INDIVIDUAL TREE SELECTION IN FOREST GENETICS

by Jonathan W. Wright

A selective breeding program includes both the phenotypic selection of individuals that are superior in some particular respect and the mating of those individuals in such a way as to produce superior progenies. Individual trees and their progenies are the units of study. This is in contrast to racial selection or species selection, where populations are the units of study. This distinction is important. If the job of unravelling the large differences among species and races were to be tackled on an individual-tree basis, it would never end. On the other hand, if the individual-tree records were to be discarded when studying variation within an ecotype, genetic improvement would be negligible.

In this field there are three major jobs ahead in the next few years. They are the determination of: (1) the relative amounts of individual-tree and racial variation within species, (2) the heritabilities of the most important characters, and (3) the best mating methods to achieve maximum improvement with the least effort.

In the time available we shall be able to discuss adequately only one aspect of this subject: the genetic gains with different breeding methods. We shall consider separately those situations in which all the genetic variance is additive and when an appreciable portion of the genetic variance is nonadditive.

With Additive Genetic Variance

If it is assumed that all the genetic variance is additive, the first- and second-generation genetic gains can be calculated for most types of situations from the following formulas given by Lerner. 2/

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(1) ΔG = Genetic gain after mass selection = $\underline{i}\ \underline{h}^2$ = Selection differential x heritability (narrow sense)

(2) $\underline{i}$ = Selection differential = Mean of selected parents - mean of unselected population

(3) $\underline{h}^2$ = Heritability (narrow sense) = $\dfrac{2\,(V_m + V_f)}{V_m + V_f + V_{fm} + V_e}$

V_m, V_f, V_{fm}, and V_e = Variances due to male parent, female parent, male-female interaction, and error respectively, as derived from a 2-parent progeny test.

Formula (1) is used to estimate gain from mass selection (from selecting the best parents, growing their progeny without records as to parentage, and re-selecting among the progeny). It is also used to estimate gain from clonal selection (selecting the best parents, clonally propagating them, and selecting the best clones as parents without reference to the performance of their progeny). In the latter case the heritability is higher than in ordinary mass selection because a clonal test gives a more reliable estimate of the genetic potentiality of a tree.

The gains from family selection (selecting the best families after a progeny test) and from combined family + mass selection (selecting the best individuals within the best families) can be computed from the following formulas:

(4) $$\frac{\Delta G_f}{\Delta G} = \frac{\text{Genetic gain from family selection}}{\text{Genetic gain from mass selection}}$$

$$= \frac{1 + (n - 1)\,r^G}{\sqrt{n\,(1 + (n - 1)\,r^P)}}$$

2/ Lerner, I. M. The genetic basis of selection. 298 pp., illus. New York. 1958.

$$(5)\quad \frac{\Delta G_c}{\Delta G} = \frac{\text{Genetic gain from family + mass selection}}{\text{Genetic gain from mass selection}}$$

$$= \sqrt{1 + \frac{(r^G - r^P)^2}{1 - r^P} \cdot \frac{n - 1}{1 + (n-1)r^P}}$$

ΔG_f = genetic gain from family selection

ΔG_c = genetic gain from combined family and mass selection

r^G = genetic correlation between individuals due to common descent

r^G = 0.5 in full-sib families

= 0.25 in half-sib families

r^P = phenotypic correlation between individuals

= $r^G h^2$ if there are no common environmental effects on members of the same family. This is true if the families are tested in 1-tree plots.

The heritability of a forest tree character is usually determined from a progeny test, in which the error variance is much lower than in a wild stand. Therefore it is necessary to multiply a "progeny test" heritability by a constant, k, when calculating genetic gains based upon selection in a wild stand. This constant is defined as:

$$(6)\quad \underline{k} = \frac{\text{Heritability in a wild stand}}{\text{Heritability determined from a progeny test}}$$

In order to calculate genetic gains it is necessary to know the general breeding procedure. Several different types of forest tree breeding methods are summarized below.

TYPE I. Mass selection of open-pollinated seedlings. Collect open-pollinated seed from selected wild females, bulk the seed, establish a first-generation seed orchard, thin the orchard to the best trees after a test rotation, and harvest the seed for F2 commercial plantings.

TYPE II. Mass selection of control pollinated seedlings. Make selected x selected matings, bulk the seed, establish an F1 seed orchard, thin to the best trees after a test rotation, and harvest seed from the F1 for F2 commercial plantings.

Thinning a seed production area to the best phenotypes constitutes a variant of this method. All matings are among selected trees even though no controlled pollination is involved. However, the selection differential and therefore the genetic gain is much lower than in a planted seed orchard where each selected phenotype can be the best of hundreds of thousands.

TYPE III. *Selection of half-sib families, using open-pollinated progenies.* Collect open-pollinated seed from selected wild females, establish a replicated 1-parent progeny test, thin to the best families after a test rotation, and harvest seed for F2 commercial plantings.

TYPE IIIa. *Selection of individuals within half-sib open-pollinated families.* Proceed as in Type III but thin the F1 progeny test to the best individuals in the best families.

TYPE IV. *Selection of half-sib control-pollinated families.* Cross each selected wild female with a pollen mix containing pollen from several selected males, establish a replicated F1 progeny test, thin the progeny test to the best families, and harvest seed for commercial production or continued experimental work.

TYPE IVa. *Selection of individuals within half-sib open-pollinated families.* Proceed as in Type IV but thin the Fl progeny test to the best individuals in the best families.

TYPE V. *Selection of full-sib families.* Cross each selected wild female with several selected males, keep the seed separate by male and female parents, establish a replicated F1 progeny test, thin to the best families, and harvest seed for commercial production or continued experimental work.

TYPE Va. *Selection of individuals within full-sib families.* Proceed as in Type V but thin the F1 progeny test to the best individuals in the best families.

TYPE VI. *Clonal selection.* Establish a clonal planting with the selected wild parents, thin at the end of a rotation to the best parental-generation clones.

TYPE VII. *Half-sib family selection plus clonal seed orchard.* Establish a 1-parent progeny test as in Types III or IV. At the same time establish a clonal planting of the same parents. After a test rotation thin the clonal planting to the clones which were the best parents.

TYPE VIII. *Full-sib family selection plus clonal seed orchard.* Establish a 2-parent progeny test as in Type V. At the same time establish a clonal planting of the same parents. After a test rotation thin the clonal planting to the two clones with the best demonstrated specific combining ability. A clonal planting thinned to the several clones with demonstrated specific combining ability belongs in Type VII rather than Type VIII. The clones will inter-pollinate among each other at random and therefore not produce the particular superior families for which they were selected.

TYPE VIIIa. Full-sib family selection plus delayed clonal seed orchard. Establish a 2-parent progeny test as in Type V. After it is evaluated, establish a planting of the two clones with the best demonstrated specific combining ability. This 2-clone planting will furnish superior seed from the time it starts to fruit until the end of the second test rotation. This is much less expensive than a Type VI$_{I}$I seed orchard but the harvest of good seed is delayed for several years.

The genetic gains for each of these breeding methods are summarized symbolically in table 1. In the preparation of that table it is assumed that the genetic variance remains constant in the first two generations and that the number of parents is approximately the same for all breeding methods.

In seed orchards of Types II, IV, V, VI, VII, and VIII, the seed produced before the orchard is thinned is k AG superior to average. This is the mass selection gain due to the phenotypic selection of the original parents in wild stands. In plantings of Types I and III the gain is only half as much because only the female parents were selected.

Any progeny test or seed orchard established with seedlings of the parental generation belongs to the F1 generation and produces seed from which the F2 generation will be grown. That is the reason for indicating two components for the genetic gain of all seedling seed orchards of Types I to V. The first component (2 k AG or k AG) is the gain from mass selection in the parental generation, and the second component is the family or mass selection gain in the first generation. The situation is different with clonal seed orchards of Types VI to VIII. In such orchards there can be only the one component of gain due to selection in the parental generation because the clones belong to the parental generation. Even if a clonal project were to be continued for 15 generations the clonal plantings would always be one generation behind the seedling progeny test which they were meant to supplement.

Table 1.--Summary of genetic gains with different methods of selection

Type of planting		Thinned to	Genetic mean of seed produced--	
			Before thinning	After thinning
MASS SELECTION METHODS. SEEDLING SEED ORCHARDS WITH NO PROGENY TESTING.				
I.	Selected x OP	Best trees	$\frac{1}{2}k\Delta G$	$(\frac{1}{2}k-1)\Delta G$
II.	Selected x selected (using pollen mix)	Best trees	$k\Delta G$	$(k+1)\Delta G$
FAMILY SELECTION METHODS. SEEDLING SEED ORCHARDS WITH PROGENY TESTS.				
III.	Selected x OP	Best families	$\frac{1}{2}k\Delta G$	$\frac{1}{2}k\Delta G + \Delta G_{hs}$
IIIa.	Selected x OP	Best trees in best families	$\frac{1}{2}k\Delta G$	$\frac{1}{2}k\Delta G + \Delta G_{c}$
IV.	Selected x selected (using pollen mix)	Best families	$k\Delta G$	$k\Delta G + \Delta G_{hs}$
IVa.	Selected x selected (using pollen mix)	Best trees in best families	$k\Delta G$	$k\Delta G + \Delta G_{c}$
V.	Selected x selected (separate pollens)	Best families	$k\Delta G$	$k\Delta G + \Delta G_{fs}$
Va.	Selected x selected (separate pollens)	Best trees in best families	$k\Delta G$	$k\Delta G + \Delta G_{c}$
CLONAL SEED ORCHARDS, WITH OR WITHOUT ACCOMPANYING PROGENY TESTS.				
VI.	Selected clones	Best clones	$k\Delta G$	ΔG_{cl}
VII.	Selected clones	Clones with best general combining ability	$k\Delta G$	ΔG_{hs}
VIII.	Selected clones	2 clones with best specific combining ability	$k\Delta G$	ΔG_{fs}
VIIIa.	Two selected clones with best specific combining ability	No thinning	ΔG_{fs}	ΔG_{fs}

Explanation of symbols used:

ΔG = gain from mass selection
ΔG_{hs} = gain from half-sib family selection
ΔG_{fs} = gain from full-sib family selection
ΔG_{c} = gain from combined family and mass selection
ΔG_{cl} = gain from clonal selection
OP = open-pollinated

Table 2 contains numerical estimates of the genetic mean of the seed produced by the different types of progeny tests or seed orchards after the end of the first test rotation. The values were calculated on the assumption that the "progeny-test" heritability is twice the "wild stand" heritability (k = 1/2) and that 100 seedlings of each family are grown in randomized 1-tree plots.

In this table it is noticeable that half-sib family selection is less productive than simple mass selection at heritabilities above approximately 0,25 (compare Types I and III or Types II and IV as to gain). But at low heritabilities the family selection methods--especially full-sib family plus mass selection (Type Va)--are the most productive. This is reasonable because the higher the heritability the more closely does the phenotype approach the genotype.

The genetic gains are less in seed harvested from clonal seed orchards than from the progeny tests which they accompany (compare Type IVa to VII, Type Va to VIII). This is because the clones belong to the parental generation. They are the same clones used to produce the superior families in the progeny test but there is no opportunity for practicing selection in two successive generations.

With Non-Additive Genetic Variance

If an appreciable portion of the genetic variance is non-additive it is impossible to find general solutions for relative genetic gains such as are given in table 2 because formulas 1 to 5 are applicable only to cases of additive variance. However, the symbolism presented in table 1 applies to cases of non-additive as well as of additive genetic variance.

If all the variance is additive the genetic mean of a progeny is equal to the genetic mean of the parents. This is not the case with non-additive variance because a progeny may be superior to the mean of its parents because of epistasis or dominance. Thus with non-additive variance the relative superiority of full-sib to half-sib and of half-sib to mass selection is greater than shown in table 2.

Whether the genetic variance is additive or non-additive the clones comprising a thinned Type VII orchard are the same parental clones used to produce the superior families of a Type IV seedling orchard. But if

Table 2.--Relative genetic gains from seed produced by various types of seed orchards after thinning. Calculated with formulas 4 and 5 on the assumptions that n = 100 seedlings per progeny planted in 1-tree plots, that the heritability in wild stands is half that in progeny tests (k = 1/2), and that all genetic variance is additive

Type of planting	Thinned to	Genetic mean of seed produced after thinning if heritability is--				
		.10	.15	.20	.25	.30
MASS SELECTION METHODS		----------------ΔG unit------------				
I. Sel. x OP	Best trees	1.25	1.25	1.25	1.25	1.25
II. Sel. x sel. (pollen mix)	Best trees	1.50	1.50	1.50	1.50	1.50
FAMILY SELECTION METHODS						
III. Sel. x OP	Best families	1.63	1.44	1.30	1.25	1.14
IIIa. Sel. x OP	Best trees in best families	1.83	1.66	1.55	1.48	1.42
IV. Sel. x sel. (pollen mix)	Best families	1.88	1.69	1.55	1.50	1.39
IVa. Sel. x sel. (pollen mix)	Best trees in best families	2.08	1.91	1.80	1.73	1.67
V. Sel. x sel.	Best families	2.56	2.25	2.02	1.86	1.76
Va. Sel. x sel.	Best trees in best families	3.08	2.37	2.12	1.97	1.88
CLONAL SEED ORCHARDS						
VI. Sel. clones	Best clones	Not calculable. Higher than ΔG				
VII. Sel. clones	Clones with best general combining ability	1.38	1.19	1.05	1.00	0.89
VIII. Sel. clones	2 clones with best specific combining ability	2.06	1.75	1.52	1.36	1.26

the variance is non-additive these superior families will not give an F2 population equal to themselves; the mean of the F2 will regress toward the population mean. Thus a Type VII clonal orchard will give better seed than the Type IV progeny test accompanying it. Similarly a Type VIII clonal orchard will give better seed than the Type V progeny test accompanying it.

This superiority of clonal orchards over seedling progeny tests does not hold if there is a significant positive parent-progeny regression and if the seedling plantings are thinned to the best trees in the best families as in progeny tests of Types IVa and Va. In such a case the presence of a positive F1-F2 correlation can be inferred from the already demonstrated parent-Fl correlation, and the F2 seed produced by a thinned Type IVa or Type Va progeny test can be assumed to be higher in quality than can be produced by a clonal planting established at the same time.

Group Discussion

Most questions concerned the differences between eastern white pine and western white pine in susceptibility to the white pine blister rust and in the apparent differences in results of selection for blister rust resistance in the two species. Some possible reasons for the apparent greater success of selection in western white pine were given as (1) differences in testing procedures, and (2) differences in apparent severity of infection. For example, 500 cankers per tree are quite common on western white pine in the West, but are rather rare on eastern white pine in the East. The selection pressure may therefore be more intense on the western species.