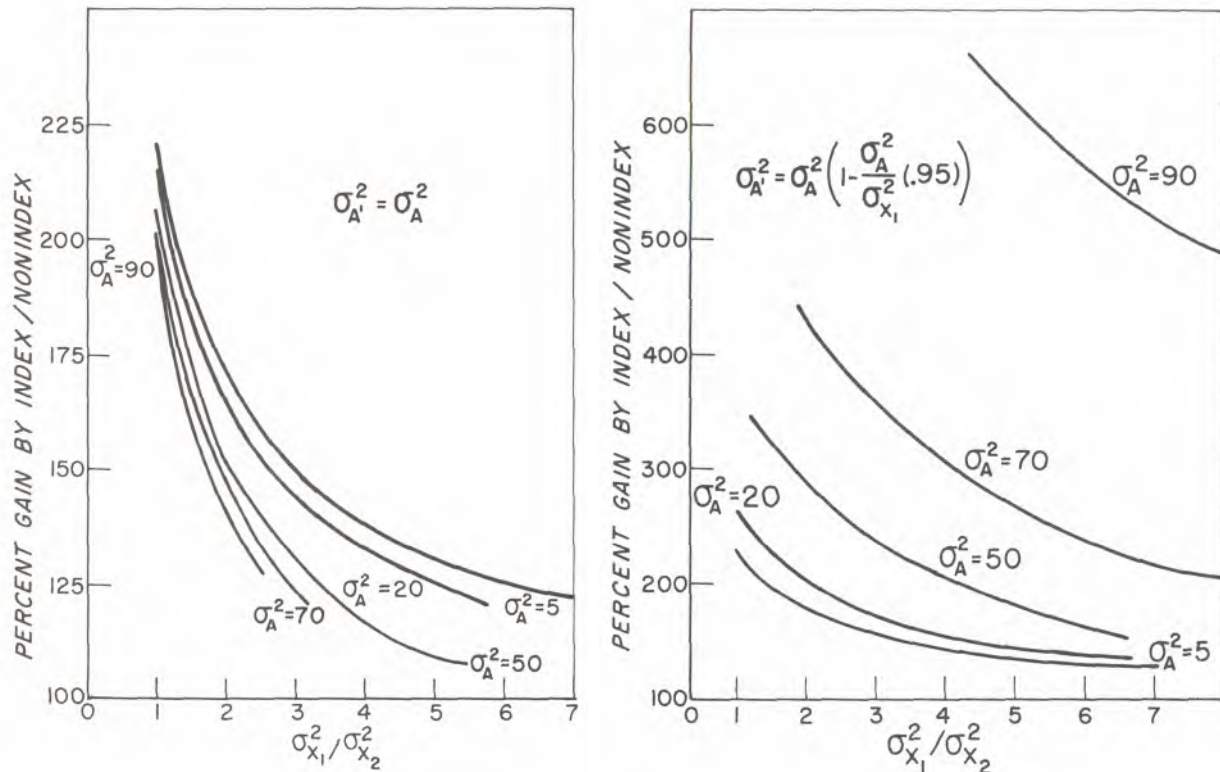


FIGURE 2. — Relative efficiency of index selection over selection on progeny-test data only.

orchard is reduced. For example, under no initial selection and even at low $\sigma_A^2 = 10$ and $\sigma_{x_1}^2 / \sigma_{x_2}^2 = 5$, index selection is 128 percent as effective in obtaining genetic gain as is selection only on the basis of progeny test means. For these same levels of σ_A^2 and $\sigma_{x_1}^2 / \sigma_{x_2}^2$ but under the initial selection of 1 : 10,000, the superiority is 138 percent.

Seedling Seed Orchards

For seedling seed orchards there are three sources of data on each potential orchard tree: the performance of the individual's wild maternal parent, its half-sib family, and its own relative performance in the orchard block. Although we must deal with three items of information, the principles remain the same. The problem is somewhat simplified by ignoring any reduction in genetic variance due to first-stage selection. If many genes at many frequencies are operating, the genetic recombination will regenerate genetic variance so that no increase or decrease is predictable for several generations of selection. It is also necessary to assume that at the time of final evaluation in the seedling orchard only one member, at most, of each half-sib family will be allowed to remain in each unit. The orchard

may be divided into breeding blocks and each unit evaluated separately.

The weights may then be computed from:

$$\begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} = \begin{bmatrix} \sigma_{x_1}^2 & \sigma_{x_1 x_2} & \sigma_{x_1 x_3} \\ \sigma_{x_1 x_2} & \sigma_{x_2}^2 & \sigma_{x_2 x_3} \\ \sigma_{x_1 x_3} & \sigma_{x_2 x_3} & \sigma_{x_3}^2 \end{bmatrix}^{-1} \begin{bmatrix} \sigma_{g x_1} \\ \sigma_{g x_2} \\ \sigma_{g x_3} \end{bmatrix}$$

- where b_1 = weight given to seed parent value
- b_2 = weight given to half-sib family performance
- b_3 = weight given to seedling's own performance
- $\sigma_{x_1}^2$ = phenotypic variance of wild population
- $\sigma_{x_2}^2$ = phenotypic variance of half-sib family means
- $\sigma_{x_1 x_2}$ = phenotypic covariance of half-sib family mean and seed parent value (i.e., $\frac{1}{2} \sigma_A^2$)
- $\sigma_{x_3}^2$ = phenotypic variance among seedlings in an orchard block

$\sigma_{x_1 x_3}$ = phenotypic covariance between wild tree and the individual seedling (i.e., $\frac{1}{2} \sigma_A^2$)

$\sigma_{x_2 x_3}$ = phenotypic covariance of an individual seedling and its half-sib family (i.e., $\frac{1}{4} \sigma_A^2$)

$\sigma_{g x_1}$ = additive genetic covariance of the seedling with its maternal parent (i.e., $\frac{1}{2} \sigma_A^2$)

$\sigma_{g x_2}$ = additive genetic covariance of the seedling with its half-sib family mean (i.e., $\frac{1}{4} \sigma_A^2$)

$\sigma_{g x_3}$ = additive genetic covariance of the seedling with itself (i.e., σ_A^2)

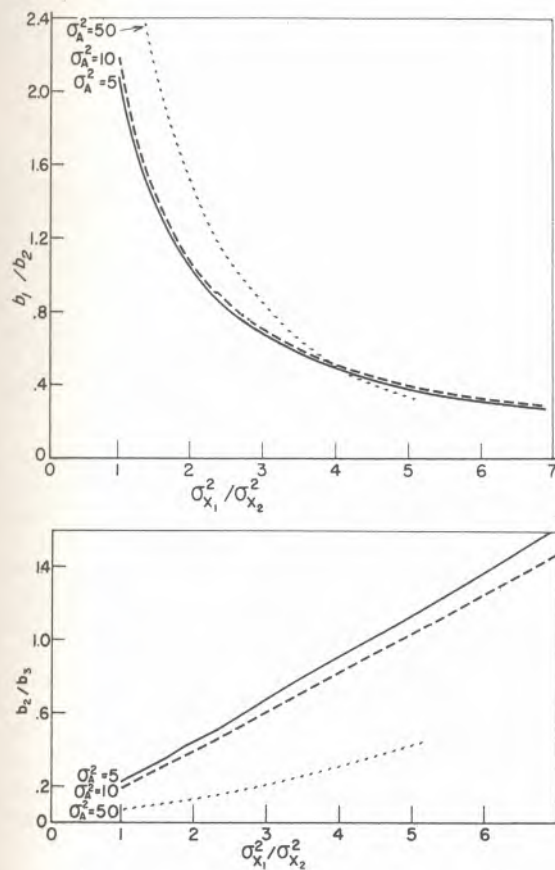


FIGURE 3. — Ratio of optimum weights to give to seed parent (b_1), half-sib family (b_2), and the seedling's own performance (b_3).

Figure 3 shows families of curves similar to those of the previous case. Three levels of σ_A^2 and a range in phenotypic variance ratios are included for estimates of optimum weighting. Again the weights are highly dependent on the relative reduction of phenotypic variance from $\sigma_{x_1}^2$ to $\sigma_{x_2}^2$. If either b_1 , b_2 , or b_3 are set equal to 1, the other two relative weights can be found from the figures. It can also be seen that, as heritability increases and the ratio ($\sigma_{x_1}^2 : \sigma_{x_2}^2$) approaches 1, the relative weight placed on family mean performance decreases very rapidly.

An evaluation of index selection can be made on the basis of an orchard selection of 1 : 10. In the tandem selection recommended by Goddard and Brown (1961) and Wright and Bull (1963), a selection would first be made on family means, and then on individuals within these families. Two cases may be arbitrarily chosen for comparison: one is the selection of 1 : 5 for family and 1 : 2 for individuals; the other is the selection of 1 : 3.16 for families and also 1 : 3.16 for individuals. Both schemes result in a final selection of 1 : 10. The ratios of gain by index vs. the former scheme are traced for several levels of genetic variance and testing effectiveness in figure 4. The ratios of gain by index vs. the latter 1 : 3.16 selections are similarly traced in figure 5. Again, the superiority of index selection is obvious.

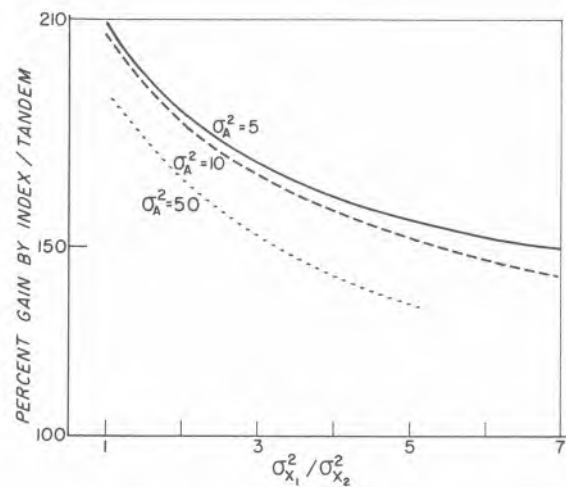


FIGURE 4. — Relative efficiency of seedling index selection over tandem selection at intensities of 1:5 for families and 1:2 for individuals.

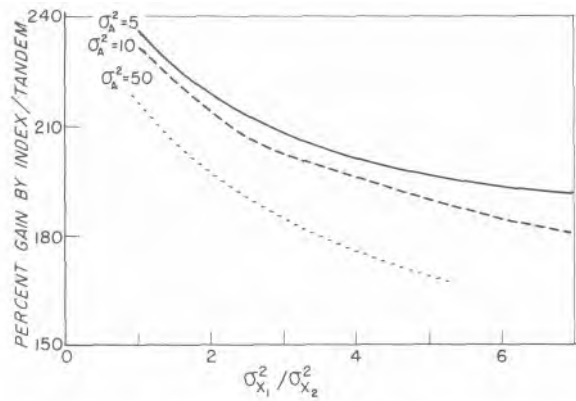


FIGURE 5. — Relative efficiency of seedling index selection over tandem selection at intensities of 1:3.16 for families and 1:3.16 for individuals.

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