Average Genetic Correlations Among Offspring From Open-Pollinated Forest Trees

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In estimating additive genetic variance and heritability, most forest tree geneticists assume that the genetic correlation among offspring (coefficient of relationship) of an open-pollinated tree is .25. Such offspring (often called a half-sib family) are all related as half-sibs only when none of them resulted from self-pollination and when all of them were sired by different males. When they are truly half-sibs and when the parents are not correlated or inbred, the correlation between all pairs of offspring is .25. Since these conditions are usually not fulfilled, geneticists are aware that the average correlation is likely to be greater than .25.

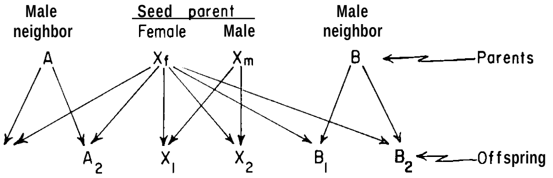
Assumption that the correlation among offpring is .25 usually results in an overestimate of additive genetic variance (NAMKOONG, 1966). Assumption that the parents are unrelated may lead to either over- or underestimates of additive genetic variance (FUJISHIMA and FREDEEN, 1972). Biases in estimates of additive genetic variance in turn cause biases in estimates of heritability and of genetic gains.

Average genetic correlations among offspring from open-pollination are computed herein for a range of hypothetical conditions. An attempt is also made to estimate the biases resulting from assumptions noted above, and recommendations are given for alleviating them.

Kinds of Relatives and Correlations Among Them

Offspring of an open-pollinated tree consist of selfs and outcrosses, and there are four possible kinds of relatives (***Fig.*** 1). Two offspring produced by selfing are self full-sibs. Two outcrossed offspring which have both parents in common are full-sibs and two which have a single parent in common are half-sibs. A self and an outcross, which have a common parent, represent a different kind of relationship. To my knowledge, this relationship has not heretofore been noted and such pairs of offspring are here termed "self half-sibs".

The genetic correlation between each of the offspring pairs was computed in several steps.



Kinds of relatives arnong offspring	Exarnples	Genetic correlation when porents are noninbred and uncorrelated
Self full-sibs	X_1 and X_2	.667
Full-sibs	A_1 and A_2	.500
Self half-sibs	A_1 and X_1	.408
Half-sibs	A_1 and B_1	.250

Fig. *1.* — Types of relatives that can occur in the offspring of an open-pollinated tree (seed parent).

1. First, pedigrees were depicted for each pair of relatives (***Table 1***). Here the parent trees were assumed to be non-inbred and uncorrelated. Thus, the genetic correlation (r) between parents of full-sibs A_1 and A_2 is 0. However, under selfing, the single parent, X, was depicted as if it were two parents, X_f and X_m, between whom the genetic correlation is 1.

2. Next, following rules for path coefficient procedures (LI, 1955, p. 158), independent paths connecting pairs of offspring through their common parents or through their correlated parents, were traced (***Table*** 1). Thus, there is one path connecting full-sibs A_1 and A_2 through parent A, and another through parent X_f. Parents of the full-sibs, A and X_f, are uncorrelated here, so paths are not traced through them. But for self full-sibs, there are two additional paths, $X_1X_fX_mX_2$ and $X_1X_mX_fX_2$ because "parents" X_f and X_m are correlated.

3. Next, the path coefficients from parents to their offspring ($p_{0.P}$) in each path were computed:

$$p_{0\,.\,P} = .5\sqrt{\frac{1 + F_P}{1 + F_O}},$$

   in which F_P and F_O are the inbreeding coefficients of the parent and offspring, respetively (LI, 1955, p. 221). For use in the above expression, the inbreeding coefficient of an offspring can be computed if the correlation between its parents, $r_{P_f\ m}$, and their inbreeding coefficients (F_{P_f} and F_{P_m}) are known (LI, 1955, p. 222):

$$F_O = .5\, r_{P_fP_m}\sqrt{(1 + F_{P_f})\,(1 + F_{P_m})}.$$

   Under the assumptions specified in ***Table*** 1, for an offspring produced by selfing F, $= .5$ and $p_{0\,.\,P} = .408$ (footnote, ***Table*** 1). For an offspring produced by outcrossing, F, $= 0$ and $p_{0\,.\,P} = .5$.

4. Finally, the product of the path coefficients and correlations involved in each connecting path was computed, and the products for all paths were summed. For example, in the case of self full-sibs of ***Table*** 1, the product of the path coefficients and correlations in each of the four paths is .1665 and the genetic correlation between self full-sibs is the sum of these, .667.

If the parent population is inbred, the correlations between offspring of an open-pollinated tree will be larger. Inbreeding coefficients for natural tree stands are not generally known. However, if the degree of effective natural selfing (proportion of selfs vs. total trees in a sexually mature stand), s, is known, we can get an approximate estimate of the general level of inbreeding in the stand from the equation

$$F_P = \frac{s}{2 - s},$$ assuming equilibrium of gene and zygotic frequencies (LI, 1955, p. 134).

Under the same assumption (equilibriurn), s is equal to the correlation among the parents. Thus, if the degree of effective natural selfing in a stand is 5%, we shall assume

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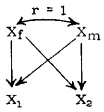
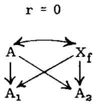
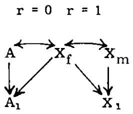
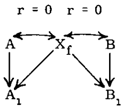
Table 1. — Computation of genetic correlations among offspring of an open-pollinated parent when the parents are neither inbred nor correlated.

Pedigrees	Connecting paths	Path coefficients and correlations[1]		Products
		Self Full-Sibs		
	$X_1X_fX_2$	.408, .408		.1665
	$X_1X_mX_2$	.408, .408		.1665
	$X_1X_fX_mX_2$	.408, 1, .408		.1665
	$X_1X_mX_fX_2$	.408, 1, .408		.1665
			$r_{X_1X_2}$ =	.667
		Full-Sibs		
	$A_1A\,A_2$	.5, .5		.25
	$A_1X_fA_2$	.5, .5		.25
			$r_{A_1A_2}$ =	.5
		Self Half-Sibs		
	$A_1X_fX_1$	.5, .408		.204
	$A_1X_fX_mX_1$	.5, 1, .408		.204
			$r_{A_1X_1}$ =	.408
		Half-Sibs		
	$A_1X_fB_1$	.5, .5		.25
			$r_{A_1B_1}$ =	.25

[1] For selfing, $F_0 = .5(1)\ \sqrt{(1+0)(1+0)} = .5$, and

$$p_{0\cdot P} = .5\sqrt{\frac{1+0}{1+.5}} = .408.$$

For outcrossing, $F_0 = .5(0)\ \sqrt{(1+0)(1+0)} = 0$, and

$$p_{0\cdot P} = .5\sqrt{\frac{1+0}{1+0}} = .5.$$

that the correlation among trees in it is .05 and that $F_P = \frac{.05}{2-.05} = .026$. Computations of correlations among offspring when the correlation among parents is .05 and the inbreeding coefficient of the parents is .026 are given in *Table 2.* Correlations among offspring for various degrees of inbreeding and relationship in the parent population are summarized in the upper half of *Table 3.*

Genetic correlations among relatives in the offspring of open-pollinated trees were also computed for situations in which the parents are inbred to various degrees but unrelated. Such a situation may, for example, occur in a clonal seed orchard in which the ortets were located in a number of natural stands, so that the clones in the orchard may be inbred but unrelated to each other. In these computations, F_0 and $p_{0\cdot P}$ for selfing remain the same as given in *Tables 1 and 2.* But in the case of outcrossing, F_O becomes 0 even if the parents are inbred because

$$r_{P_fP_m} = 0,$$

$$\text{and } p_{0\cdot P} = .5\sqrt{\frac{1+F_P}{1+0}}.$$

Computation for the correlation among full-sibs, when the inbreeding coefficient in the original parental stand is .026, will serve as an example. The pedigree diagram is the same as that for full-sibs *(Table 1).* Thus,

$$r_{AX_f} = 0,$$

$$F_O = .5(0)\sqrt{(1+.026)(1+.026)} = 0,$$

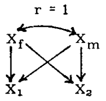
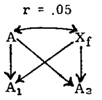
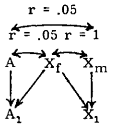
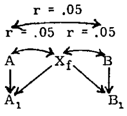
$$p_{0\cdot P} = .5\sqrt{\frac{1+.026}{1+0}} = .5064.$$

Since there are two paths through common parents and none through correlated parents, the correlation between the full-sibs becomes

$$r_{A_1A_2} = 2(.5064)^2 = .513.$$

Results of the remaining computations are shown in the lower half of *Table 3.* In some situations, one of the male parents of a half-sib pair may be correlated with the seed

Table 2. — Computation of genetic correlations among offspring of an open-pollinated parent when the parent population is inbred to the extent that the correlation among parents is .05 and the inbreeding coefficient, .026.

Pedigrees	Connecting paths	Path coefficients and correlations[1]		Products
		Self Full-Sibs		
	$X_1X_fX_2$	.412, .412		.1695
	$X_1X_mX_2$	.412, .412		.1695
	$X_1X_fX_mX_2$	.412, 1, .412		.1695
	$X_1X_mX_fX_2$	.412, 1, .412		.1695
			$r_{X_1X_2}$ =	.678
		Full-Sibs		
	$A_1A\,A_2$	.5, .5		.25
	$A_1X_fA_2$	.5, .5		.25
	$A_1A\,X_fA_2$	.5, .05, .5		.0125
	$A_1X_fA\,A_2$	.5, .05, .5		.0125
			$r_{A_1A_2}$ =	.525
		Self Half-Sibs		
	$A_1X_fX_1$	.5, .412		.206
	$A_1X_fX_mX_1$	.5, 1, .412		.206
	$A_1A\,X_fX_1$	.5, .05, .412		.010
	$A_1A\,X_mX_1$	.5, .05, .412		.010
			$r_{A_1X_1}$ =	.432
		Half-Sibs		
	$A_1X_fB_1$	.5, .5		.25
	$A_1A\,X_fB_1$	.5, .05, .5		.0125
	$A_1X_fB\,B_1$	.5, .05, .5		.0125
	$A_1A\,B\,B_1$	.5, .05, .5		.0125
			$r_{A_1B_1}$ =	.288

[1] For selfing, $F_0 = .5(1)\ \sqrt{(1+.026)(1+.026)} = .513$, and

$$p_{0\cdot P} = .5\sqrt{\frac{1+.026}{1+.513}} = .412.$$

For outcrossing:

$$F_0 = .5\,(.05)\ \sqrt{(1+.026)(1+.026)} = .026, \text{ and}$$

$$p_{0\cdot P} = .5\sqrt{\frac{1+.026}{1+.026}} = .5.$$

Table 3. — Genetic correlations between specific relatives in the offspring of an open-pollinated tree under various conditions.

Correlation among parents	Inbreeding coefficient of parents	Self full-sibs	Full-sibs	Self half-sibs	Half-sibs[1]
		Correlations			
Parents Inbred and Correlated to Various Degrees					
.00	.000	.667	.500	.408	.250
.05	.026	.678	.525	.432	.288
.10	.053	.690	.550	.457	.325
.15	.081	.702	.575	.482	.362
.20	.111	.714	.600	.507	.400
Parents Inbred to Various Degrees But Uncorrelated					
.00	.000	.667	.500	.408	.250
.00	.026	.678	.513	.418	.256
.00	.053	.690	.526	.426	.263
.00	.081	.702	.540	.435	.270
.00	.111	.714	.556	.445	.278

[1] The correlations given for half-sibs in the upper half of the table are for the situation in which the male parents of a half-sib pair are correlated with the seed parent and with each other. If only one of the males is correlated with the seed parent and the two males are uncorrelated, the offspring correlations are .250, .262, .275, .288, and .300 for parental correlations of .00, .05, .10, .15, and .20, respectively.

parents, while the two males are uncorrelated. Half-sib offspring correlations for this special case are given in the footnote of *Table 3*.

Proportions of the Various Relatives

Proportions of various types of relatives in the offspring of an open-pollinated tree can easily be determined for hypothetical cases. Suppose there are 10 offspring produced by open-pollination of tree X and that tree X sired 2 of them (selfs) while neighboring trees A, B, C, and D sired 3, 3, 1, and 1 trees, respectively. The type of relative for each pair of offspring can then be specified as in *Table 4*. Finally, the numbers of each type can be counted and divided by the total pairs of offspring to obtain relative frequencies.

When the family is large, the above procedure becomes tedious. In such cases, the proportions (p) of the various relatives can be obtained from the following formulas:

$$p_{sfs} = \frac{s(sn - 1)}{n - 1},$$

$$p_{fs} = \sum_{i=1}^{j} \frac{[m_i(m_i n - 1)]}{n - 1},$$

$$p_{shs} = \frac{2sn(1 - s)}{n - 1},$$

$$p_{hs} = \frac{(1 - s)\,[n(1 - s) - 1]}{n - 1} - p_{fs},$$

where n = total number of offspring
s = proportion of selfs in the offspring,
m_i = proportion of offspring sired by male parent i, $i = 1 \dots j$,
j = number of male parents (excluding the seed parent).

(*Note:* In all cases, if $s > 0$, sn must be equal to or greater than 1. Similarly, if $m_i > 0$, $m_i n \geqslant 1$).

As an example, if we substitute the basic data of *Table 4* ($n = 10$, $s = .2$, $m_1 = m_2 = .3$, and $m_3 = m_4 = .1$) into the above equations, we obtain $p_{sfs} = .022$, $p_{fs} = .133$, $p_{shs} = .356$, and $p_{hs} = .489$, as was obtained earlier by the direct procedure of *Table 4*.

Table 4. — Relationhips between 10 offspring in a hypothetical family produced by open-pollination.

Offspring[1])	Offspring[1])									
	X_1	X_2	A_1	A_2	A_3	B_1	B_2	B_3	C_1	D_1
X_1		sfs	shs	shs	shs	shs	shs	shs	shs	shs
X_2			shs	shs	shs	shs	shs	shs	shs	shs
A_1				fs	fs	hs	hs	hs	hs	hs
A_2					fs	hs	hs	hs	hs	hs
A_3						hs	hs	hs	hs	hs
B_1							fs	fs	hs	hs
B_2								fs	hs	hs
B_3									hs	hs
C_1										hs
D_1										

Proportions of different kinds of relatives, obtained by counting the entries in table and dividing by the total entries (45):

sfs = self full-sibs	=	.022
fs = full-sibs	=	.133
shs = self half-sibs	=	.356
hs = half-sibs	=	.489
Total		1.000

[1] The X_i offspring were produced by self-pollination of seed parent X; A_i, B_i, C_i and D_i were produced by outcrossing of X with male parents A, B, C, and D, respectively.

Utility of the above formulas is restricted to the situation in which all of the pairs of offspring within a type of relative are correlated to the same degree. Such would be the case if all of the parents are correlated to the same degree. However, suppose that a seed parent is pollinated by neighboring trees (local males) which may be correlated with each other and with the seed parent, and also by distant trees (non-local males) which are not correlated with each other or with the seed parent. In this event, the total proportion of self half-sib pairs will consist of

p'_{shs} = proportion of pairs of self half-sibs in which the parents are not correlated

$$= \frac{2asn}{n - 1}$$

and p''_{shs} = proportion of pairs of self half-sibs in which parents are correlated

$$= \frac{2sn(1 - s - a)}{n - 1}$$

where a = proportion of offspring sired by non-local males

$p_{shs} = p'_{shs} + p''_{shs}$.

The half-sibs will consist of three groups:

p'_{hs} = proportion of half-sib pairs in which none of the parents are correlated

$$= \frac{a(an - 1)}{n - 1}$$

p''_{hs} = proportion of half-sib pairs in which one of the males is correlated with the seed parent

$$= \frac{2an(1 - s - a)}{n - 1}$$

and p'''_{hs} = proportion of half-sib pairs in which all parents are correlated

$$= \frac{(1 - s - a)\,[n(1 - s - a) - 1]}{n - 1} - p_{fs}$$

where $p_{hs} = p'_{hs} + p''_{hs} + p'''_{hs}$.

The Average Genetic Correlations

The average genetic correlation ($\bar{r}$) in a family produced by open-pollination is the average of correlations among specific relatives weighted by the proportions of each type of relative. Thus, where the offspring within each type of relative are correlated to the same degree,

$$\bar{r} = r_{sfs}p_{sfs} + r_{fs}p_{fs} + r_{shs}p_{shs} + r_{hs}p_{hs}.$$

As an example, suppose the five parents of the hypothetical family of *Table 4* are not inbred and not correlated. The correlations among specific relatives in the offspring would then be $r_{sfs} = .667$, $r_{fs} = .500$, $r_{shs} = .408$, and $r_{hs} = .250$ (*Table 3*). The average correlation then would be

$$\bar{r} = .667(.022) + .500\,(.133) + .408(.356) + .250(.489) = .349.$$

Computation of the average correlation among offspring of an open-pollinated tree under field conditions is complicated by the fact that parameters involved under various situations are not accurately known. For example, the degree of selfing seems to vary rather high both within and between species (*Table 5*). The number of males that might sire offspring of a tree under open-pollination is open to question. It is generally believed that most of the offspring are sired by few parents, perhaps 5 to 15 because

Table 5. — Estimates of the degree of effective natural selfing in some coniferous species[1]).

Species	Trees studied	Effective natural selfing		Author
		Range	Average	
	number	*percent*	*percent*	
Picea abies (L.) Karst.	6	3—10	6	Koski (1973)
Picea mariana (Mill.) B.S.P.	—[2])	6—15	10	Morgenstern (1972)
Pinus banksiana Lamb.	3	11—26	20	Fowler (1965 a)
Pinus banksiana Lamb.	5	9—25	17	Rudolph (1966)
Pinus densiflora Sieb. et Zucc.	22	0—24	< 5	Ohba *et al.* (1971)
Pinus elliottii Engelm.	11	0—27	6	Squillace and Kraus (1963)
Pinus pungens Engelm.	1	—	18	Cram (1960)
Pinus radiata D. Don	3	1—27	13	Bannister (1965)
Pinus resinosa Ait.	2	2—22	12	Fowler (1965 b)
Pinus sylvestris L.	—	3—13	7	Sarvas (1962)
Pinus sylvestris L.	1	—	6	Koski (1973)
Pinus taeda L.	25	0—13	2	Franklin (1968)
Pinus thunbergii Parl.	1	—	40	Ohba (1972)
Pseudotsuga menziesii (Mirb.) Franco	19	0—27	7	Sorensen (1973)

[1]) From a practical standpoint, the estimates given here are somewhat high, because in most cases they were based upon newly germinated seedlings. Mortality of selfs is usually greater than outcrosses (Franklin, 1970). Judging from plantation data in several reports, selfing at 10 years would probably be 80% of that at time of germination. Under natural growing conditions, it may be considerably less.

[2]) The values given here are based on estimates of the inbreeding coefficient given by the author, .08 for southern regions and .03 for northern regions. Estimates of s were computed from the equation $F = \frac{s}{2-s}$.

of limitations on dispersal of pollen, non-synchronous flowering, etc. This may be especially true in a clonal seed orchard (Eriksson *et al.*, 1973). Pollen coming from long distances (background pollen) may be as high as 25% (Silen, 1962). Trees contributing to the background pollen may not be correlated with the seed parent, while neighboring trees may be correlated. Therefore, computations were made for a range of conditions that is likely to occur in the field. Computations were made separately for 1) parents inbred and related to various degrees and 2) parents inbred but not related.

Parents inbred and correlated to various degrees

Here it is assumed that the seed parents are inbred and correlated with neighboring trees (local males) siring it, but not correlated with "non-local" trees (contributing to background pollen) siring the seed parent. It is assumed further that local males sire equal numbers of offspring and more than one offspring in a 100-tree family, while non-local males sire a single offspring. The correlation among related parents is assumed to be equal to the proportion of selfing.

Computations were made for five levels of selfing (0%, 5%, 10%, 15%, and 20%), four levels of local males (5, 10, 15, and 20 trees), and four levels of non-local males (0, 10, 20, and 30 trees) (*Table 6*). Family size held constant at 100 individuals.

As an example, consider the situation involving 5% selfing, 10 local males, and 20 non-local males (*Table 6*). Steps in the computation follow.

1. The following offspring correlations are obtained from *Table 3*.

$r_{sfs} = .678$

$r_{fs} = .525$ (parents correlated)

$r'_{shs} = .418$ (parents uncorrelated)

$r''_{shs} = .432$ (parents correlated)

$r'_{hs} = .256$ (parents uncorrelated)

$r''_{hs} = .262$ (one of male parents correlated with seed parent)

$r'''_{hs} = .288$ (parents correlated)

2. Under the assumptions given, the seed parent sired five offspring and the 20 non-local males each sired one offspring. Therefore, the 10 local males each sired an average of $\frac{100-5-20}{10} = 7.5$ offspring. Thus, in this example

$$m_1 \ldots m_{10} = .075$$
$$m_{11} \ldots m_{30} = .01$$
$$s = .05$$
$$n = 100$$
$$\text{and } a = .20$$

From the formulas given earlier, the proportions of the relatives in the offspring are:

$$p_{sfs} = \frac{.05[(.05)(100)-1]}{100-1} = .002$$

$$p_{fs} = \frac{10(.075)[.075(100)-1] + 20(.01)[.01(100)-1]}{100-1} = .049$$

$$p'_{shs} = \frac{2(.20)(.05)(100)}{100-1} = .020$$

$$p''_{shs} = \frac{2(.05)(100)(1-.05-.20)}{100-1} = .076$$

$$p'_{hs} = \frac{.20[(.20)(100)-1]}{100-1} = .038$$

$$p''_{hs} = \frac{2(.20)(100)(1-.05-.20)}{100-1} = .303$$

$$p'''_{hs} = \frac{(1-.05-.20)[100(1-.05-.20)-1]}{100-1} - .049 = .512.$$

3. Finally, the average correlation among offspring is the sum of the products of the proportions of each group of relatives by their respective correlations:

$$\bar{r} = .678(.002) + .525(.049) + .418(.020) + .432(.076) + .256(.038) + .262(.303) + .288(.512) = .30,$$

as shown in *Table 6*.

The average genetic correlation increases strongly with increasing degree of effective selfing, as expected *(Table 6)*. In contrast, the effect of differing numbers of local and non-local males is relatively small.

The average genetic correlation also increases with family size, although in *Table 6*, family size was held constant at 100. The effect of changes in family size is small when it exceeds 50 individuals. For example, if $s = .1$ with all parents correlated to the same degree and $m = .1$ for all males, r is .351, .363, .369, .370, and .372 for family sizes 10, 20, 50, 100, and 1,000, respectively.

Contrary to the assumption that the local males sire equal numbers of offspring, it is more realistic to assume that the nearest male shedding pollen at the proper time would sire the most offspring, while those further removed, or less well synchronized as to time of pollen shedding, would sire fewer offspring. Failure of the assumption of equal effectiveness of males causes only small underestimates of the average genetic correlation. For example, in computing the entry given for 5% selfing, 10 local males and 20 non-local males, it was assumed that the local males sired an average of 7.5 offspring each. But if they sired 18, 14, 11, 9, 7, 5, 4, 3, 2, and 2 offspring, respectively, the average genetic correlation would be .311 instead of .305.

Table 6. — Average genetic correlation among offspring of open-pollinated parents in stands in which the parents are inbred and related to various degrees. Family size = 100.

Number of equally effective non-local males[2])	Number of equally effective local males[1])			
	5	10	15	20
20% Selfing				
0	.47	.46	.45	.45
10	.45	.44	.43	.43
20	.43	.42	.42	.42
30	.41	.40	.40	.40
15% Selfing				
0	.43	.41	.41	.41
10	.41	.40	.39	.39
20	.39	.38	.38	.38
30	.37	.37	.37	.36
10% Selfing				
0	.39	.37	.36	.36
10	.37	.36	.35	.35
20	.36	.34	.34	.34
30	.34	.33	.33	.33
5% Selfing				
0	.34	.32	.32	.31
10	.33	.31	.31	.30
20	.32	.30	.30	.30
30	.31	.30	.29	.29
0% Selfing				
0	.30	.27	.26	.26
10	.29	.27	.26	.26
20	.28	.26	.26	.26
30	.27	.26	.26	.25

[1]) These are nearby neighbors pollinating the seed parent. Each is assumed to sire offspring equal to

$$\frac{100 - \% \text{ selfing} - \text{no. non-local males}}{\text{no. of local males}}$$

[2]) These are males remotely situated from the seed parent (trees that make up the "background pollen"). Each is assumed to sire a single offspring.

Table 7. — Average genetic correlations among offspring of open-pollinated parents in stands in which the parents are inbred to various degrees but unrelated. Family size = 100.

Number of equally effective non-local males[2])	Number of equally effective local males[1])			
	5	10	15	20
20% Selfing				
0	.38	.36	.36	.36
10	.37	.36	.36	.35
20	.37	.36	.35	.35
30	.36	.35	.35	.35
15% Selfing				
0	.36	.34	.33	.33
10	.35	.34	.33	.33
20	.34	.33	.33	.33
30	.34	.33	.33	.32
10% Selfing				
0	.34	.32	.31	.30
10	.33	.31	.31	.30
20	.32	.31	.30	.30
30	.31	.30	.30	.30
5% Selfing				
0	.32	.29	.28	.28
10	.31	.29	.28	.28
20	.30	.28	.28	.28
30	.29	.28	.28	.28
0% Selfing				
0	.30	.27	.26	.26
10	.29	.27	.26	.26
20	.28	.26	.26	.26
30	.27	.26	.26	.25

[1]) See footnote 1, *Table 6*.

[2]) See footnote 2, *Table 6*.

Parents inbred but not correlated

Here it is assumed that the parent trees are inbred to various degrees but not correlated. This situation may be approximately true in plantations established from seed collected from a number of stands or in seed orchards in which the parents originated from a number of stands.

The computations here are similar to those made for inbred and related parents. The only difference is that correlations among specific relatives in the offspring given in the lower half of *Table 3* are used throughout since all of the parents are assumed to be uncorrelated. The resulting average correlations among offspring under these conditions *(Table 7)* are lower than in the case where parents are related *(Table 6)*.

Implications

In estimating genetic parameters, what is the effect of assuming that the correlation among offspring is only .25 when it is actually greater? Suppose an analysis of variance is computed for a group of unrelated families produced by open-pollination and a component of variance associated with families (σ^2_f) is obtained. If it is assumed that individuals within families are all half-sibs ($r_{00} = .25$), this variance would be interpreted as one-fourth of the additive genetic variance (σ^2_A). Thus, $\sigma^2_f = .25\sigma^2_A$ and $\sigma^2_A = \frac{\sigma^2_f}{.25}$. But if the genetic correlation among individuals within families is actually .30, the estimate of σ^2_A should be $\frac{\sigma^2_f}{.30}$ instead of $\frac{\sigma^2_f}{.25}$. Clearly, the false assumption results in an overestimate of genetic variance and of heritability (h^2), since

Table 8. — Analysis of variance for a progeny test containing families from open-pollination.

Source of variation	df	Mean squares	Expected mean squares
Families	$m - 1$	MS_f	$\sigma^2_w + k\sigma^2_f$
Individuals/families	$m(k - 1)$	MS_w	σ^2_w

m = number of families

k = number of individuals in families

$$\sigma^2_w = MS_w = (1 - r_{00})\sigma^2_A + \sigma^2_E$$

$$\sigma^2_f = \frac{MS_f - MS_w}{k} = (r_{00} - r_{PP})\sigma^2_A$$

r_{00} = Correlation among offspring within families

r_{PP} = Correlation among parents

$$\sigma^2_A = \text{additive genetic variance} = \frac{\sigma^2_f}{r_{00} - r_{PP}}$$

$$\sigma^2_E = \text{environmental variance} = \sigma^2_w - (1 - r_{00})\sigma^2_A$$

$$= \sigma^2_w - (1 - r_{00})\frac{\sigma^2_f}{r_{00} - r_{PP}}$$

$h^2 = \frac{\sigma^2_A}{\sigma^2_P}$ where σ^2_P = phenotypic variance.

Genetic variance and heritability estimates should also take into account any correlation that may occur among parents (Fujishima and Fredeen, 1972). For a hierarchical mating design with families and individuals within families, the analysis is relatively simple, assuming that all genetic effects are additive (*Table 8*). Additive genetic variance decreases with increasing correlation among offspring within families and increases with increasing correlations among parents. Correlations affect heritability estimates in the same manner. By substitution of variances given in *Table 8* into the usual equation for heritability

$$h^2 = \frac{\sigma^2_A}{\sigma^2_A + \sigma^2_E} = \frac{\sigma^2_f}{(r_{00} - r_{PP})\sigma^2_w + r_{00}\sigma^2_f}.$$

If parents are uncorrelated and if the correlation among trees within families is .25, the above reduces to the familiar form,

$$h^2 = \frac{\sigma^2_f}{.25(\sigma^2_w + \sigma^2_f)} \quad \text{or} \quad \frac{4\sigma^2_f}{\sigma^2_w + \sigma^2_f}.$$

If the parents are assumed to be uncorrelated when they are acually correlated, heritability is underestimated. In contrast, assuming that the correlation among offspring is only .25 when it is actually greater, tends to cause an overestimate of heritability.

What is the net result of the two opposing factors under normal conditions? If values given in *Tables 6 and 7,* for 15 local males and 20 nonlocal males, are reasonable estimates of the average correlation among offspring of open-pollinated trees for various degrees of selfing, then estimates of the average correlations, extracted from *Tables 6 and 7,* are as follows:

Proportion of selfing (Average correlation among seed parents)	Correlations among offspring	
	Parents inbred and related	Parents inbred but not related
r_{PP}	r_{00}	r_{00}
.00	.26	.26
.05	.30	.28
.10	.34	.30
.15	.38	.33
.20	.42	.35

Heritability estimates can then be adjusted for both correlations among seed parents and among individuals within families. Suppose open-pollinated seed were collected from trees in a natural stand and grown in a designed test. If $\sigma^2_f = 1$ and $\sigma^2_w = 4$ and the average correlation among parents was .10, then $r_{PP} = .10$ and from the above tabulation, $r_{00} = .34$. Adjusted heritability can then be computed:

$$h^2 = \frac{1}{(.34 - .10)(4) + (.34)(1)} = .77.$$

In contrast, unadjusted heritability (i.e., assuming that $r_{PP} = 0$ and $r_{00} = .25$) would be

$$\frac{4(1)}{1 + 4} = .80.$$

The relation between adjusted and unadjusted heritabilities for a range of conditions is given in *Table 9*. Data were obtained by letting σ^2_f equal unity, then computing the corresponding values of σ^2_w for a range of unadjusted heritabilities, and finally computing corresponding adjusted heritabilities. Note that if the correlations among parents and among offspring are assumed to be 0 and .25, respectively, heritability will usually be overestimated. However, the overestimate is rather small if the seed trees are correlated (such as in a natural stand), in which case, a slight underestimate may occur where selfing is high and heritability is low. In contrast, if the seed trees are uncorrelated (such as in some artificial stands), heritability is appreciably overestimated, especially if selfing is high.

Full-sibs are almost certain to occur in offspring from open-pollination and at least some inbreeding must occur in natural stands. Therefore, it would seem wise to adjust heritabilities estimated from data obtained from open-pollinated families. With reliable data on stand structure, good estimates can be made, using the correlation data and formulas presented. Approximate adjustments can be made directly with *Table 9*. For example, suppose that a progeny test consists of offspring from open-pollinated trees in a clonal orchard in which the clones came from several different stands. If unadjusted heritability was found to be .50 and if effective natural selfing for the species is known to be about 10%, adjusted heritability would be .42. If the seed trees are in a natural stand, and unadjusted heritability is low, adjustment is hardly necessary.

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Table 9. — Heritabilities[1]) adjusted for correlations among offspring (r_{00}) being greater than .25 and/or correlations among seed parents (r_{PP}) being greater than 0.

Unadjusted heritability	Proportion of effective natural selfing				
	.00	.05	.10	.15	.20
			Seed Parents Correlated[2]) (Natural Stand)		
(r_{PP} = .00, r_{00} = .25)	(r_{PP} = .00, r_{00} = .26)	(r_{PP} = .05, r_{00} = .30)	(r_{PP} = .10, r_{00} = .34)	(r_{PP} = .15, r_{00} = .38)	(r_{PP} = .20, r_{00} = .42)
.01	.01	.01	.01	.01	.01
.10	.10	.10	.10	.11	.11
.20	.19	.20	.20	.21	.22
.30	.29	.30	.30	.31	.32
.40	.38	.39	.40	.41	.42
.50	.48	.49	.50	.50	.51
.60	.58	.58	.59	.60	.60
.70	.67	.68	.68	.68	.68
.80	.77	.77	.77	.77	.77
.90	.87	.86	.86	.85	.85
1.00	.96	.95	.94	.93	.92
1.10	1.06	1.04	1.03	1.01	1.00
1.20	1.15	1.13	1.11	1.09	1.07
			Seed Parents Uncorrelated (Artificial Stand)		
(r_{PP} = .00, r_{00} = .25)	(r_{PP} = .00, r_{00} = .26)	(r_{PP} = .00, r_{00} = .28)	(r_{PP} = .00, r_{00} = .30)	(r_{PP} = .00, r_{00} = .33)	(r_{PP} = .00, r_{00} = .35)
.01	.01	.01	.01	.01	.01
.10	.10	.09	.08	.08	.07
.20	.19	.18	.17	.15	.14
.30	.29	.27	.25	.23	.21
.40	.38	.36	.33	.30	.29
.50	.48	.45	.42	.38	.36
.60	.58	.53	.50	.45	.43
.70	.67	.62	.58	.53	.50
.80	.77	.71	.67	.61	.57
.90	.87	.81	.75	.68	.64
1.00	.96	.89	.83	.76	.71
1.10	1.06	.98	.92	.83	.78
1.20	1.15	1.07	1.00	.91	.86

[1]) Based on offspring of open-pollinated trees.

[2]) Correlation assumed to be equal to the proportion of effective natural selfing.

Summary

Average genetic correlations among offspring produced by open-pollination were computed for a range of hypothetical conditions. Results suggest that correlations under real situations will usually be appreciably larger than .25, the commonly used half-sib correlation. Assumption that the correlation is .25 causes an overestimate of genetic variance and of heritability. However, according to earlier workers, genetic correlations that may occur among the parents also affect estimates of these parameters — in the problem at hand they cause underestimates. Under a range of correlations among parents and among their offspring that are expected to occur in forest tree populations, the two opposing factors usually result in a net overestimate of genetic variance and heritability. The overestimate is usually small if the seed parents are correlated but appreciable when not. Biases can be removed if approximate estimates of the degree of selfing are known.

Key words: Open-pollination, wind-pollination, genetic correlation, coefficient of relationship, heritability, genetic variance, natural inbreeding.

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Unterschiede im Kronenaufbau bei Klonen und Herkünften der Fichte (Picea abies (L.) Karst.)

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1. Problemstellung

Die Mannigfaltigkeit der Formen der Fichtenkrone ist seit langem bekannt, und es hat nicht an Versuchen für eine kausale Erklärung des ihr zugrundeliegenden genetischen Polymorphismus gefehlt. Die meisten Autoren, die sich mit diesem Fragenkomplex auseinandergesetzt haben, machen verschiedene Selektionswerte der Kronentypen mit Hinblick auf Konkurrenzfähigkeit im Bestand, *Widerstandsfähigkeit gegen Schneeauflage bzw. Eisanhang* für die Vielfalt der Ausformung der Fichtenkrone und für ihre geographische Verteilung verantwortlich. Es sei hier auf die Veröffentlichungen von Hoffmann (1968) und Schmidt-Vogt (1972) für zusammenfassende Darstellungen dieser Forschungsergebnisse und Beobachtungen hingewiesen. Die Eisbruchuntersuchung von Antoine (1974) im Harz sowie auch frühere Forschungsergebnisse über dieses Thema heben die Zweckmäßigkeit der gleichzeitigen Betrachtung mehrerer miteinander korrelierter Merkmale hervor, um verschiedene Kronenmorphe der Fichte auseinanderzuhalten. Bei der jetzigen Untersuchung soll überprüft werden, inwieweit bestimmte anbaufähige Klone und Herkünfte sich in der Batterie der für Eisbruch relevanten sowie zusätzlichen interessanten Wipfelmerkmale unterscheiden.

2. Untersuchungsmaterial

Die Untersuchungsobjekte (es sind Fichtenwipfel) stammen von zwei Fichtenversuchen: einem 17- bis 20jährigen Klonversuch in Escherode (Bundesrepublik Deutschland) und einem Herkunftsversuch in Dönjelt (Südschweden). Der Fichtenklonversuch Escherode liegt in 52^0 nördlicher Breite und 340 m Seehöhe. Der Fichtenherkunftsversuch Dönjelt ist einer der Versuche, die 1938 von der IUFRO in mehreren Ländern Europas angelegt wurden. Langlet hat diesen Versuch geplant und durchgeführt (vgl. Langlet 1964). Der Ort Dönjelt befindet sich in 57^0 nördlicher Breite und in 170 m über NN. Der Versuch enthält 36 Provenienzen aus verschiedenen Gebieten Europas, die in 5 vollständigen Blocks verteilt sind.

Die Quirlzahl wurde bei den untersuchten Wipfeln konstant gehalten: 4 für das Escheroder Material, 6 für Dönjelt. Vom Escheroder Material wurden folgende Merkmale erhoben:

1— Gesamtzahl der Quirläste
2— Gesamtzahl der Fülläste
3— Wipfellänge
4— Triebdicke oberhalb der Schnittstelle
5— Gesamtlänge der Quirläste
6— Astdicke eines repräsentativen Hauptastes am untersten Quirl
7— Astwinkel 1 = Winkel zwischen Stammachse und einem Hauptast am untersten Quirl
8— Astwinkel 2 = Winkel gemessen an einem Hauptast am obersten Quirl
9— Brusthöhendurchmesser
10— Baumlänge

Die ersten 5 Wipfelmerkmale sind gleichzeitig diejenigen, die den Eisbruch in den untersuchten Harzbeständen (Antoine 1974) wesentlich mitbeeinflußten. Diese Merkmale wurden in beiden Versuchen aufgenommen, während sich die zusätzlich herangezogenen Wipfel- und Stammesmerkmale in den zwei Versuchen zum Teil unterscheiden. Für Dönjelt heißen die zusätzlichen Merkmale:

6— Astbreite, gemessen an der breitesten Stelle eines repräsentativen Hauptastes an jedem Quirl. Die Meßwerte für die Äste an den verschiedenen Quirlen wurden aufsummiert.
7— Asttiefe (wie im Punkt 6)
8— Astdicke (wie in Escherode)
9— Astwinkel 1 (wie in Escherode)
10— Astwinkel 2 (wie in Escherode)
11— Baumlänge

Im Escheroder Versuch wurden die Messungen an 7 verschiedenen Klonen mit 5 Wiederholungen vorgenommen. Da die Messungen im Zuge einer Durchforstung erfolgten, waren die Probebäume nicht streng zufällig auf die Versuchsfläche verteilt. In Dönjelt sind die oben aufgeführten Merkmale an 10 ausgewählten Herkünften gemessen worden. Die Stichprobe umfaßte 100 Bäume der oberen Kronenschicht: 10 Individuen je Provenienz und jeweils zwei Bäume in jeder Parzelle der 5 vorhandenen Blocks.

3. Das biometrische Verfahren

Als statistisches Entscheidungsmittel wird die multivariate Varianzanalyse benutzt, die bei der Behandlung biologischer Fragestellungen mit korrelierten Merkmalen mehr und mehr Anwendung findet (Schneider 1967). Sie kann als Verallgemeinerung der univariaten Varianzanalyse aufgefaßt werden. Der wesentlichste Unterschied