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Heritability and Gain Concepts for Evaluating Breeding Systems such as Seedling Orchards¹⁾

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Introduction

Unbiased estimates of the gains and the time it takes to achieve them are required to weigh costs against benefits for various selection and mating systems. Methods for computing genetic gain are numerous, and various and sometimes contradictory concepts have been published (e.g., WRIGHT, 1960; HATTEMER, 1963; HANSON, 1963). As a guide for the tree breeder the anatomy of heritability is here examined, procedures for estimating gain are simplified by a method of accumulating the gains from the various selection stages, and comparisons are made of expected progress for several methods.

The statistical basis for the concept of genetic gain is simple linear regression $(Y - \bar{Y}) = b(X - \bar{X})$, or $y = bx$. Let us assume that the independent variable (X) is the yield or value measured on selected units of a large population: trees within a macrosite, replicated families in a plantation, or any natural unit of trees. It is more convenient to use (x), the difference between the mean of the original unselected population and the mean of the selected individuals (i.e. the selection differential). If (y) is the predicted gain, then the regression coefficient (b) represents the expected rate of response between the selection attempted and the magnitude of the genetic gain expected. This is heritability in the sense of HANSON (1963). The regression coefficient is,

by standard definition, $\frac{\text{Cov}(x, y)}{\text{Var}(x)}$, i.e. the ratio of the covariance between the predictor variable (x) and the predicted variable (y) in the numerator to the variance of the predictor in the denominator. No discussion will be presented on methods for obtaining estimates of the components of variance and covariance except when the method of estimation affects the meaning and use of the component. Rather, it is assumed that proper estimation experiments will supply precise values for the components, and that the principal problem addressed is that of using the components appropriately for specific ways of obtaining genetic gain.

First consider the *denominator* (variance of x). It is commonly regarded as being composed of two distinct parts, i.e. genetic differences and sampling error, either experimental or genetic. The sampling error can be reduced by

more extensive sampling of effects that cause errors in properly rating a selection unit with respect to the other units:

- 1) The genotype-macrosite error variance. Since most programs specify selection only when gross environmental or macrosite effects are comparable, these effects contribute little to error. However, the interaction between macrosite effects and genotypes, independent of the macrosite effects themselves, may be large. In at least some environments, the genotypes depart from their relative average behavior, the size of the departure being measured by the interaction variance (σ_{ge}^2). The interaction will cause an error in evaluating relative merit.
- 2) The error variance of large plots. This is the failure of the genotypes to behave relatively the same between the blocks or environmental replications within a macrosite (σ_p^2).
- 3) The error variance of the small plot or microsite. This error (σ_t^2) is due to within-plot differences, i.e., microsite differences (σ_w^2) plus the remaining genetic variability among individuals within plots.

For instance, if unrelated trees are scattered at random within a macrosite class, the variance among them will be: $V(x) = \sigma_w^2 + \sigma_p^2 + \sigma_{ge}^2 + \sigma_G^2$ (the total genetic variance).

If the trees are in families with n to a plot and with r blocks on e macrosites, the variance among family means will be: $V(x) = \sigma_t^2/nre + \sigma_p^2/re + \sigma_{ge}^2/e + \sigma_f^2$ (genetic variance among families). An optimum allocation of n, r, and e in properly designed experiments can minimize this sampling error portion of the variance for a given cost, or can minimize cost for a given variance. By the definition of heritability, the denominator cannot be smaller than the numerator.

In some cases, sampling errors of genetic nature must be considered. For example, when the predicted (y) populations are half sibs but the predictor (x) population estimates are based on a finite sample of full-sib families, the covariance is based on general combining ability but the variance includes specific combining ability. The contribution of this sampling error to the denominator is the specific combining ability variance divided by the number of males.

Secondly, the *numerator* of the regression coefficient Cov(x, y) can be similarly examined once it is known which selection units are being used, the degree to which they vary, and how sampling errors can be reduced. This numerator is the genetic covariance between the material measured in tests, such as those designed to assess the value of the wild-tree selections or progeny mean, and the future

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material on which the actual gain is to be achieved, such as the expected growth of trees grown from seed-orchard seeds. Because this covariance is an expected cross-product between the two materials, its size depends on their common effects.

Generally speaking, two types of effects control the covariance between the test and expected materials: the genotype-environment interaction effects and those more purely genetic. The former can be included in the covariance if the test sites are similar to the intended planting sites. This situation may exist when selection is for single special sites, or for response to specific fertilizers. Since relations between test and forest environments usually are not very clear, the interaction should generally be eliminated from the covariance. Often, however, genotypes are tested and compared on a single site. Then the interaction of genotypes and environments is inseparable from the genetic effects and, if large, appreciably reduces the accuracy with which the genotypes can be compared and causes gain overestimation. Thus, any interaction between particular genotypes on special sites will be lost when the genotypes are planted elsewhere. This interaction should therefore be estimated and separated from the more purely genetic effects.

The other genetic effects common to the test and commercial materials include all genetic sources of variability that are repeatable in the ensuing generation. When clones, pure lines, or varieties are selected for self propagation, all of the genetic variability is included in the covariance of test to commercial material. When genetic recombination occurs, the ancestral relationships between the test and commercial materials must be sought for determination of the covariance numerator. The covariances are actually derived from genetic variance components as detailed elsewhere (e. g., FALCONER, 1960).

To illustrate that the desired covariance is estimated by the genetic components, consider several forms of family selection. If half-sib families are selected on the basis of their half-sib collateral relatives, the proper numerator is the half-sib covariance ($\frac{1}{4} \sigma_A^2$). If unrelated full-sib families are tested and the selected families are reproduced by remating their specific parents, the numerator is the full-sib covariance ($\frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_D^2$), where σ_D^2 is the dominance genetic variance. Epistatic variances are assumed to be negligible and are ignored here.

If selection for general combining ability is to be effective, family differences must exist, or synonymously, the additive variance (σ_A^2) must be greater than zero. Therefore, such procedures as the F-test of family differences are good for establishing the possibilities of gain, provided that the experiments are sufficiently sensitive. Tests of significance of constructed heritabilities are unnecessary except as fiducial statements may be useful (Bogyo, 1964).

Composition of Published Heritabilities

If the concepts of the previous section are accepted the meanings of published heritabilities require review. Table 1 lists interpretable heritabilities according to our understanding of the published information. We accept the assumption, implicit or stated in many of the papers, that the open-pollinated progenies of a tree represent half-sibs, though its strict validity is doubtful (NAMKOONG, in press). Also, it is evident from the genetic component column that effects of genotype-location interaction have not been

estimated but are included in the genetic component. Therefore, some of these heritabilities are of doubtful value.

Worse than these defects, however, were errors which precluded our listing 50 percent of the heritabilities reviewed. Often the composition of the numerator or denominator was unclear and hence the heritability was uninterpretable. The other errors were faulty or inaccurate procedures such as:

- 1) Incorrect analysis of the mating design. For instance, diallels were analyzed as if the same trees did not often serve as both male and female.
- 2) Lack of true replication.
- 3) Intentionally selected populations analyzed for the selected trait.
- 4) Incorrect estimators or assumptions in the analysis.

It is apparent from Table 1 that the effects of genotype-location interactions have not been estimated thus far, and that heritability contains a variety of components and meanings in forestry literature.

Estimating Gain for Various Seed-Orchard Methods

To estimate genetic gain with a properly constructed heritability regression, it is only necessary to determine the mean selection differential. The breeding programs most common in forestry involve several stages of selection, each having its own selection differential and regression. It is easiest to consider the gain from each stage separately. To illustrate the procedure of estimating gains, several breeding schemes in use or proposed will be compared first in general terms and then as actual gains for fictitious test materials.

Since selection is on the basis of a culling level or a fraction of the selection population saved, the selection differential is indirectly measured. If a normal distribution of values (i. e., evaluation of individual wild trees or of average family performance) exists with a variance of σ_u^2 , the mean difference can be derived to be $i\sigma_u$ where i is the selection intensity. The values of i for various population sizes are given by FISHER and YATES (1953, Table XX), and FALCONER (1960, pages 193–194). Gain, therefore, is $i\sigma_u b$, where b = heritability for the selection system

$$b = \frac{k\sigma_A^2}{\sigma_u^2}$$

$$\text{Therefore, gain} = \frac{i k \sigma_A^2}{\sigma_u}$$

where k = fraction of the total additive genetic variance in the covariance of additive values (e. g., $k = \frac{1}{4}$ for half-sibs).

Gains for Individual Cases

One simple method of breeding would be to establish a clonal seed orchard without any testing beyond comparison of the ortets' wild performances. This is simple mass selection. As an example, hereafter referred to as Case 1, it may be assumed that phenotypic selections are made in the wild and a clonal orchard established for the production of commercial seed by free mating among the selected genotypes. These ortets are to be evaluated on their deviations from locality averages or otherwise adjusted for direct effects of macrosite and age. The commercial seed will be planted within a region to which it is adapted but otherwise on sites relatively uncorrelated with the site of the wild tree. The proper heritability for gain estimates includes the covariance numerator, which is the individual's genetic co-

Table 1. — Composition of heritabilities reported for forest trees.

Species and trait studied	Numerator		Denominators			h ² Construction
	Genetic nature of materials	Genetic ¹⁾ components reported	Trees in replications	Replications in locations	Locations	
<i>Betula verrucosa</i> Height (STERN 1962)	16 half-sib and 8 full-sib families (among others reported)	$\sigma_A^2 + \sigma_{AE}^2$	20 in plots	4	1	$\frac{\sigma_A^2 + \sigma_{AE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_A^2 + \sigma_{AE}^2}$
<i>Cryptomeria</i> Height and others (SAKAI and HATAKEYAMA 1963)	Unrelated plantation trees	$\sigma_G^2 + \sigma_{GE}^2 + \sigma_p^2$	1—10 in plots	1	1	$\frac{\sigma_G^2 + \sigma_{GE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_{GE}^2 + \sigma_G^2}$
(TODA 1958)	Unrelated plantation trees	$\sigma_G^2 + \sigma_{GE}^2 + \sigma_p^2$	7 in plots	1	1	$\frac{\sigma_G^2 + \sigma_{GE}^2 + \sigma_p^2}{\sigma_w^2 + \sigma_p^2 + \sigma_{GE}^2 + \sigma_G^2}$
<i>Picea abies</i> Rooting and others (MERGEN 1962)	30 clones	$\sigma_G^2 + \sigma_{GE}^2$	2 random	5	1	$\frac{\sigma_G^2 + \sigma_{GE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_G^2 + \sigma_{GE}^2}$
<i>Pinus elliottii</i> Wood characters (EINSPAHR <i>et al.</i> 1964)	5 clones	$\sigma_G^2 + \sigma_{GE}^2$	4 random	1	1	$\frac{\sigma_G^2 + \sigma_{GE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_G^2 + \sigma_{GE}^2}$
(SQUILLACE <i>et al.</i> 1962)	8 half-sib families	$\sigma_A^2 + \sigma_{AE}^2$	2—6 random	7	1	$\frac{\sigma_A^2 + \sigma_{AE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_A^2 + \sigma_{AE}^2}$
	7 clones	$\sigma_G^2 + \sigma_{GE}^2$	2—8 in plots	7	1	$\frac{\sigma_G^2 + \sigma_{GE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_G^2 + \sigma_{GE}^2}$
(ZOBEL <i>et al.</i> 1962)	39 clones	$\sigma_G^2 + \sigma_{GE}^2$	1 single-tree plots	5+6	1+1	$\frac{\sigma_G^2 + \sigma_{GE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_G^2 + \sigma_{GE}^2}$
Height and others (BARBER 1964)	19—21 half-sib families	$\sigma_A^2 + \sigma_{AE}^2$	± 15—20 in plots	3—4	1	$\frac{\sigma_A^2 + \sigma_{AE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_A^2 + \sigma_{AE}^2}$
(SQUILLACE and BENGTSON 1961)	8 half-sib families	$\sigma_A^2 + \sigma_{AE}^2$	2—6 random	7	1	$\frac{\sigma_A^2 + \sigma_{AE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_A^2 + \sigma_{AE}^2}$
<i>Pinus elliottii</i> Branch diameter (STRICKLAND 1964)	15 half-sib families	$\sigma_A^2 + \sigma_{AE}^2$	1 single-tree plots	5	1	$\frac{\sigma_A^2 + \sigma_{AE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_A^2 + \sigma_{AE}^2}$
Gum yield (GODDARD <i>et al.</i> 1962)	158 clones	$\sigma_G^2 + \sigma_{GE}^2$	1 single-tree plots	2	1	$\frac{\sigma_G^2 + \sigma_{GE}^2}{\frac{\sigma_w^2 + \sigma_p^2}{2} + \sigma_G^2 + \sigma_{GE}^2}$
<i>Pinus monticola</i> Height and epicotyl height (HANOVER and BARNES 1963)	4 ♂ × 5 ♀	$\sigma_A^5 + \sigma_{AE}^2$	± 24 in plots	4	1	$\left[\frac{\sigma_A^2 + \sigma_{AE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_A^2 + \sigma_{AE}^2} + \frac{(\sigma_D^2 + \sigma_{DE}^2)}{4} \right]$
<i>Pinus ponderosa</i> Height (CALLAHAM and HASEL 1961)	80 half-sib families	$\sigma_A^2 + \sigma_{AE}^2$	16 in plots	2	1	$\frac{\frac{1}{4}(\sigma_A^2 + \sigma_{AE}^2)}{\frac{\sigma_w^2}{16} + \sigma_p^2 + \frac{1}{4}(\sigma_A^2 + \sigma_{AE}^2)}$
<i>Pinus radiata</i> Wood characters (NICHOLLS <i>et al.</i> 1964)	33 half-sib families	$\sigma_A^2 + \sigma_{AE}^2$	3 in plots	5	1	$\frac{\sigma_A^2 + \sigma_{AE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_G^2 + \sigma_{GE}^2}$
<i>Pinus sylvestris</i> Foliage characters (WRIGHT 1963)	130 half-sib families	$\sigma_A^2 + \sigma_{AE}^2$	12—20 in plots	4	1	$\frac{\frac{1}{4}(\sigma_A^2 + \sigma_{AE}^2)}{\frac{\sigma_w^2 + k\sigma_p^2}{4k} + \frac{1}{4}(\sigma_A^2 + \sigma_{AE}^2)}$
<i>Pinus taeda</i> Wood characters (GOGGANS 1962)	6+7 half-sib families	$\sigma_A^2 + \sigma_{AE}^2$	5+8 in plots	2+2	1	$\frac{\frac{1}{4}(\sigma_A^2 + \sigma_{AE}^2)}{\frac{\sigma_w^2}{20 \text{ or } 32} + \frac{\sigma_p^2}{2} + \frac{\sigma_A^2 + \sigma_{AE}^2}{4}}$
Wood and diameter (STONECYPHER <i>et al.</i> 1964)	100 half-sib families	$\sigma_A^2 + \sigma_{AE}^2$	5 or 3 in plots	4	1	$\frac{\sigma_A^2 + \sigma_{AE}^2}{\sigma_w^2 + \sigma_p^2 + \sigma_G^2 + \sigma_{GE}^2}$

¹⁾ $\sigma_G^2 = \sigma_A^2 + \sigma_D^2$ (ignoring epistasis) = Total genetic variance. σ_{GE}^2 = Total genetic by gross environment interaction.

variance with its own performance, and a denominator composed of the variance among individuals unrelated ancestrally or environmentally. The gain, therefore, is:

$$i_1 \frac{\sigma_A^2}{\sigma_1} \text{ where } k \text{ of the previous formula} = 1.$$

Generally, i_1 will be for the upper 1 percent of the population of total tree values or higher and therefore will be 2.66 or greater. For a selected proportion of .001, i_1 would be 3.36. σ_A^2 is the total additive genetic variance for a large, random-mating population and the phenotypic variance of the wild stand is $\sigma_1^2 = \sigma_w^2 + \sigma_p^2 + \sigma_{ge}^2 + \sigma_G^2$.

A second example (Case 2) would be a clonal seed orchard with additional culling of the poorer clones on the basis of progeny tests (ZOBEL and McELWEE, 1964). Initial procedures would be similar to those for Case 1, except that, say, four times as many ortets might be included in the orchard. Culling according to progeny-test results will remove up to three-fourths of the original clones and the rest will intermate freely. Some additional gain could be obtained by properly weighting the phenotypic with the progeny-test information, but this additional complication will not be considered here. For the progeny tests, let us assume that 4 tester males will produce the progeny for planting n seedlings per plot in r replications on e environments. In all progeny tests the genotype-environment interaction will be omitted from the numerator.

To the initial mass-selection gain, a gain from progeny testing will be added. It can be estimated if a normal distribution of the original wild population is assumed. Thus, two stages of gain are achieved, that of the second stage being obtained at the cost of a lower first-stage selection intensity. The second-stage gain is on the basis of the half-sib relationship between test and predicted materials, because the offspring of the progeny test are derived from matings in which usually only the female ortet is of interest; i.e., the covariance is that of half-sibs. However, the commercial seeds are derived from ortets of which both male and female are selected participants. The selection differential is therefore double that for half sibs. Because the judgment of ortet value is made on the basis of family means, the denominator of heritability is the variance of family means σ_2^2 . The gain from this procedure may, therefore, be written as:

$$i_2 \frac{\sigma_A^2}{\sigma_1} + 2i_3 \frac{1/4 \sigma_A^2}{\sigma_2}$$

$$\text{where } \sigma_2^2 = \frac{\sigma_t^2}{nre} + \frac{\sigma_p^2}{re} + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_{mf}^2}{4} + \frac{\sigma_A^2}{4}$$

and, σ_{mf}^2 = male \times female interaction component.

σ_A^2 is smaller than σ_1^2 because the population has been phenotypically reduced, but the population will be nearly normal unless σ_A^2 is very high. According to FINNEY (1956), $\sigma_A^2 = \sigma_1^2 (1 - \beta v')$ where $\beta = \sigma_A^2 / \sigma_1^2$, and v' is a variable dependent on i_2 and tabulated by FINNEY.

For a .004 (or 1/250) selection in the wild, and a .25 (or 1/4) selection in families, a combined selection intensity of .001 (or 1/1000) is derived. Therefore, $i_2 = 2.96$ and $i_3 = 1.27$ in sufficiently large population for this final selection percentage.

An alternative is seedling seed orchards with open pollination, as proposed by WRIGHT and BULL (1963). In this Case 3, let us assume that wild trees are first selected on

the basis of their own phenotypes and that open-pollinated seeds are collected. These seeds are grown and the presumed half-sib families allowed to mate among other selected families to produce the commercial seed. The family and individual performances at a suitable age will later serve for culling families and individuals. These open-pollinated families must be planted on representative macro-sites. This is family and individual selection wherein the test materials themselves are used for seed production.

Assume the same number of seedling families as for Case 2, and that the seedlings will not be treated to vitiate the family test design, and that inbreeding among selections within families is prevented. Families and individuals within families at each location will be selected for commercial seed production. For the final seed orchard, reduction to about a tenth of the original number of individuals was recommended by GODDARD and BROWN (1960). The data of WRIGHT and BULL (1963) indicated an approximate 14 percent family selection and 33 percent selection intensity of individuals in families. This is a combined intensity of slightly better than 1 in 20. An approximate apportionment of the selection intensities as recommended in the literature would therefore be in the range of .25 (1/4) for family selection and .20 (1/5) for individual selection, i.e., $i_3 = 1.27$ for family and $i_4 = 1.40$ for individual within-family selection. The gain for this system is based on a initial mass selection at half the intensity of Case 2 plus two second-generation gain components. The first gain is in the family-testing stage; it is made on the basis of a numerator of the covariance of half-sibs ($1/4 \sigma_A^2$) since the open-pollinated families are being mated among one another. The second gain is based on individual variation within half-sib families and, therefore, is made on the basis of the total within-family genetic variance, or $3/4 \sigma_A^2$ (FALCONER, 1960). This is the total genetic variance after the variance among the half-sib families is removed. Therefore, the gain for Case 3 is composed of half the mass selection gain of Case 2 and two progeny-test gains as follows:

$$1/2 i_2 \frac{\sigma_A^2}{\sigma_1} + i_3 \frac{1/4 \sigma_A^2}{\sigma_3} + i_4 \frac{3/4 \sigma_A^2}{\sigma_4} \text{ where}$$

$$\sigma_3^2 = \frac{\sigma_t^2 + n\sigma_p^2}{nre} + \frac{\sigma_{ge}^2}{e} + 1/4 \sigma_A^2$$

$$\sigma_4^2 = \sigma_w^2 + \sigma_p^2 + \sigma_{ge}^2 + (3/4) \sigma_A^2 + \sigma_D^2$$

$$\sigma_D^2 = \text{the genetic dominance variance.}$$

Since genetic recombination occurs between the wild tree selection and family selection among many trees, the genetic variance may be assumed to be regenerated, so that $\sigma_A^2 = \sigma_1^2$. These formulations are different from those published by WRIGHT (1960) and by STERN and HATTEMER (1964).

Another alternative (Case 4) would be to establish a seedling seed orchard system as above for Case 3 but to make controlled pollinations among the first-stage selections. The first-stage mass-selection gain would not be halved as in Case 3, but otherwise the same procedures could be followed. The gain is:

$$i_2 \frac{\sigma_A^2}{\sigma_1} + i_3 \frac{(1/4) \sigma_A^2}{\sigma_3} + i_4 \frac{(3/4) \sigma_A^2}{\sigma_4}$$

The procedures outlined for Cases 1-4 are the only ones presently used, but many others exist. The last method (Case 5) is an untried possibility exemplifying the way in which the specific combining ability or dominance variance

may be used. Mass selection is followed by the establishment of several seed orchards, each containing only two clones. Each clone is used only once and is paired with another at random, or according to flowering time, or by any method that may enhance hybrid combining ability. The test matings will be made between these two ortets, and testing will, therefore, be on the basis of unrelated full-sib families. All of the original seed orchards may be kept and graded according to information from all the progeny tests and other sources. The commercial seed may be taken from the best orchards only, or, in years when demand is high, from all or almost all of the orchards. Thus, selection intensity may be varied according to yearly requirements. Of several practical difficulties in such a procedure, the costs of increased border areas, and increased selfing, are paramount.

In terms of gain this alternative has sizable advantages. A system comparable in selection intensity to Cases 1-4 might include the first-stage acceptance of eight times the number of clones in the first stage of Case 2. The progeny test would be the same size as that of Case 2, for two clones provide one test cross per family instead of the eight from four male testers. The selection intensity of the progeny test may then be quadrupled since there are four times as many clonal pair families to select among as there are single-clone families in Case 2.

The system would add a progeny test gain to the mass selection gain. The former is based on full-sib relations that include a portion of the dominance variability. The success of the method depends on the strength of this dominance variance. The expected gain is:

$$i_5 \frac{\sigma_A^2}{\sigma_1} + i_6 \frac{(1/2) \sigma_A^2}{\sigma_5} + i_6 \frac{(1/4) \sigma_D^2}{\sigma_5}$$

where $\sigma_5^2 = \frac{\sigma_t^2}{nre} + \frac{\sigma_p^2}{re} + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_A^2}{2} + \frac{\sigma_D^2}{4}$

For a mass selection intensity of .032, or 1/8 of that of Case 2, $i_5 = 2.24$ and $i_6 = 1.97$ (for progeny test selection of 1/16).

Other procedures are possible. For instance, the method of testing with clones, as suggested by LIBBY (1964), is an attractive alternative presently limited only by the uncer-

tainties of cloning and the size of nonadditive genetic variances. However, the methods illustrated above by the five cases provide several alternatives, and four are in common use. Schedules of operations and modifications (B and C) are explained in Table 2.

Gain Comparisons

The gains for the five cases can be directly compared by the formulae above, but Table 3 offers simplified comparisons between pairs of systems. These comparisons are correct when the total selection intensity of .001 is subdivided as indicated by the footnote. The gain comparisons depend on the size of the heritability denominators.

It is instructive to simulate near-maximum and near-minimum effectiveness in progeny or family tests for given heritabilities. The breeder will obtain results between these extremes. One may simulate by assigning a value of 100 to the total of the variance components of the heritability denominator. That is, $\sigma_t^2 + \sigma_p^2 + \sigma_{ge}^2 + \sigma_A^2 = 100$. Then the contributions of the components are varied according to what may happen under conditions of varying testing effectiveness.

For example, a highly effective test may be simulated by allotting 95 percent of the total variance to within plots (σ_t^2) by assuming that the test consists of 100 seedlings per family ($nr = 50, e = 2$). The reducible variance in the denominator is thus 1 percent of its former size.

An ineffective test may be simulated by allotting 95 percent of the total variance to σ_{ge}^2 . With two testing locations, the reducible variance in the denominator is now decreased by 50 percent. Here the breeder has failed to distribute his seedlings optimally.

The total gains calculated for each type of orchard at 20 percent and at 5 percent heritability under highly effective and under ineffective testing are given in Tables 4 and 5. They show that the choice of method depends on the heritability and the effectiveness with which the error is reduced in testing.

The time required to obtain gains has seldom been considered in breeding annual crops. DICKERSON and HAZEL (1944) evaluated generation or cycling time in animal breeding and CAMPBELL (1964) presented data for forestry. A cycle is defined as the interval between initial selection and the time when the same phase in the breeding cycle is available

Table 2. — Assumed schedules of operations in orchard cycles.

Type of orchard	Selection and seed collection, 1 yr.	Grafting, 2 yr.	Controlled pollinations		Seed available in quantity from grafts, 7 yr.	Tests, 17 yr. ¹⁾	Second generation old enough to select, 15 yr.	Total years to second-generation orchard
			In stands 6 yr.	In orchards 4 yr.				
(1) Mass-selection clonal orchard	x	x			x		x	25
(2) Progeny-tested clonal orchard	x	x		x		x	x	39
				(x)	x	(x)	x	25
(3) Open-pollinated seedling orchard	x					x	x	33
(4) Control-pollinated seedling orchard	x		x			x	x	39
(5) Two-clone orchard	x	x		x		x-2	x	37
				(x)	x	(x-2)	x	25

¹⁾ Selection is at 15 years but 2 years are added because, in pines, the cones on selected trees were previously pollinated by unwanted males. For simplicity of calculations, the partially improved seed during these 2 years is ignored.

The 2-year interval does not occur in the 2-clone orchards, since males are not rogued. Here the selection is complete at 15 years and is designated as x-2.

²⁾ A is the clonal orchard procedure in which the second generation is started after progeny testing.

B and C use commercial plantings as the sources of the second generation. Since the progeny tests are grown simultaneously with the second generation, parentheses have been used to indicate that neither the years for pollination nor for testing are included in total time: In B only female parentage can be identified; in C both parents are identified.

Table 3. — Formulae for comparing gains expected from five breeding methods.¹⁾

	Case 1. — Mass-selection clonal orchard	Case 2. — Progeny-tested clonal-orchard	Case 3. — Open-pollinated seedling orchard	Case 4. — Control-pollinated seedling orchard
Case 2	2 vs. 1 $1.27/\sigma_2$ vs. $0.80/\sigma_1$			
Case 3	3 vs. 1 $\frac{.32}{\sigma_3} + \frac{1.05}{\sigma_4}$ vs. $\frac{1.91}{\sigma_1}$ or if $\sigma_1 \approx \sigma_4$, $\frac{\sigma_1}{\sigma_3}$ vs. 2.7	3 vs. 2 $\frac{.32}{\sigma_3} + \frac{1.05}{\sigma_4}$ vs. $\frac{1.49}{\sigma_1} + \frac{.57}{\sigma_2}$ or if $\sigma_1 \approx \sigma_4$, $\sigma_2 \approx \sigma_3$, 2 is always greater than 3		
Case 4	4 vs. 1 $\frac{.32}{\sigma_3} + \frac{1.05}{\sigma_4}$ vs. $\frac{.42}{\sigma_1}$ or if $\sigma_1 \approx \sigma_4$ 4 is always greater than 1	4 vs. 2 $\frac{.32}{\sigma_3} + \frac{1.05}{\sigma_4}$ vs. $\frac{.57}{\sigma_2}$ or if $\sigma_2 \approx \sigma_3$, 4.34 vs. $\frac{\sigma_4}{\sigma_2}$	4 vs. 3 $\frac{1}{2}$ vs. $\frac{1}{4}$ 4 is always greater than 3	
Case 5 (two-clone orchards)	5 vs. 1 $\frac{\sigma_1}{\sigma_5} (76 + .42 \frac{\sigma_D^2}{\sigma_A^2})$ vs. 1	5 vs. 2 $\frac{.89}{\sigma_5} + \frac{.49}{\sigma_5} \frac{\sigma_D^2}{\sigma_A^2}$ vs. $\frac{.74}{\sigma_1} + \frac{.57}{\sigma_2}$ or if $\sigma_2 \approx \sigma_5$	5 vs. 3 $\frac{.75}{\sigma_1} + \frac{.89}{\sigma_5} + \frac{.49}{\sigma_5} \frac{\sigma_D^2}{\sigma_A^2}$ vs. $\frac{.32}{\sigma_3} + \frac{1.05}{\sigma_4}$ or if $\sigma_1 \approx \sigma_4$, $\sigma_3 \approx \sigma_5$ 5 is always greater than 3	5 vs. 4 $\frac{.89}{\sigma_5} + \frac{.49}{\sigma_5} \frac{\sigma_D^2}{\sigma_A^2}$ vs. $(\frac{.74}{\sigma_1} + \frac{.32}{\sigma_3} + \frac{1.05}{\sigma_4})$ or if $\sigma_1 \approx \sigma_4$, $\sigma_3 \approx \sigma_5$, $\frac{\sigma_1}{\sigma_5} (.32 + .28 \frac{\sigma_D^2}{\sigma_A^2})$ vs. 1

¹⁾ On the basis of a .001 final selection intensity and the arbitrary allocation of selection intensities described in the literature:
 $i_1 = 3.36$, $i_2 = 2.96$, $i_3 = 1.27$, $i_4 = 1.40$, $i_5 = 2.24$, and $i_6 = 1.97$

Table 4. — Genetic gains from different types of orchards at a 5% heritability with effective and ineffective progeny testing.

Type of orchards		Selection intensity	Genetic gain			Operational value	
			Total gain	Years in cycle	Rate of gain per year	Years in cycle	Value per year
Highly effective testing							
(1) Mass-selection clonal orchard		$i_1 = 3.36$	1.68	25	.067	35	1.20
(2) Progeny-tested clonal orchard	A	$i_2 = 2.96$	3.33	39	.085	49	2.12
		B	$i_3 = 1.27$	2.40	25	.096	35
(3) Open-pollinated seedling orchard	}	$i_2 = 2.96 \times 1/2$	2.35	33	.071	51	1.52
		$i_3 = 1.27$					
		$i_4 = 1.40$					
(4) Control-pollinated seedling orchard			3.08	39	.079	63	1.91
(5) Two-clone orchard	A	$i_5 = 2.24$	2.96	37	.080 ¹⁾	47	1.86
	C	$i_6 = 1.97$	2.96	25	.118 ¹⁾	35	1.48
Ineffective testing							
(1) Mass-selection clonal orchard		$i_1 = 3.36$	1.68	25	.067	35	1.20
(2) Progeny-tested clonal orchard	A	$i_2 = 2.96$	1.90	39	.049	49	1.39
		B	$i_3 = 1.27$	1.69	25	.068	35
(3) Open-pollinated seedling orchard	}	$i_2 = 2.96 \times 1/2$	1.49	33	.045	51	.96
		$i_3 = 1.27$					
		$i_4 = 1.40$					
(4) Control-pollinated seedling orchard			2.23	39	.057	63	1.38
(5) Two-clone orchard	A	$i_5 = 2.24$	1.99	37	.054 ¹⁾	47	1.34
	C	$i_6 = 1.97$	1.99	25	.079 ¹⁾	35	1.12

¹⁾ This rate of gain is partially dependent on dominance effects and may not be wholly cumulative unless a form of reciprocal recurrent selection is followed.

Table 5. — Genetic gains from different types of orchards at 20% heritability with effective and ineffective testing.

Types of orchards	Selection intensity	Genetic gain			Operational value		
		Total gain	Years in cycle	Rate of gain per year	Years in cycle	Value per year	
Highly effective testing							
(1) Mass-selection clonal orchard		$i_1 = 3.36$	6.72	25	.269	35	4.80
(2) Progeny-tested clonal orchard	A	$i_2 = 2.96$	9.92	39	.254	49	6.75
	B	$i_3 = 1.27$	7.92	25	.317	35	4.86
(3) Open-pollinated seedling orchard		$i_2 = 2.96 \times \frac{1}{2}$	7.72	33	.234	51	5.00
		$i_3 = 1.27$					
		$i_4 = 1.40$					
(4) Control-pollinated seedling orchard			10.68	39	.274	63	6.61
(5) Two-clone orchard	A	$i_5 = 2.24$	10.72	37	.290 ¹⁾	47	6.85
	C	$i_6 = 1.97$		25	.429 ¹⁾	35	5.52
Ineffective testing							
(1) Mass-selection clonal orchard		$i_1 = 3.36$	6.72	25	.269	35	4.80
(2) Progeny-tested clonal orchard	A	$i_2 = 2.96$	7.36	39	.189	49	5.45
	B	$i_3 = 1.27$	6.64	25	.266	35	4.46
(3) Open-pollinated seedling orchard		$i_2 = 2.96 \times \frac{1}{2}$	6.01	33	.182	51	3.89
		$i_3 = 1.27$					
		$i_4 = 1.40$					
(4) Control-pollinated seedling orchard			8.97	39	.230	63	5.55
(5) Two-clone orchard	A	$i_5 = 2.24$	7.36	37	.199 ¹⁾	47	5.06
	C	$i_6 = 1.97$	7.36	25	.287 ¹⁾	35	4.27

¹⁾ This rate of gain is partially dependent on dominance effects and may not be wholly cumulative unless a form of reciprocal recurrent selection is followed.

for starting a new generation at the improved level. Conceivably, some agencies will strive for maximum one-cycle gain even though it takes somewhat longer. Others will want fast one-cycle gains at the cost of less total gain in the cycle. In the long run, frequent cycles of lesser gains may give higher returns than fewer cycles of greater gain.

For illustration, assume that the times required for the various stages of operation are as in Table 2. The rate of

gain per year is calculated by dividing the total gain by the time from start of initial selection to start of a new cycle; e. g., in Table 5, Case 2A, highly effective testing, 9.92 is divided by 39 years = .254 units of genetic gain per year. The rate-of-gain values are given in Tables 4 and 5 and some are illustrated in Figure 1.

The foregoing rates of genetic gain are based on the gain obtained at the end of a cycle and are the figures of use to

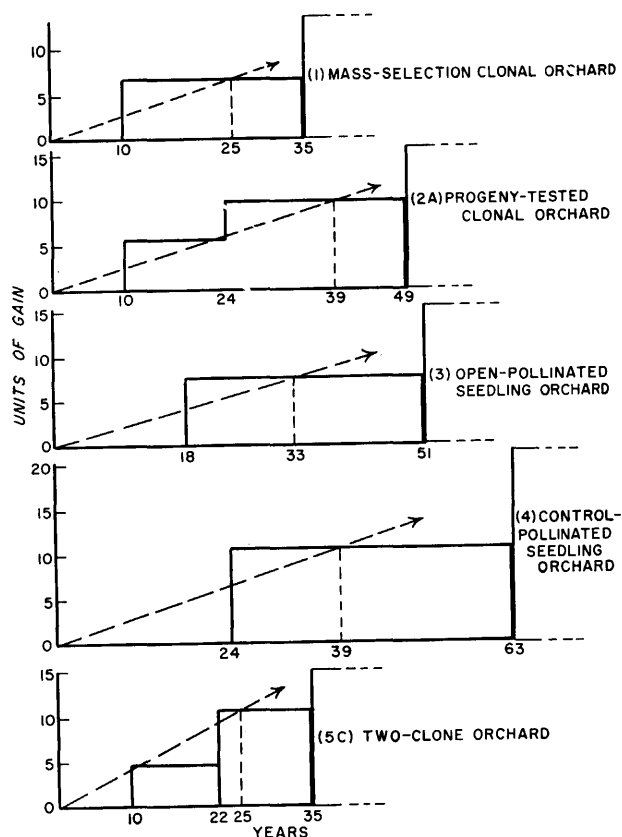


Figure 1. — Breeding cycles, with rates of gain.

tree breeders. However, a seed producer may wish to determine the value of the orchard on the basis of realized gains over the lifetime of the orchard. We call this evaluation "cumulative operational value" to distinguish it from rate of genetic gain; for example, in Case 2A, ineffective testing, Table 5.

The origin represents the beginning of a selection program. The first solid vertical line indicates the first year of commercial seed production and, for seedling orchards, also when roguing becomes effective. The dotted vertical line indicates the year when the new population is old enough to permit recurrent selection; the arrow indicates rate of genetic gain, the stepped terminal line is the time when the first-cycle orchard may be abandoned, and when the second-cycle orchard begins producing.

The diagrams assume 20 percent heritability, effective progeny testing, and the arbitrary breeding-cycle intervals listed in Table 2. The reader should consult Tables 4 and 5 for numerical examples and for calculations based on other combinations of heritability and effectiveness of testing and for systems 2B and 5A.

$$\begin{array}{l} \text{1st stage} \qquad \qquad \text{1st and 2nd stage} \\ \hline 5.92 \text{ gain} \times 14 \text{ years} + 7.36 \text{ gain} \times 25 \text{ years} = 5.45 \text{ units of} \\ \hline \text{(10 + 39) years} \qquad \qquad \text{cumulative} \\ \qquad \qquad \qquad \qquad \text{operational} \\ \qquad \qquad \qquad \qquad \text{value per year} \end{array}$$

Of the 7.36 units of total gain, 5.92 were obtained in the first stage or unrogued orchard, and 1.44 by roguing. The first-stage gain was realized when the orchard was between 10 and 24 years old — that is, between the times the uncultured orchard first produced quantities of seed and when roguing first yielded its additional value. The total gain of 7.36 units is then maintained until age 49, when the pro-

duction of second-cycle orchards is expected to start. Other values are computed in Tables 4 and 5.

Discussion

Relative total gain of the breeding methods may change radically with the many factors in the computations. Not all of the factors can be kept comparable for fair comparison of the systems. For instance, in a particular situation, selection may be more efficient in Case 2 than 4, or vice versa; also, with increased selection intensities (because of a possible expanded selection program) one or the other of the systems would be favored. In some cost situations Cases 1 and 3 may be much better than the other programs. Similarly, the sizes and distribution of the variances obviously have profound influence in the comparisons.

A second basis for comparing systems is on the rates of gain. Gain per year depends on the time required to bring the improved generation to the stage at which a new cycle of selection may be initiated. The possibility of reducing time factors, with consequent improvements in rate of gain, may influence the choice of system. For example, in some systems it may be feasible to shorten the time required for profuse flowering, for an adequate test, or for growing the trees. Production of a new generation simultaneously with progeny testing is preferable to a tandem schedule and in some schemes may be accomplished by keeping track of the parentage of the commercial plantings so they can be used for recurrent selection.

Finally, gains should be expressed in terms of unit cost, especially since costs enter even into the determination of the selection intensity and hence the size of the gain. If costs are roughly known, evaluations are that: If progeny testing is inefficient or expensive, clonal orchards without tests are attractive. If testing is desired but seedling seed orchards are difficult to establish, clonal orchards with tests would seem best. If clonal orchards are expensive, the seedling orchard with testing would be highly commendable. If flexibility and genetic diversity are desirable, two-clone orchards become attractive.

We feel that this paper establishes the principles and derives the formulas by which various breeding systems can be compared. Individual organizations may now wish to make evaluations considering their own policies and using their own figures instead of our fictitious ones.

Summary

Tabulation of heritability ratios in publications on forest trees showed that many ratios contained unclear or unestimated components in the variance denominator and covariance numerator. Estimates of gain are inaccurate unless they include all major components; and usually genotype-environment interactions should be excluded.

The problem of how to determine the expected gain from multistage breeding systems was solved by developing a simple method of accumulating gains at each stage.

Various breeding system, including clonal and seedling seed orchards, were evaluated for total gain and rate of gain. No one system was superior under all variations of heritabilities, selection intensities, and other factors considered.

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Studies of Selection of Frost-Hardy *Cryptomeria* I.

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1. Introduction

Every winter, 5 to 12 year cryptomerias growing in southern Hokkaido invariably suffer frost damage to some extent. This area is near the northern economical limit of growing cryptomeria. The minimum and average temperatures in this area are about -17°C and -5°C , respectively. In this area, the snow cover differs considerably with the year and locality. During the winter of 1964–65, the snow depth ranged from 10 to 20 cm in flat lands. The soil continues to freeze from early December to late March and the depth of frozen soil is about 15 cm in midwinter. When the snow cover exceeds 30 to 50 cm from early winter, the soil generally remains unfrozen, but the cryptomeria stems at 5 to 10 cm below the snow surface usually remains in a frozen state for a considerable length of time.

Investigations of the damage of cryptomeria over several years revealed that most of the cryptomerias growing on the lee side of wind breaks and in low lands were generally undamaged, but those in wind-swept areas or on raised ground were seriously damaged during winter. In addition, the leaves and small twigs on the northwest side of trees suffered serious damage. It may be added that even in a considerably damaged trees, the lower parts of the stem and the roots usually remained undamaged.

Frost damage of young cryptomeria in Japan Proper is usually observed on the south side of the stem 10 to 15 cm above ground. However, frost damage seldom occurs in Matsumae district.

From these results, it may be surmized that wintering young cryptomerias in frozen soil and wind-swept areas are damaged by desiccation due to an unbalance of water in leaves, small twigs and terminal buds resulting from freezing of soil or stem for a considerable length of time. It may also be surmized that dry winds are one of the main factors contributing to damage in the wintering young trees in frozen soil.

As result of investigations of damage during winter continued for several years, it was also observed that even in the same meteorological and topographical conditions, the degree of damage differs remarkably among trees, even among trees in the same stands or groves, and that there seems to be some relation between the degree of winter damage and tree-type of cryptomeria.

To obtain more information and to establish a method of selecting hardier trees, cryptomeria grown in Matsumae district in southern Hokkaido was classified into 3 groups and the degrees of desiccation resistance and frost-hardiness in these tree-types were studied under varying conditions for 3 years.

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