MORE ARGUMENTS AGAINST INTERMATING F₂ PLANTS OF A SELF-FERTILIZING CROP

I. BOS

Institute of Plant Breeding (IvP), Agricultural University, Wageningen, the Netherlands

SUMMARY

If no selection is applied on the F_2 of a self-fertilizing crop, the effect of random mating F_2 plants upon following generations (F'_3, F'_4, F'_5, ..., F'_∞) is scanty:
i) F'_3 contains less plants with the desired genotype $A_1A_1B_1B_1$ than the normal F_3.
ii) F'_∞ contains – if the loci segregate independently – as many plants with the optimal genotype as F_∞. When the loci are linked F'_∞ contains at most 25% more plants with the optimal genotype than F_∞.
When selection takes place in the F_2, the effect of random mating plants of the remaining F_2 on the F_3 is negative and nil where the F_∞ is concerned.

1 INTRODUCTION

Plant breeding very often attempts to combine good levels of expression for different characters in one variety. To this end complementary parents are chosen: P_1 with a good level for one character and P_2 with a good level for another character. The breeder hopes that, after crossing, he will find plants in the F_2 (or a later generation) which combine the desired levels of expression. In other words: he mates these two parents in the hope that he may come across the desired recombinant.

Another much pursued goal is the creation of a new, higher yielding variety. Two varieties with good yielding capacity each are crossed in the hope of obtaining a new variety with yet better yielding capacity. In fact, the goal is the same as above: a recombinant genotype that, as a whole, surpasses both parents.

Assume: $A_1–A_2$ is a locus for character A and $B_1–B_2$ a linked locus for character B. This notation does not indicate which of the alleles is the dominant. A_1 and B_1 are the 'plus-alleles' and A_2 and B_2 the 'minus-alleles'. A 'minus-allele' may be desired or not, depending on the character (compare earliness with yield).

The suboptimal parent varieties P_1 and P_2 with the respective genotypes $A_1A_1B_2B_2$ and $A_2A_2B_1B_1$ are crossed to give the desired recombinant with the optimal genotype $A_1A_1B_1B_1$. The 'plus-alleles' are here assumed to be favourites. Thus: the homozygous parental genotypes are:

$$P_1: \frac{A_1B_2}{A_1B_2} \text{ and } P_2: \frac{A_2B_1}{A_2B_1}, \text{ and}$$

the recombinant desired is $\dfrac{A_1B_1}{A_1B_1}$.

The F_1 has the genotype $\dfrac{A_1B_2}{A_2B_1}$ and produces gametes with the:

genotypes A_1B_1 A_1B_2 A_2B_1 A_2B_2
in the relative frequencies   u   v   v   u
A conventional notation is:

$$u = \tfrac{1}{2}r \tag{1}$$

$$v = \tfrac{1}{2}(1-r) \tag{2}$$

A fraction r of the gametes has a recombinant genotype i.e. A_1B_1 or A_2B_2. For independent segregating loci, thus $r = \frac{1}{2}$, $u = v = \frac{1}{4}$.

The F_2 arises from random fusion of gametes produced by the F_1; the F_3 from self-fertilization of F_2 plants. Continued self-fertilization eventually results in the F_∞. The derivation of the genotypic composition of the F_3 is given in Appendix I. The genotypic composition of the F_∞ was given by NELDER (1952). Table 1 presents the genotypic composition of the F_2, the F_3 and the F_∞. Table 2 provides marginal genotype frequencies for the F_2, the F_3 and the F_∞.

For 2 situations we will verify if intermating the F_2 plants is an advantage to attaining our objective, which is the maximization of the relative frequency of plants with the optimal genotype $A_1A_1B_1B_1$. These situations are:
(i) the parents are different for 2 linked loci (see section 2);
(ii) the parents are different for m independent segregating loci (see section 3).
Intermating was propagated by HANSON (1959), who says: 'It appears evident, based on the analysis of the breakup of linkage blocks, that a breeding program for a self-pollinated species should include at least one, and preferably three of four generations of intermating if at all feasible.'

Table 1. Genotypic composition of the F_2, the F_3 and the F_∞ for linked loci if the F_1 is in repulsion phase; r is the fraction of gametes originating from recombination; $u = \frac{1}{2}r$, $v = \frac{1}{2}(1\text{-}r)$.

Genotype	Code (ij)	Relative frequency (f_{ij})		
		F_2	F_3	F_∞
$A_1A_1B_1B_1$	22	u^2	$\frac{1}{2}u + 4u^2v^2$	$r(1+2r)^{-1}$
$A_1A_1B_1B_2$	21	$2uv$	$uv + 4uv(u^2+v^2)$	0
$A_1A_1B_2B_2$	20	v^2	$\frac{1}{2}v + 2v^4 + 2u^4$	$(2+4r)^{-1}$
$A_1A_2B_1B_1$	12	$2uv$	$uv + 4uv(u^2+v^2)$	0
$A_1B_2A_2B_1$	11r*	$2v^2$	$4u^4 + 4v^4$	0
$A_1B_1A_2B_2$	11c*	$2u^2$	$8u^2v^2$	0
$A_1A_2B_2B_2$	10	$2uv$	$uv + 4uv(u^2+v^2)$	0
$A_2A_2B_1B_1$	02	v^2	$\frac{1}{2}v + 2v^4 + 2u^4$	$(2+4r)^{-1}$
$A_2A_2B_1B_2$	01	$2uv$	$uv + 4uv(u^2+v^2)$	0
$A_2A_2B_2B_2$	00	u^2	$\frac{1}{2}u + 4u^2v^2$	$r(1+2r)^{-1}$

* r = repulsion phase; c = coupling phase.

Table 2. Marginal genotype frequencies for the F_2, the F_3 and the F_∞. Code for genotypes as in Table 1.

i \ j	2	1	0	F_2	F_3	F_∞
2	f_{22}	f_{21}	f_{20}	$\frac{1}{4}$	$\frac{3}{8}$	$\frac{1}{2}$
1	f_{12}	f_{11}	f_{10}	$\frac{1}{2}$	$\frac{2}{8}$	0
0	f_{02}	f_{01}	f_{00}	$\frac{1}{4}$	$\frac{3}{8}$	$\frac{1}{2}$
F_2	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	1		
F_3	$\frac{3}{8}$	$\frac{2}{8}$	$\frac{3}{8}$		1	
F_∞	$\frac{1}{2}$	0	$\frac{1}{2}$			1

HÄNSEL (1964) also advocated the application of several generations with intermating. He calculated for different numbers of parent varieties and for different numbers of generations from intermating the probability distribution of the number of parent varieties that are represented in an individual offspring: the greater the number of intercrossing generations for a given number of parent varieties, the better the probability that a high number of parent varieties is represented in an individual offspring.

A third advocate for intermating after the F_1 generation is JENSEN (1970).

In this paper the number of plants with the optimal genotype $A_1A_1B_1B_1$ (or the optimal phenotype $A_1.B_1.$) to be expected in a population of 10000 plants forms the object of study.

2 THE PARENTS ARE DIFFERENT FOR 2 LINKED LOCI

2.1 No selection in the F_2

2.1.1 F_2 plants produce progenies by continued self-fertilization

If the bulk-population breeding method is applied, i.e. selection starts in a population of homozygous plants (the F_∞), continued spontaneous self-fertilization will give an F_2, F_3, F_4, ...

2.1.1.1 The number of plants with the optimal genotype (in F_2, F_3 and F_∞)
Table 3 presents, for some values of r, the number of plants with the optimal genotype $A_1A_1B_1B_1$ that can be expected according to Table 1 in an F_2, F_3 or an F_∞ population of 10000 plants. From the fifth column it appears that, as coupling becomes tighter (r smaller), there is relatively more advantage in selecting plants with the genotype $A_1A_1B_1B_1$ (if recognizable!) in the F_3 than in the F_2. Delay of selection from the F_3 to the F_∞, especially for weak coupling, will give rather few additional advantages.

2.1.1.2 The number of plants with the optimal phenotype (in F_2, F_3 and F_∞)
If the 'plus-alleles' (A_1 and B_1) are completely dominant then the portion of plants with the optimal phenotype $A_1.B_1.$ equals

Table 3. The expected number of plants with the optimal genotype $A_1A_1B_1B_1$ (n_g) in an F_2, F_3 or F_∞ population of 10000 plants.

r	$n_g(F_2)$	$n_g(F_3)$	$n_g(F_\infty)$	$\dfrac{n_g(F_3)}{n_g(F_2)}$	$\dfrac{n_g(F_\infty)}{n_g(F_3)}$
0.5	$625 \simeq (\frac{1}{4})^2$	$1406.25 \simeq (\frac{3}{8})^2$	$2500 \simeq (\frac{1}{2})^2$	2.25	1.78
0.25	156	712.89	1667	4.57	2.34
0.125	39	342.41	1000	8.78	2.92
0.0625	9.8	164.83	556	16.82	3.37
0.03125	2.4	80.42	294	33.5	3.66
0.01562	0.6	39.65	152	66.1	3.83
0.00781	0.15	19.68	77	131.2	3.91
0.0039	0.04	9.78	38.6	244.5	3.95
0	0	0	0	$\lim\limits_{r \to 0} \dfrac{n_g(F_\infty)}{n_g(F_3))} = 4$	

$$f_{22} + f_{21} + f_{12} + f_{11} = 1 - (f_{0.} + f_{.0} - f_{00}) \tag{3}$$

(see Table 2) and therefore, according to Table 1 :

$$\text{in the } F_2: \tfrac{1}{2} + f_{00} = \tfrac{1}{2} + f_{22} = \tfrac{1}{2} + u^2 = a^{-1} \tag{4}$$

$$\text{in the } F_3: \tfrac{1}{4} + f_{00} = \tfrac{1}{4} + f_{22} \tag{5}$$

$$\text{in the } F_\infty: f_{00} = f_{22} \tag{6}$$

Table 4 shows, for some values of r, the number of plants with the optimal phenotype that can be expected in an F_2, F_3 or an F_∞ population of 10000 plants according to Eq. 4, 5 and 6. Table 4 is based on Table 3. From the fifth column it appears that, if dominance is complete, the proportion of F_3 plants with the optimal phenotype as against those with the optimal genotype increases as r decreases.

In case of dominance and thight coupling it is comparatively better to select the phenotype $A_1.B_1.$ only in advanced generations because $n_f(F_\infty) = n_g(F_\infty)$ for each

Table 4. The expected number of plants with the optimal phenotype $A_1.B_1.$ (n_f) in an F_2, F_3 or F_∞ population of 10000 plants.

r	$n_f(F_2)$	$n_f(F_3)$	$n_f(F_\infty) = n_g(F_\infty)$	$\dfrac{n_f(F_3)}{n_g(F_3)}$
0.5	$5625 \simeq (\frac{3}{4})^2$	3906.25	$2500 \simeq (\frac{1}{2})^2$	2.78
0.25	5156	3212.89	1667	4.51
0.125	5039	2842.41	1000	8.30
0.0625	5009.8	2664.83	556	16.17
0.03125	5002.4	2580.42	294	32.09
0.01562	5000.6	2539.65	152	64.05
0.00781	5000.15	2519.68	77	128.03
0.0039	5000.04	2509.78	38.6	256.62
0	5000	2500	0	

value of r. Selection in the F_3 and growing F_4 lines in order to separate plants with the genotype $A_1A_1B_1B_1$ cannot be considered as a profitable procedure when there is dominance and thight coupling.

2.1.2 F_2 plants are intermated

It is assumed that the F_2 plants are crossed randomly (e.g. by crossing neighbouring plants or by pollinating male sterile F_2 plants with male fertile F_2 plants). This results in an F_3' population, which after continued spontaneous self-fertilization transforms in an F_∞' population.

2.1.2.1 The number of plants with the optimal genotype (in F_3' and F_∞')

The relative frequencies of the gametes produced by a population that originated from random mating (e.g. F_2, F_3'), follow from Eq. 7 (see VAN DER VEEN, 1973):

$$(g_{ij}^{(k)} - \tfrac{1}{4}) = (1 - r)(g_{ij}^{(k-1)} - \tfrac{1}{4}); i, j = 0,1 \tag{7}$$

In this equation $g_{ij}^{(k-1)}$ and $g_{ij}^{(k)}$ stand for the relative frequencies of the gametes of 2 successive generations. It should further be true for the gene frequencies that $p_{A1} = q_{A2} = p_{B1} = q_{B2} = \tfrac{1}{2}$, which is the case for F_1, F_2, F_3, etc. if there is no selection. The relative frequencies of the gametes from the F_1, the F_2 and the F_3 will be indicated by g_{ij}, g_{ij}' and g_{ij}''.

From Eq. 7 it follows that

$$g_{ij}' = g_{ij}(1-r) + \tfrac{1}{4}r \tag{8}$$

Applying Eq. 1 and 2, one finds for the gametic output of the F_2 that:

$$g_{11}' = \tfrac{3}{4}r - \tfrac{1}{2}r^2 \tag{9}$$

$$g_{10}' = \tfrac{1}{2} - \tfrac{3}{4}r + \tfrac{1}{2}r^2 = \tfrac{1}{2} - g_{11}' \tag{10}$$

$$g_{01}' = g_{10}'$$

$$g_{00}' = g_{11}'$$

Define:

$$g_{11}' = \tfrac{1}{2}r'; u' = \tfrac{1}{2}r'; v' = \tfrac{1}{2}(1-r').$$

This gives:

$$g_{11}' = u'; g_{10}' = v'; g_{01}' = v'; g_{00}' = u'.$$

Random fusion of these gametes produces F_3' (see Table 5).

For the gametes from F_3' it is true that, analogous to Eq. 8:

$$g_{11}'' = g_{11}'(1-r) + \tfrac{1}{4}r = r - \tfrac{5}{4}r^2 + \tfrac{1}{2}r^3 \tag{11}$$

$$g_{10}'' = g_{10}'(1-r) + \tfrac{1}{4}r = (\tfrac{1}{2} - g_{11}')(1-r) + \tfrac{1}{4}r = \tfrac{1}{2} - g_{11}'' \tag{12}$$

$$g_{01}'' = g_{10}''$$

$$g_{00}'' = g_{11}''.$$

VAN DER VEEN (1973) derived the following formula for the relative frequency of

Table 5. Genotype composition of the F_3' and the F_∞' for linked loci if the F_1 is in repulsion phase; r is the fraction gametes originating from recombination; $u' = \frac{1}{2}r'$, $v' = \frac{1}{2}(1\text{-}r')$, $\frac{1}{2}r' = \frac{3}{4}r - \frac{1}{2}r^2$.

Genotype	Code (ij)	Relative frequency (f_{ij})	
		F_3'	F_∞'
$A_1A_1B_1B_1$	22	u'^2	$(5r - 2r^2)(4 + 8r)^{-1}$
$A_1A_1B_1B_2$	21	$2u'v'$	0
$A_1A_1B_2B_2$	20	v'^2	$\frac{1}{2} - (5r - 2r^2)(4 + 8r)^{-1}$
$A_1A_2B_1B_1$	12	$2u'v'$	0
$A_1B_2A_2B_1$	11r	$2v'^2$	0
$A_1B_1A_2B_2$	11c	$2u'^2$	0
$A_1A_2B_2B_2$	10	$2u'v'$	0
$A_2A_2B_1B_1$	02	$v'2$	$\frac{1}{2} - (5r - 2r^2)(4 + 8r)^{-1}$
$A_2A_2B_1B_2$	01	$2u'v'$	0
$A_2A_2B_2B_2$	00	u'^2	$(5r - 2r^2)(4 + 8r)^{-1}$

gametes with genotype A_1B_1 produced by a population which originates – after many generations of self-fertilization – from an arbitrary initial population:

$$\lim_{k \to \infty} g_{11}^{(k)} = g_{11}^{(i)} - \frac{r(1 - 2r)}{2(1 + 2r)} (f_{11c}^{(i)} - f_{11r}^{(i)}) \tag{13}$$

In this equation (i) denotes: in the initial population. If F_3' is considered to be the initial population, i.e. the first population which produces progeny by self-fertilization, i.e. $g_{11}^{(i)} = g_{11}'$, and

$f_{11c}^{(i)} - f_{11r}^{(i)} = 2u'^2 - 2v'^2 = u' - v' = r' - \frac{1}{2} = -r^2 + \frac{3}{2}r - \frac{1}{2}$ (see Table 5), then

$$g_{11}^{(\infty)} = (r - \tfrac{5}{4}r^2 + \tfrac{1}{2}r^3) - \frac{r(1 - 2r)}{2(1 + 2r)} (-r^2 + \tfrac{3}{2}r - \tfrac{1}{2})$$

$$= (5r - 2r^2)(4 + 8r)^{-1}, \tag{14}$$

which is in agreement with BAKER (1968).

For F_∞' we have $g_{11} = f_{22}$; $g_{10} = f_{20}$; $g_{01} = f_{02}$; and $g_{00} = f_{00}$, and because F_∞' does not contain heterozygotes it follows (according to Table 2) that

$$g_{10}^{(\infty)} = \tfrac{1}{2} - g_{11}^{(\infty)} = (2 - r + 2r^2)(4 + 8r)^{-1} \tag{15}$$

$$g_{01}^{(\infty)} = g_{10}^{(\infty)}$$

$$g_{00}^{(\infty)} = g_{11}^{(\infty)}.$$

Table 5 presents the relative genotype frequencies of F_3' and F_∞'. For some values of r, Table 6 reports the number of plants with the optimal genotype $A_1A_1B_1B_1$ to be expected, according to Table 5, in an F_3' or an F_∞' population of 10000 plants.

a. Comparison of F_3 and F_3' (Table 6, column 4). For independent segregating loci $(r = \frac{1}{2})$ the F_2 is in linkage equilibrium and then random mating of F_2 plants will

Table 6. The expected number of plants with the optimal genotype $A_1A_1B_1B_1$ (n_g) in an F_3' or F_∞' population of 10 000 plants.

r	$n_g(F_3')$	$n_g(F_\infty')$	$\dfrac{n_g(F_3)}{n_g(F_3')}$	$\dfrac{n_g(F_\infty')}{n_g(F_\infty)}$
0.5	625	2500	2.25	1
0.25	244.1	1875	2.92	1.12
0.125	73.9	1187.5	4.63	1.19
0.0625	20.2	677.1	8.16	1.22
0.03125	5.3	363.1	15.17	1.235
0.01562	1.3	188.2	30.5	1.238
0.00781	0.3	95.8	65.6	1.244
0.0039	0.1	48.3	97.8	$\simeq 1.25$
0	0	0		$\lim\limits_{r \to 0} \dfrac{n_g(F_\infty')}{n_g(F_\infty)} = 1.25$

originate an F_3' with the genotypic composition of the F_2. In spite of extra investments for such loci intermating of F_2 plants implies stagnation in the shifting of the genotype frequencies.

When the loci are linked ($r < \frac{1}{2}$; F_1 in repulsion phase) F_3 contains more plants with genotype $A_1A_1B_1B_1$ than F_3', and relatively more as linkage is tighter. This disappointing result follows from the fact that intermating of F_2 plants does not produce plants with genotype $A_1A_1B_1B_1$ in preference to others, but will yield all types of homozygous and heterozygous individuals. On the contrary, self-fertilization of F_2 plants will yield especially homozygotes, such as $A_1A_1B_1B_1$.

b. Comparison of F_∞ and F_∞' (Table 6, column 5). For independent segregating loci F_∞ and F_∞' are identical and intermating of F_2 plants has no effect.

For linked loci ($r < \frac{1}{2}$; F_1 in repulsion phase) F_∞' contains more plants with genotype $A_1A_1B_1B_1$ than F_∞, and increasingly so as linkage is tighter. This extra portion, however, amounts at most to only 25 % of the number in the F_∞. This can be shown as follows: define $\Delta f_{11} = f_{11}(F_\infty') - f_{11}(F_\infty)$. From Eq. 14 and Table 1 it can be derived that

$$\Delta f_{11} = (r - 2r^2)(4 + 8r)^{-1}.$$

The relative increment is therefore

$$\Delta f_{11}/f_{11}(F_\infty) = \tfrac{1}{4}(1 - 2r), \text{ being } \tfrac{1}{4} \text{ at the most.}$$

2.1.2.2 The number of plants with the optimal phenotype (in F_3' and F_∞')
If the 'plus-alleles' are completely dominant the portion of plants with the optimal phenotype $A_1.B_1.$ is, according to Eq. 3 and Table 5:

in the F_3' : $\frac{1}{2} + u'^2$ (16)

in the F_∞' : $f_{00}.$ (17)

Table 7. The expected number of plants with the optimal phenotype $A_1.B_1$. (n_f) in an F'_3 or an F'_∞ population of 10000 plants.

r	$n_f(F'_3)$	$n_f(F'_\infty)$	$\dfrac{n_f(F'_3)}{n_g(F'_3)}$
0.5	5625	2500	9
0.25	5244.1	1875	21.5
0.125	5073.9	1187.5	68.6
0.0625	5020.2	677.1	248.5
0.03125	5005.3	363.1	944.4
0.01562	5001.3	188.2	—
0.00781	5000.3	95.8	—
0.0039	5000.1	48.3	—
0	5000	0	

Table 7 presents, for some values of r, the number of plants with the optimal phenotype to be expected, according to Eq. 16 and 17, in an F'_3 or an F'_∞ population of 10000 plants. Table 7 is based on Table 6. From the fourth column it appears that, if dominance is complete, the proportion of F'_3 plants with the optimal phenotype as against those with the optimal genotype increases as r decreases. It is therefore advisable, in the case of dominance and tight linkage, to start selection in an advanced generation.

2.2 Selection in the F_2

When the 2 characters for which one tries to combine desired levels of expression, are observable before flowering, selection may take place before flowering. It is assumed that the plus-alleles are completely dominant. After selection the F_2 contains only plants with the phenotype $A_1.B_1$. The result of spontaneous self-fertilization of F_2 plants with the optimal phenotype (see section 2.2.1) will be compared with the result of intermating the F_2 plants with the optimal phenotype (see section 2.2.2).

2.2.1 The remaining F_2 plants produce progenies by continued self-fertilization

According to Eq. 4 a fraction a^{-1} of the plants of the original F_2 population has the optimal phenotype and therefore the composition of this F_2 population after selection (see Table 8) can easily be derived from Table 1. The F_3 originates from spontaneous self-fertilization of the remaining F_2 plants. The genotypic composition of the F_3 (see Table 8) follows from Appendix 1. The relative frequency of the gametes with genotype A_1B_1 produced by this F_3 is, according to Appendix 2,

$$g'_{11} = a \left(\tfrac{7}{8} - r^2 + \tfrac{1}{2}r^3 \right) \tag{18}$$

For the F_∞ it applies, according to Appendix 3, that

$$f^{(\infty)}_{22} = 4r \left\{ (2 + r^2)(1 + 2r) \right\}^{-1} \tag{19}$$

Table 8. Genotypic composition of the F_2 and the F_3 after positive mass-selection of F_2 plants with the optimal phenotype; r is the fraction of gametes originating from recombination; $u = \frac{1}{2}r$, $a = (\frac{1}{2} + u^2)^{-1}$.

Genotype	Code (ij)	Relative frequency (f_{ij})	
		F_2	F_3
$A_1A_1B_1B_1$	22	$a(u^2)$	$a(\frac{1}{2}u + 4u^2v^2)$
$A_1A_1B_1B_2$	21	$a(2uv)$	$a\{uv + 4uv(u^2 + v^2)\}$
$A_1A_1B_2B_2$	20	0	$a(\frac{1}{2}uv + 2u^4 + 2v^4)$
$A_1A_2B_1B_1$	12	$a(2uv)$	$a\{uv + 4uv(u^2 + v^2)\}$
$A_1B_2A_2B_1$	11r	$a(2v^2)$	$a(4u^4 + 4v^4)$
$A_1B_1A_2B_2$	11c	$a(2u^2)$	$a(8u^2v^2)$
$A_1A_2B_2B_2$	10	0	$a\{4uv(u^2 + v^2)\}$
$A_2A_2B_1B_1$	02	0	$a(\frac{1}{2}uv + 2u^4 + 2v^4)$
$A_2A_2B_1B_2$	01	0	$a\{4uv(u^2 + v^2)\}$
$A_2A_2B_2B_2$	00	0	$a(4u^2v^2)$

2.2.1.1 The number of plants with the optimal genotype (in F_3 and F_∞)

Table 9 presents, for some values of r, the number of plants with the optimal genotype $A_1A_1B_1B_1$ that can be expected, according to Table 8 and Eq. 19 in an F_3 or F_∞ population, respectively, of 10000 plants. Because

$$\frac{N_g(F_3)}{n_g(F_3)} = a \text{ (see Table 1 and Table 8), and also}$$

$$\frac{N_g(F_\infty)}{n_g(F_\infty)} = \frac{4}{2 + r^2} = a \text{ (see Table 1 and Eq. 19),}$$

positive mass-selection of F_2 plants with the optimal phenotype has for result that both F_3 and F_∞ contain a times as many plants with the optimal genotype $A_1A_1B_1B_1$ as when selection in the F_2 was not applied (see Table 9, column 4).

Table 9. The expected number of plants with the optimal genotype $A_1A_1B_1B_1$ (N_g) in an F_3 or an F_∞ population of 10000 plants after selection in the F_2.

r	$N_g(F_3)$	$N_g(F_\infty) = N_f(F_\infty)$	$\frac{N_g(F_3)}{n_g(F_3)} = \frac{N_g(F_\infty)}{n_g(F_\infty)} = a$
0.5	2500	4444.4	1.78
0.25	1382.6	3232.3	1.94
0.125	679.5	1984.5	1.98
0.0625	329.0	1108.9	1.99
0.03125	160.8	587.9	2.0
0.01562	79.3	302.9	2.0
0.00781	39.3	153.8	2.0
0.0039	19.6	77.4	2.0
0	0	0	2

In short, selection in the F_2 will give in later generations not more than 2 times as many plants with genotype $A_1A_1B_1B_1$.

2.2.2 *The remaining F_2 plants are intermated*

Just like in section 2.1.2, it is assumed that the F_2 plants are intermated at random. The relative frequency of gametes with genotype A_1B_1 that are produced by the F_2, is derived from Appendix 3:

$$g'_{11} = \tfrac{1}{4}a (3r - 2r^2) \tag{20}$$

Likewise:

$$g'_{10} = f_{20} + \tfrac{1}{2}f_{21} + \tfrac{1}{2}f_{10} + vf_{11r} + uf_{11c} \tag{21}$$

$$= \tfrac{1}{4}a (1 - 2r + 2r^2) \tag{22}$$

$$g'_{01} = f_{02} + \tfrac{1}{2}f_{12} + \tfrac{1}{2}f_{01} + vf_{11r} + uf_{11c} = g'_{10} \tag{23}$$

$$g''_{00} = f_{00} + \tfrac{1}{2}f_{10} + \tfrac{1}{2}f_{01} + uf_{11r} + vf_{11c} \tag{24}$$

$$= \tfrac{1}{4}a (r - r^2) \tag{25}$$

Random mating of the remaining F_2 plants results in F'_3 (see Table 10). According to VAN DER VEEN (1973) the relative frequency of gametes with genotype A_1B_1 equals

$$g''_{11} = g'_{11} - r (g'_{11}g'_{01} - g'_{10}g'_{01}) \tag{26}$$

For F'_∞ it then applies that

$$f^{(\infty)}_{22} = \frac{r(8 + 5r - 2r^3)}{(2 + r^2)^2 (1 + 2r)} \text{ (see Appendix 4).} \tag{27}$$

Table 10. Genotypic composition of the F'_3 and the F'_∞ for linked loci if the F_1 is in repulsion phase and after selection in the F_2; $g'_{11}, g'_{10}, g'_{01}$ and g''_{00} are the relative frequencies of the gametes from the F_2, r is the fraction gametes originating from recombination.

Genotype	Code (ij)	Relative frequency (f_{ij})	
		F_2	F_3
$A_1A_1B_1B_1$	22	g'^2_{11}	$r(8 + 5r^2 - 2r^3)\{(2 + r^2)^2(1 + 2r)\}^{-1}$
$A_1A_1B_1B_2$	21	$2g'_{11}g'_{10}$	0
$A_1A_1B_2B_2$	20	g'^2_{10}	*
$A_1A_2B_1B_1$	12	$2g'_{11}g'_{01}$	0
$A_1B_2A_2B_1$	11r	$2g'_{10}g'_{01}$	0
$A_1B_1A_2B_2$	11c	$2g'_{11}g''_{00}$	0
$A_1A_2B_2B_2$	10	$2g'_{10}g''_{00}$	0
$A_2A_2B_1B_1$	02	g'^2_{01}	*
$A_2A_2B_1B_2$	01	$2g'_{01}g''_{00}$	0
$A_2A_2B_2B_2$	00	g'^2_{00}	*

* Not derived.

2.2.2.1 The number of plants with the optimal genotype (in F_3' and F_∞')

Table 11 (derived from Table 10) presents, for some values of r, the number of plants with the optimal genotype $A_1A_1B_1B_1$ to be expected in an F_3' or an F_∞' population of 10000 plants.

a. Comparison of F_3 and F_3' (Table 11, column 4). It appears that after positive mass-selection of F_2 plants with the optimal phenotype $A_1.B_1$. the introduction of random mating of F_2 plants implies extra expenses. These expenses will only result in an even smaller number of plants with the desired genotype than with continued self-fertilization, especially for small values of r.

b. Comparison of F_∞ and F_∞'. Because

$$\frac{N_g(F_\infty')}{N_g(F_\infty)} = \frac{8 + 5r^2 - 2r^3}{8 + 4r^2} \simeq 1 \text{ (see Eq. 19 and 27),}$$

it must be concluded that introduction of random mating of selected F_2 plants has no effect what so ever on the ultimate fraction of plants with genotype $A_1A_1B_1B_1$.

3 THE PARENTS ARE DIFFERENT FOR M INDEPENDENT SEGREGATING LOCI

If the homozygous parental varieties are different for m independent segregating loci $(A_1 - A_2, B_1 - B_2, ..., M_1 - M_2)$ then the F_1 plants have the genotype $A_1A_2B_1B_2....$ M_1M_2. The F_1 plants will form gametes with 2^m different genotypes, each of which has a relative frequency 2^{-m} (= the product of the gene frequencies). The F_2 population will be a population in linkage equilibrium. Random mating of the plants of the F_2 yields an F_3' with the same genotypic composition as the F_2. Continued self-fertilization of the F_2 or the F_3' results therefore in F_∞ populations with identical genotypic compositions. In this case intermating of F_2 plants will involve only extra costs.

Table 11. The expected number of plants with the optimal genotype $A_1A_1B_1B_1$ (N_g) in an F_3' or an F_∞' population of 10000 plants after selection in the F_2.

r	$N_g(F_3')$	$N_g(F_\infty')$	$\dfrac{N_g(F_3)}{N_g(F_3')}$
0.5	1975.3	4444.4	1.27
0.25	918.3	3232.3	1.51
0.125	290.8	1984.5	2.34
0.0625	80.4	1108.9	4.09
0.03125	21.0	587.9	7.66
0.01562	5.37	302.9	14.77
0.00781	1.36	153.8	28.90
0.0039	0.34	77.4	57.65
0	0	0	

4 DISCUSSION

For 2 linked loci (and if the F_1 is in repulsion phase) the following can be concluded.

If there is no selection in the F_2 population then the effect of random mating F_2 plants is scanty as far as following generations (F'_3, F'_4, F'_5, ..., F'_∞) are concerned:

i) F'_3 contains less plants with the desired genotype $A_1A_1B_1B_1$ than the normal F_3. This follows from the fact that random mating yields all kinds of homozygous and heterozygous genotypes and not – as in the case of self-fertilization – an increased fraction of homozygotes.

ii) F'_∞ contains – if the loci segregate independently – as many plants with the optimal genotype as F_∞. When the loci are linked, F'_∞ (i.e. in case of tight linkage) contains at most 25 % more plants with the optimal genotype than F_∞.

When selection is applied to the F_2 population then random mating of the remaining plants of the F_2 has a negative effect on the F_3 and no effect at all on the F_∞.

The conclusion is that intermating of F_2 plants can not be considered to be a possibility of increasing the expected number of plants with the desired genotype. This conclusion holds too for any number of independent segregating loci. This result confirms the results of PEDERSON (1974) where he compares the variances of the F_∞ populations gained after 0, 1, 2, ... generations with random mating.

Intermating of selected F_2 plants has no effect on the expected number of plants with genotype $A_1A_1B_1B_1$ in the F . Selection in F_2 as such, however, is effective: one should compare Table 3, column 4 with Table 9, column 3. Also PEDERSON (1974) concludes: 'Directional selection is preferred as a method for increasing the frequency of desirable homozygotes.'

The advocates for intermating that were mentioned in the Introduction did not report experiments to evaluate their considerations and therefore experiences of some others will be discussed.

REDDEN & JENSEN (1974) investigated in barley and wheat the effect of intermating plants of segregating populations. They did this both for absence and presence of selection and conclude: 'There is reason to believe that outcrossing concurrent with selection may be worth considering as a tool for breeding programs for naturally inbreeding crops, provided that the additive component of the genetic variance is important.'

MILLER & RAWLINGS (1967) investigated in cotton the negative genetic correlation of yield and fibre strength. This correlation could be caused by linkage in repulsion phase. The negative correlation was weakened by intermating of the plants during 6 generations. The conclusion was: 'It appears that the intermated populations should provide a better source of material for selection than the original F_2 population, perhaps due to a partial break up of linkage blocks in the original material.'

MEREDITH & BRIDGE (1971), who also worked with cotton, found the same after 2 generations with intermating.

The foregoing outcomes of experiments are opposite to those of this study. Two possible explanations are:

i) the positive conclusions are based on observations on segregating generations. Conclusions about the result in the F_∞ are impossible;

ii) no data are delivered about the proportion of the plants showing an optimal phe-

notype in both the normal generations and the generations gained after intermating.

APPENDICES

Appendix 1

Genotype	code (ij)	$f_{ij}(F_2)$	Genotypic composition F_3 line									
			22	21	20	12	11r	11c	10	02	01	00
$A_1A_1B_1B_1$	22	u^2	1	0	0	0	0	0	0	0	0	0
$A_1A_1B_1B_2$	21	$2uv$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	0	0	0	0	0	0	0
$A_1A_1B_2B_2$	20	v^2	0	0	1	0	0	0	0	0	0	0
$A_1A_2B_1B_1$	12	$2uv$	$\frac{1}{4}$	0	0	$\frac{1}{2}$	0	0	0	$\frac{1}{4}$	0	0
$A_1B_2A_2B_1$	11r*	$2v^2$	u^2	$2uv$	v^2	$2uv$	$2v^2$	$2u^2$	$2uv$	v^2	$2uv$	u^2
$A_1B_1A_2B_2$	11c*	$2u^2$	v^2	$2uv$	u^2	$2uv$	$2u^2$	$2v^2$	$2uv$	u^2	$2uv$	v^2
$A_1A_2B_2B_2$	10	$2uv$	0	0	$\frac{1}{4}$	0	0	0	$\frac{1}{2}$	0	0	$\frac{1}{4}$
$A_2A_2B_1B_1$	02	v^2	0	0	0	0	0	0	0	1	0	0
$A_2A_2B_1B_2$	01	$2uv$	0	0	0	0	0	0	0	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$
$A_2A_2B_2B_2$	00	u^2	0	0	0	0	0	0	0	0	0	1

* r = repulsion phase; c = coupling phase.

Appendix 2

When deriving g'_{11} the following equalities are used:

$$u^4 + v^4 = (u^2 - v^2)^2 + 2u^2v^2 = \tfrac{1}{4}(u-v)^2 + 2u^2v^2 \tag{a1}$$

$$u^2 + v^2 = (u+v)^2 - 2uv = \tfrac{1}{4} - 2uv \tag{a2}$$

According to Table 8

$$
\begin{aligned}
g'_{11} &= f_{22} + \tfrac{1}{2}f_{21} + \tfrac{1}{2}f_{12} + uf_{11r} + vf_{11c} \\
&= a\{\tfrac{1}{2}u + 4u^2v^2 + \tfrac{1}{2}uv + 2uv(u^2+v^2) + \tfrac{1}{2}uv + 2uv(u^2+v^2) + 4u(u^4+v^4) + 8u^2v^3\} \\
&= a\{\tfrac{1}{2}u + 2uv + u(u-v)^2\} \\
&= a\{\tfrac{1}{4}r + \tfrac{1}{2}r(1-r) + \tfrac{1}{2}r(r-\tfrac{1}{2})^2\} = a(\tfrac{7}{8}r - r^2 + \tfrac{1}{2}r^3)
\end{aligned} \tag{a3, a4}
$$

Appendix 3

For the F_2 holds (see Table 8):

$$f_{11c} - f_{11r} = 2a(u^2 - v^2) = a(r - \tfrac{1}{2}) \tag{a5}$$

For an F_∞ holds

$$f_{22}^{(\infty)} = g_{11}^{(\infty)} \text{ and } f_{22}^{(\infty)} = \lim_{k\to\infty} g_{11}^{(k)}$$

The F_2 population remaining after selection is the first generation which produces progenies by self-fertilization, and therefore g'_{11} is substituted for $g_{11}^{(i)}$ in Eq. 13.

According to Eq. a3 and Table 8 one finds

$$g_{11}' = a(\tfrac{3}{4}r - \tfrac{1}{2}r^2)$$ (a6)

Eq. 13 gives, with application of Eq. a5,

$$f_{22}^{(\infty)} = a\left\{(\tfrac{3}{4}r - \tfrac{1}{2}r^2) - \frac{r(1-2r)}{2(1+2r)}(r-\tfrac{1}{2})\right\}$$
$$= 4r\left\{(2+r^2)(1+2r)\right\}^{-1}$$ (a7)

Appendix 4

Eq. 13, together with Table 10 and Eq. 26, 20, 22, 23 and 24, gives

$$f_{22}^{(\infty)} = g_{11}'' - \frac{r(1-2r)}{2(1+2r)}(2g_{11}'g_{00}' - 2g_{10}'g_{01}')$$

$$= g_{11}' - \frac{2r}{1+2r}(g_{11}'g_{00}' - g_{10}'g_{01}')$$

Because $a = (\tfrac{1}{2} + u^2)^{-1} = \dfrac{4}{2+r^2}$ one can derive:

$$f_{22}^{(\infty)} = \frac{r(8+5r^2-2r^3)}{(2+r^2)^2(1+2r)}$$

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