Theoretical and Applied Genetics 45, 96–103 (1974)

Analysis of Means in the Case of Nonequivalent Reciprocal Crosses in Autogamous Plants[1]

RUSTEM AKSEL

Department of Genetics, University of Alberta, Edmonton, Alberta (Canada)

Summary. The analysis of means dealt with in this paper applies to two homozygous lines of an autogamous plant species and to their reciprocal crosses and backcrosses considered jointly. The analysis is based on a set of assumptions with respect to the parents, to the expressivity of alleles at differential loci in the crosses when acting in a plasmatype different from that of the parent contributing them and to the gene-dosis effects. The observed family means together with their expectations, formulated in terms of parameters implied by the assumptions postulated, consitute two independent systems of linear equations. The solution of these systems by means of weighted least squares yields the parameter estimates and their standard errors. The adequacy of the genetical model can be tested by chi-square method.

Introduction

The quantitative expressions of character-differences between the hybrids from reciprocal crosses have been studied in a number of plants such as *Zea mays* (Richey 1920, St. John 1934, Fleming et al. 1960, Bhat and Dhavan 1970), *Vicia faba* (Sirks 1931), *Epilobium* (Michaelis 1954), *Oryza sativa* (Chandraratna and Sakai 1960, Sakai et al. 1961), *Hordeum sativum* (Nečas 1961, 1962, 1963, 1966), *Linum usitatissimum* (Smith and Fitzsimmons 1964, 1965; Durrant 1965, 1973; Tyson 1973) and *Nicotiana rustica* (Jinks, Perkins and Gregory 1972). Chandraratna and Sakai (op. cit.) and Sakai et al. (op. cit.) have developed a method of biometrical analysis of matroclinous inheritance. Durrant (1965) has worked out a method of analysis of reciprocal differences in diallel crosses. Models of biometrical analysis for reciprocal crosses between inbred lines and for multiple crosses, maternal effects taken into consideration, were given by Mather and Jinks (1971). A detailed analysis and interpretation of differences between reciprocal crosses of *Nicotiana rustica* varieties was made by Jinks, Perkins and Gregory (op. cit.). The intent of this paper is to discuss the genetic situation in reciprocal crosses and backcrosses of autogamous plants when character differences are controlled by both the genotype and the plasmatype and to explore the possibility of a somewhat different and perhaps more detailed approach to their quantitative genetic analysis. The analysis presented here centers on the parametric composition of the means of reciprocal families. With an appropriate experimental design it can be extended to second degree statistics calculated from the set of families, and possibly to diallel crosses provided the parents used are inbred lines selected from a cross and its reciprocal after a sufficiently long period of self fertilisation.

[1] This topic was presented partially and under a different form at the 16th Annual Meeting of the Genetics Society of Canada at l'Université Laval, Quebec, P. Quebec, Canada.

Notation, Assumptions and the Formulation of the Expectations

The nth ($n = 1, 2, \ldots$) filial generation of a cross between a female X and a male Y can be denoted generally as $(XY)F_n$, with X and Y written always in that order. In the present case $X = A, B, (AB), (BA)$ and $Y = A, B, (AB), (BA)$, where A and B are two homozygous lines of an autogamous plant species, and (AB) and (BA) stand for the first generation of their reciprocal crosses.

Let us postulate:

Assumption 1. The parents A and B differ from one another with respect to a quantitative character both genotypically and plasmatypically.

Assumption 2. Genotypically the character is controlled by nuclear genes some or all which have different effects in different cytoplasms, or plasmatypes. Such genes are said to be *plasmon sensitive*, or *plasma sensitive* (Caspari 1948, Michaelis 1954, Hagemann 1964, Jinks 1964).

Assumption 3. The plasmatype of the hybrid is the same as that of its female parent and maintains its reaction norm in the subsequent generations of autofertilization (see, e. g. Michaelis, op. cit.).

Assumption 4. The nuclear genes controlling the character are independent in their action, i. e., the contribution of a locus to the character-measurement is independent of the rest of the genotype.

Some other assumptions will be postulated in due course.

A notation similar to that of von Wettstein (see Michaelis, op. cit.) will be used to denote an idiotype, viz., $I = \{\pi, G\}$, where π and G stand for plasmatype and genotype respectively. Both π and G may refer to one, several, or all the characters with respect to which similarities and differences between individuals or groups of individuals belonging to the same species are recordable. In the present case they refer to a quantitative character.

Let $G(A)$ and $G(B)$ be the genotypes, and $\pi(A)$ and $\pi(B)$ the plasmatypes of the parents A and B. Since A and B are assumed to be homozygous, $G(A)$ and $G(B)$ denote their genotypes in both the zygotic and the gametic states (Aksel 1967). As usual, $G(A)$ and $G(B)$ are defined as sets of loci at which A and B are assumed to differ with respect to the character considered.

Any XY cross implies the union of sets of alleles contributed by the gametes of the two parents. Since in this case $X = A, B, (AB), (BA)$ and $Y = A, B, (AB), (BA)$, all $(XY)\ F_n$ have the same nuclear-genetic constitution, viz., $G(A) \cup G(B)$. If A and B differ at N loci and the two alleles controlling this difference at the kth locus ($k = 1, 2, \ldots, N$) are denoted as unit sets $\{a\}_k \subset G(A)$ and $\{b\}_k \subset G(B)$ then $G(A) = \cup_k\{a\}_k$, $G(B) = \cup_k\{b\}_k$ and $G(A) \cup G(B) = \cup_k\{a, b\}_k$. By assumption the offspring has the same plasmatype as its female parent. Consequently,

$$I(XY)F_n = \{\pi(X{:}X = A, B)\ ,\ \cup_k \{a, b\}_k\} \quad (1)$$

where $X = A, B, (AB), (BA)$ and $Y = A, B, (AB), (BA)$, as already given. Expression (1) may refer to a single individual or to a group of individuals sharing jointly the same $\cup_k\{a, b\}_k$ set of alleles.

The set of the possible genotypes at the kth locus is $\{a, b\}_k \times \{a, b\}_k = \{(aa), (ab), (bb)\}_k$, assuming $(ab) = (ba)$. If the probabilities of (aa), (ab) and (bb) at the kth locus in a population are p, q and r, respectively, such that $0 \leq p \leq 1$, $0 \leq q \leq 1$, $0 \leq r \leq 1$ and $p + q + r = 1$, then

$$\cup_k\{a, b\}_k \Rightarrow \sum_k \{p(aa) + q(ab) + r(bb)\}_k$$

or, with p, q and r assumed the same for each locus involved

$$\cup_k \{a, b\}_k \Rightarrow p \sum_k (aa)_k + q \sum_k (ab)_k + r \sum_k (bb)_k \quad (2)$$

where $\Rightarrow$ reads *implies* or *results in*.

By definition, a moment M of order t with respect to an arbitrary origin c is $M_t = \left(\sum_i f_i(x_i - c)^t\right) \div \sum_i f_i$ where $i = 1, 2, \ldots,$ and $t = 1, 2, \ldots$. With $t = 1$ and the addition of c to both its sides, this equation becomes

$$c + M = c + \left(\sum_i (x_i - c)\right) \div \sum_i f_i\ . \quad (3)$$

Let $x_1 = x_{aa}$, $x_2 = x_{ab}$ and $x_3 = x_{bb}$ be the character-measurements of $\sum_k (aa)_k$, $\sum_k (ab)_k$ and $\sum_k (bb)_k$, respectively, and $f_1 = p$, $f_2 = q$ and $f_3 = r$ be their corresponding relative frequencies. The appropriate substitutions in (2) and (3) obtain:

$$\cup_k\{a, b\}_k \Rightarrow px_{aa} + qx_{ab} + rx_{bb}$$

and

$$c + M = c + p(x_{aa} - c) + q(x_{ab} - c) + r(x_{bb} - c)\ ,$$

respectively. Since $p + q + r = 1$, the right sides of these expressions are the same and, therefore, we can write:

$$\cup_k\{a, b\}_k \Rightarrow c + p(x_{aa} - c) + q(x_{ab} - c) + r(x_{bb} - c). \quad (4)$$

The differences $(x_{aa} - c)$, $(x_{ab} - c)$ and $(x_{bb} - c)$ define the genotypic values of $\sum_k (aa)_k$, $\sum_k (ab)_k$ and $\sum_k (bb)_k$ generally. In particular, with $c = 0.5(x_{aa} + x_{bb}) = m$ as the common reference and assuming $x_{aa} < x_{bb}$ for instance, these genotypic values are denoted as $-[d]$, $[h]$ and $[d]$, respectively (see: e. g., Mather and Jinks 1971).

By assumption $\pi(A) \neq \pi(B)$ and therefore expression (1) refers to two nuclear-genetically the same but plasmatypically different sets of crosses, viz., to sets implied by $I(XY)F_n = \{\pi(A), \cup_k\{a, b\}_k\}$ and $I(XY)F_n = \{\pi(B), \cup_k\{a, b\}_k\}$, where either $\cup_k\{b\}_k \subset \cup_k\{a, b\}_k$ is sensitive to $\pi(A)$ or $\cup_k\{a\}_k \subset \cup_k\{a, b\}_k$ is sensitive to $\pi(B)$ or both. Since one can write $A = P_1, P_2$ and $B = P_1, P_2$ such that $A \neq B$ and $P_1 \neq P_2$, in sequel it is sufficient to consider only one of the two sets of crosses, the set implied by $\{\pi(A), \cup_k, \{a, b\}_k\}$ for instance. These crosses and the relative frequencies of $\sum_k (aa)_k$, $\sum_k (ab)_k$ and $\sum_k (bb)_k$ expected in the nth generation of selving are given in Table 1.

The set of crosses in Table 1 implies a system of nonhomogeneous linear equations. The number of equations in the system is dependent upon the number of generations considered for each cross, and their parametric constitution is dependent upon the assumptions postulated in regard to the manifestation of the $\pi(A)$ — sensitivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$.

By definition plasma-sensitive genes are nuclear genes which have different effects, or expressivities, in different plasmatypes. The allelic set $\cup_k\{b\}_k$ occurs in the progeny of the crosses considered in both the heterozygous and the homozygous states, viz., as $\sum_k (ab)_k$ and $\sum_k (bb)_k$ (see expression (2)) and may have been contributed by an idiotypically $\{\pi(A), \cup_k\{a, b\}_k\}$, $\{\pi(B), \cup_k\{a, b\}_k\}$ or $\{\pi(B), \cup_k\{b\}_k\}$ parent, or by both the parents plasmatypically and/or genotypically the same or different. Therefore, various assumptions can be postulated with respect to the circumstances under which the $\pi(A)$ — sensitivity of the set $\cup_k\{b\}_k$ manifests itself in the progeny.

The plasma-sensitivity of $\cup_k\{b\}_k$ means that its expressivity in $\pi\{(A), \cup_k\{a, b\}_k\}$ is not the same as

Table 1. *The crosses implied by* $\{\pi(A), \cup_k\{a, b\}_k\}$ *and the relative frequencies p, q and r of* $\sum_k (aa)$, $\sum_k (ab)_k$ *and* $\sum (bb)_k$, *respectively, expected in the nth generation of selfing*

Crosses	p	q	r
1. (AA) = self	1	0	0
2. $(AB)F_n$	$(1/2)\ (1 - 1/2^{n-1})$	$1/2^{n-1}$	$(1/2)\ (1 - 1/2^{n-1})$
3. $[(AB)\ (BA)]F_n^*$	$(1/2)\ (1 - 1/2^{n-1})$	$1/2^{n-1}$	$(1/2)\ (1 - 1/2^{n-1})$
3. $[(AB)\ A]\ F_n$	$(1/4)\ (3 - 1/2^{n-1})$	$(1/2)\ (1/2^{n-1})$	$(1/4)\ (1 - 1/2^{n-1})$
5. $[A(AB)]\ F_n$	$(1/4)\ (3 - 1/2^{n-1})$	$(1/2)\ (1/2^{n-1})$	$(1/4)\ (1 - 1/2^{n-1})$
6. $[A(BA)]\ F_n$	$(1/4)\ (3 - 1/2^{n-1})$	$(1/2\ )(1/2^{n-1})$	$(1/4)\ (1 - 1/2^{n-1})$
7. $[(AB)B]\ F_n$	$(1/4)\ (1 - 1/2^{n-1})$	$(1/2)\ (1/2^{n-1})$	$(1/4)\ (3 - 1/2^{n-1})$

* $[(AB)\ (BA)]F_n$ corresponds to $(AB)F_{n+1}$.

in $\{\pi(B), \cup_k\{a, b\}_k\}$; conceivably it is either increased or decreased. In the former case the inheritance of the character consired will be quasi-patroclinous and in the latter case quasi-matroclinous. If the change of expressivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ results in increments $\Delta_{[h]}$ and $\Delta_{[d]}$ to the measurement of a complete heterozygote and of a homozygote of the paternal type, then the genotypic values of $\sum(ab)_k$ and $\sum(bb)_k$ become $([h] + \Delta_{[h]})$ and $([d] + \Delta_{[d]})$, in that order. We shall assume, as before, that $x_{aa} < x_{bb}$. The substitution of m, $-[d]$, $([h] + \Delta_{[h]})$ and $([d] + \Delta_{[d]})$ in expression (4) for c, $(x_{aa} - c)$, $(x_{ab} - c)$ and $(x_{bb} - c)$, respectively, obtains the following generalized expression for the expected mean, $E\bar{x}$, of an idiotypically $\{\pi(A), \cup_k\{a, b\}_k\}$ cross:

$$E\bar{x}(XY)F_n = m - p[d] + q([h] + \Delta_{[h]}) + r[d] + \Delta_{[d]})$$

or (5)

$$E\bar{x}(XY)F_n = m - (p - r)[d] + q([h] + \Delta_{[h]}) + r\Delta_{[d]}$$

where the parameters $[h]$ and $\Delta_{[h]}$ are considered jointly because otherwise the system of equations implied has no solution.

Assumption 5. The expressivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ is affected by $\pi(A)$ when heterozygous only. This assumption implies that in expression (5) $\Delta_{[h]} \neq 0$ but $\Delta_{[d]} = 0$. Table 1 shows that $q = 1/2^{n-1}$, $1/2^n$ and since $\lim_{n\to\infty} q = 0$, the effect of $\pi(A)$ on $\cup_k\{b\}_k$, like that of dominance, is expected to vanish when the hybrid population considered reaches the state of complete homozygosity.

Assumption 6. The expressivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ is affected by $\pi(A)$ in both the heterozygous and the homozygous states. On this assumption both $\Delta_{[h]}$ and $\Delta_{[d]}$ in (5) are expected to be different from zero, and since $\lim_{n\to\infty} r > 0$ (see table 1) the effect of $\pi(A)$ on $\cup_k\{b\}_k$ is expected to persist even when the hybrid population considered becomes wholly homozygous.

The question of interdependence between the $\pi(A)$-sensitivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ and the idiotype of the parent, or parents, contributing it is basically the same in the case of both the assumptions 5 and 6. We shall consider assumption 6 as being the more complex one, and restate it specifically for different, supposedly possible, situations.

Assumption 6a. The effect of $\pi(A)$ on the expressivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ depends neither on the plasmatype nor the genotype of the parent, or parents, contributing it. This assumption implies expression (5) with $\Delta_{[h]} \neq 0$ and $\Delta_{[d]} \neq 0$ beginning with the first filial generation of the crosses in question.

Assumption 6b. The effect of $\pi(A)$ on the expressivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ depends on the plasmatype of the parent contributing it, such that when $\cup_k\{b\}_k$ is contributed by a plasmatypically $\pi(A)$ parent its expressivity is affected, but when contributed by a plasmatypically $\pi(B)$ parent its expressivity is not affected by $\pi(A)$.

The idiotypically $\{\pi(A), \cup_k\{a, b\}_k\}$ crosses listed in Table 1 fall into three groups: one group consisting of crosses 4 and 5 which obtain $\cup_k\{b\}_k$ from a plasmatypically $\pi(A)$ parent, viz., from (AB), a second group consisting of crosses 2 and 6 which obtain $\cup_k\{b\}_k$ from plasmatypically $\pi(B)$ parents, viz., from B and (BA), respectively, and a third group consisting of crosses 3 and 7 which obtain $\cup_k\{b\}_k$ from both the parents plasmatypically different, viz., from (AB) and (BA) and from (AB) and (B), respectively. Consequently, for the crosses 4 and 5 the situation remains the same as by assumption 6a. For crosses 2 and 6 assumption 6b implies expression (5) with $\Delta_{[h]} = \Delta_{[d]} = 0$ in $F_{n=1}$, but $\Delta_{[h]} \neq 0$ and $\Delta_{[d]} \neq 0$ in $F_{n>1}$ since beginning with the $F_{n=2}$ generation the allelic set $\cup_k\{b\}_k$ is obtained from parents which by assumption 3 are plasmatypically $\pi(A)$.

The case of crosses 3 and 7 is rather complicated. Let $\{b'\}_k$ denote $\{b\}_k \subset \cup_k\{b\}_k$ when $\cup_k\{b\}_k$ is contributed by B or by (BA), and $\{b''\}_k$ denote $\{b\}_k \subset \cup_k\{b\}_k$ when $\cup_k\{b\}_k$ is contributed by (AB). In other words, the gametic gene-sets produced by parents B, (BA) and (AB) are $\cup_k\{b'\}_k$, $\cup_k\{b''\}_k$ and $\cup_k\{a\}_k$. Consequently, the zygotic gene-sets in the F_1 generation of the crosses in question will be as

follows:

Cross 3: $\cup_k\{a\}$, $\cup_k\{a, b'\}_k$, $\cup_k\{a, b''\}_k$ and $\cup_k\{b', b''\}$ (6)

in equal proportions, and

Cross 7: $\cup_k\{a, b'\}_k$ and $\cup_k\{b', b''\}$ (7)

in equal proportions.

By assumption 6b the set $\cup_k\{b''\}_k$ is, but $\cup_k\{b'\}_k$ is not affected by $\pi(A)$. Supposing the gene-set $\cup_k\{b''\}_k \subset \{\pi(A), \cup_k\{b', b''\}_k\}$ to be completely dominated by $\cup_k\{b'\}_k$, the F_1 mean measurements of crosses 3 and 7 are expected to be:

$$E\bar{x}\,[(AB)\,(BA)]\,F_{n=1} = m + \left(\frac{1}{4}\right)[h] + \left(\frac{1}{4}\right)([h] + \Delta_{[h]}) + \left(\frac{1}{4}\right)\Delta_{[d]} \quad (8)$$

and

$$E\bar{x}[(AB)\,B]\,F_{n=1} = m + \left(\frac{1}{2}\right)[d] + \left(\frac{1}{2}\right)([h] + \Delta_{[h]})\,. \quad (9)$$

Obviously, the subsequent selfed generations obtain $\cup_k\{b\}_k$ from plasmatypically $\pi(A)$ parents only. Therefore, $E\bar{x}\,[(AB)\,(BA)]\,F_{n>1} = E\bar{x}(AB)\,F_{(n+1):\,n\geq 1}$ and

$$E\bar{x}\,[(AB)\,B]\,F_{n>1} = m + \left(\frac{1}{2}\right)[d] + (1/2^n)\,([h] + \Delta_{[h]}) + \left(\frac{1}{4}\right)(3 - 1/2^{n-1})\,\Delta_{[d]}\,. \quad (10)$$

Assumption 6c. The expressivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ is affected by $\pi(A)$ when contributed either by (AB) or (BA) or both and not affected when contributed by B. This means that $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ is assumed to manifest its sensitivity to $\pi(A)$ only after being associated with its allelic set $\cup_k\{a\}_k$ for one, or at least one, generation. Consequently, the expected means of crosses 3, 4, 5 and 6 in Table 1 will be the same as by assumption 6a, i.e., as given by expression (5) with $\Delta_{[h]} \neq 0$ and $\Delta_{[d]} \neq 0$, beginning with the first filial generation, whereas for crosses 2 and 7 assumption 6c implies expression (5) with $\Delta_{[h]} = \Delta_{[d]} = 0$ in their first filial generation, but with $\Delta_{[h]} \neq 0$ and $\Delta_{[d]} \neq 0$ in their subsequent generations.

By assumption 6c the gene-set $\cup_k\{b'\}_k$ contained in the idiotypically $\{\pi(A), \cup_k\{b', b''\}_k\}$ individuals in F_1 of cross 7 can not be affected by $\pi(A)$ in the subsequent generations unless the effect of $\{\pi(A), \cup_k\{b''\}_k\}$ on $\cup_k\{b'\}_k \subset \{\pi(A), \cup_k\{b, b''\}_k\}$ is the same as that of $\{\pi(A), \cup_k\{a\}_k\} \subset \{\pi(A), \cup_k\{a, b'\}_k\}$, which we shall assume not to be the case. Furthermore, it is likely that the genotypic value of an $\{\pi(A), \cup_k\{b', b''\}_k\}$ idiotype is the same as that of $\{\pi(B), \cup_k\{b\}_k\}$, i.e., $[d]$, and persist as such in the subsequent generations of selfing. Consequently,

$$E\bar{\iota}\,[(AB)\,B]\,F_{n>1} = m + \left(\frac{1}{2}\right)[d] + (1/2^n)\,([h] + \Delta_{[h]}) + \left(\frac{1}{4}\right)(1 - 1/2^{n-1})\,\Delta_{[d]}\,. \quad (11)$$

A system of linear equations formulated on the basis of any one of the combinations of assumptions considered in this paper, can be solved by the method of unweighted or weighted least squares. In the latter case the reciprocals of the squares of standard errors of the family means are used as weights. The test of the adequacy of the genetic situation postulated is based on the assumption that the weighted sum of squares of differences between the expected and the observed family means is distributed as a chi-square. The number of degrees of freedom for this chi-square test is equal to the number of equations in the system minus the number of parameters to be fitted to them. The same number of degrees of freedom applies when testing the significance of the parameter estimates (see, e.g., Mather and Jinks 1971, pp. 73–76). With two different sets of families, viz., the sets implied by $\{\pi(A), \cup_k\{a, b\}_k\}$ and $\{\pi(B), \cup_k\{a, b\}_k\}$, two systems of linear equations similar or not, depending upon the assumptions underlying their formulation, are available for calculating the parameter estimates. Of these parameters the estimates of m and $[d]$ or of m, $[d]$ and $[h]$, as the case may be, are expected to be the same for both sets.

The change in expressivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ may result, as already stated, in a quasi-matroclinous or a quasi-patroclinous inheritance of the character. With a quasi-matroclinous inheritance the direction of the effect of this change will be toward the measurement-mean of the line used as the female parent, viz., toward $\bar{x}(A)$ in the present case. With a quasipatroclinous inheritance the situation will be reversed. It is sufficient to discuss only the case of quasi-matroclinous inheritance.

By assumption $\bar{x}(A) < \bar{x}(B)$ and, therefore $\Delta_{[h]}$ and $\Delta_{[d]}$ must have negative sign. In extreme cases the expressivity of $\cup_k\{b\}_k \subset \{\pi(A), \cup_k\{a, b\}_k\}$ is either affected to the extent that it becomes effectively indistinguishable from its allelic set $\cup_k\{a\}_k$, or is not affected at all. This means that in the former case $([h] - \Delta_{[h]}) = ([d] - \Delta_{[d]}) = -[d]$ and, implicitly, $\Delta_{[h]} = ([d] + [h])$ and $\Delta_{[d]} = 2[d]$, and in the latter case, trivially, $\Delta_{[h]} = \Delta_{[d]} = 0$. Consequently we can write: $0 \leq \Delta_{[h]} \leq [(d] + [h])$ and $0 \leq \Delta_{[d]} \leq 2[d]$.

On the assumption that the inheritance of the character considered is quasi-matroclinous and that $\bar{x}(A) < \bar{x}(B)$, the effect of the substitution of $\cup_k\{b\}_k$ for both $\cup_k\{a\}_k$'s in $I(A) = \{\pi(A), \cup_k\{a\}_k\}$ is $2[d] - \Delta_{[d]}$. The substitution of $\cup_k\{b\}_k$ for only one of the two $\cup_k\{a\}_k$'s in $I(A)$ results in a heterozygote and the effect of such a substitution is expected to be $(1/2)\,(2[d] - \Delta_{[d]}) + [h] = [d] + [h] - (1/2)\,\Delta_{[d]}$. With reference to m instead of $\bar{x}(A)$, the above gene-set substitution effects are $([d] - \Delta_{[d]})$ and $([h] - (1/2)\,\Delta_{[d]})$ i.e., the same as the genotypic values of $\sum (bb)_k$ and $\sum (ab)_k$, respectively, with $(1/2)\,\Delta_{[d]}$ substituted for $\Delta_{[h]}$ in $([h] - \Delta_{[h]})$. Consequently, in the absence of zygosity effect $\Delta_{[h]} = (1/2)\,\Delta_{[d]}$.

The parameters $\Delta_{[h]}$ and $\Delta_{[d]}$ refer to the effects of change of expressivity of the entire set $\bigcup_{k=1}^{k=N} \{b\}_k \subset \subset \{\pi(A), \bigcup_{k=1}^{k=N} \{a, b\}_k\}$. It was stated, however, that the character considered is controlled genotypically by nuclear genes some or all of which have different effects in different plasmotypes (see: assumption # 2). The assumption that not all but only some of the alleles $\{b\}_k \subset \cup_k\{b\}_k$, $k = 1, 2, ..., N$, are affected by $\pi(A)$ means that the set $G(B) = \cup_k\{b\}_k$ is considered to consist of two disjoint and exhaustive subsets S and R of which S is affected and R is not affected by $\pi(A)$. If the alleles contained in S and R are denoted as $\{b\}_i$ and $\{b\}_j$, respectively, ($i = 1, 2, ..., n_i$; $j = 1, 2, ..., n_j$; $i \neq j$; $n_i + n_j = N$) then $\{\pi(A), \cup_k\{a, b\}_k\} = \{\pi(A), [(\cup_i\{a, b\}_i) \cup (\cup_j\{a, b\}_j)]\}$. If it is assumed that the set $\cup_i\{b\}_i$ when acting in $\pi(A)$ has expressivity zero, i.e., that it becomes effectively undistinguishable from its allelic set $\cup_i\{a\}_i$ then, given $\pi(A)$, the set $\cup_k\{a, b\}_k$ becomes equivalent to $(\cup_i\{a\}_i) \cup (\cup_j\{a, b\}_j)$. Consequently,

$$(\cup_i\{a\}_i) \cup (\cup_j\{a, b\}_j) \Rightarrow \sum_{i=1}^{n_i} (aa)_i + p \sum_{j=1}^{n_j} (aa)_j + q \sum_{j=1}^{n_j} (ab)_j + r \sum_{j=1}^{n_j} (bb)_j . \quad (12)$$

The average genotypic values per locus for $\sum_{i=1} (aa)_i$, $\sum_{=1} (aa)_j$, $\sum_{j=1} (ab)_j$ and $\sum_{j=1} (bb)_i$ are $-(1/n_i) \sum_{i=1} d_i$, $-(1/n_j) \sum_{j=1} d_j$, $(1/n_j) \sum_{j=1} h_j$ and $(1/n_j) \sum_{j=1} d_j$, respectively. Obviously, $-(1/n_j) \sum_{j=1} d_j = (-1)(1/n_j) \sum_{j=1} d_j$. If it is assumed that $(1/n_i) \sum_{i=1} d_i = (1/n_j) \sum_{j=1} d_j = (1/N)[d]$ and $(1/n_j) \sum_{j=1} h_j = (1/N)[h]$, and $N - n_i$ is used for n_j ($n_j = N - n_i$) then appropriate substitutions in (12) obtain:

$$E\bar{x}(XY) F_n = m - (p - r)[d] + q[h] - u\{(1 - (p - r)[d] + q[h]\} \quad (13)$$

where $u = n_i/N$, $(p - r) = 0$ and $q = 1/2^{n-1}$ for $(AB) F_n$ and $[(AB)(BA)] F_n$, and $(p - r) = \pm 1/2$ and $q = 1/2^n$ for the remaining crosses implied by $(\cup_i\{a\})_i \cup (\cup_j\{a, b\}_j)$.

The system of equations derivable from (13) does not have a solution if only one and the same generation of the crosses involved is considered.

The assumption that $\cup_i\{b\}_i \subset \{\pi(A), (\cup_i\{a, b\}_i) \cup \cup (\cup_j\{a, b\}_j)\}$ has expressivity zero implies a quasi-matroclinous inheritance. With this kind of inheritance equation (5) becomes:

$$E\bar{x}(XY) F_n = m - (p - r)[d] + q[h] - q\Delta_{[h]} - r\Delta_{[d]} . \quad (14)$$

Assuming (13) and (14) to pertain to the same generation of the same cross, the difference between them is:

$$u\{(1 - (p - r))[d] + q[h]\} - (q\Delta_{[h]} + r\Delta_{[d]}) = 0 \quad (15)$$

and, consequently:

$$u(F_n) = \frac{q\Delta_{[h]} + r\Delta_{[d]}}{(1 - (p - r))[d] + q[h]} . \quad (16)$$

Substitution from Table 1 for p, q and r in (16) obtains:

$$u(F_n) = \frac{(1/2^{n-1})\Delta_{[h]} + (1/2)(1 - 1/2^{n-1})\Delta_{[d]}}{[d] + (1/2^{n-1})[h]} \quad (17)$$

for all crosses shown in the table, except for $[(AB) B] F_n$ if assumption 6a or 6b and not 6c apply, in which case

$$u([(AB) B] F_n) = \frac{(1/2^{n-1})\Delta_{[h]} + (1/2)(3 - 1/2^{n-1})\Delta_{[d]}}{3[d] + (1/2^{n-1})[h]} . \quad (18)$$

For $n = 1$ equations (17) and (18) obtain $u = \Delta_{[h]}/([d] + [h])$ and $u = (\Delta_{[h]} + \Delta_{[d]})/(3[d] + [h])$, respectively. For both equations $\lim_{n\to\infty} u = \Delta_{[d]}/2[d]$. The ratio $u = \Delta_{[d]}/2[d]$ denotes the relative number of genes which have completely lost their expressivity only if prior to this loss all genes had equal effects or if, at least, $(1/n_i) \sum_{i=1} d_i = (1/n_j) \sum_{j=1} d_j = (1/N)[d]$ was true.

The difference between the $u = n_i \div N$ ratios in two different generations of the same cross is:

$$u(F_n) - u(F_m) = \frac{a(q - q')[d]\Delta_{[h]} + a(r - r')[d]\Delta_{[d]} + (q'r - qr')[h]\Delta_{[d]}}{(a[d])^2 + a(q + q')[d][h] + qq'[h]^2} , \quad (19)$$

where $a = 1$ if $p \geq r$, $a = 3/2$ if $p < r$, and q' and r' are the same as q and r with the difference that they refer to the mth generation of the cross considered ($m < n$, $m \geq 1$). The substitutions for q, q', r and r' in (19) show that $q - q'$, $r - r'$ and $q'r - qr'$ in the numerator are either multiples or fractions of $(2^n - 2^m)/2^{m+n} = (2^{n-m} - 1)/2^n = z$. Thus, if $p = r$ then $q - q' = -2z$ and $r - r' = q'r - qr' = z$; if $p > r$ then $q - q' = -z$, $r - r' = (1/2)z$ and $q'r - qr' = (1/4)z$; and if $p < r$ then $q - q' = -z$, $r - r' = (1/2)z$ and $q'r - qr' = (3/4)z$ when either assumption 6a or 6b applies, or $q'r - qr' = (1/4)z$ when assumption 6c applies. In the denominator $q + q' = (2^{n-m} + 1)/2^{n-1}$ and $qq' = 1/2^{n+m-2}$ if $p = r$, and $q + q' = (2^{n-m} + 1)/2^n$ and $qq' = 1/2^{n+m}$ if $p \neq r$. For two consecutive generations of the same cross $m = n - 1$ and, therefore, in the numerator $z = 1/2^n$ and in the denominator $q + q' = 3/2^n$ and $aa' = 1/2^{2n-1}$. Thus, for example, for the $m = (n - 1)$th and the nth generations of the $A \times B$ cross appropriate substitutions in (19) and simple algebraic transformations obtain:

$$u(F_n) - u(F_{n-1}) = \frac{([d] + [h])\Delta_{[d]} - 2[d]\Delta_{[h]}}{2^n[d]^2 + 6[d][h] + (1/2^n)8[h]^2} \quad (20)$$

which shows that this difference becomes smaller and smaller with each generation of selfing. Obviously $\lim_{n\to\infty} 2^n[d]$ is infinitely large and since the numerator is finite and constant $\lim_{n\to\infty} [u(F_n) - u(F_{n-1})] = 0$.

Up to this point the absence of gene-dosis effects was tacitly assumed. The expected ratio, or dosis, of paternal and maternal alleles in a cross is 1:1, whereas in a backcross this ratio is either $3 \div 1$ or $1 \div 3$. Conceptually a gene-dosis effect is the effect of the dosis of $\cup_k\{a\}_k$ gene-set on the expressivity of its allelic set $\cup_k\{b\}_k$ and *vice versa*. Bhat and Dhavan (op. cit.) have reported on such effects in plasmatypically different maize crosses.

In the absence of $\pi(A)$ effect on the expressivity of the paternal set of alleles $\cup_k\{b\}_k \subset \cup\{\pi(A), \cup_k\{a, b\}_k\}$, the comparison

$$\bar{x}(AB)\,F_n - (1/2^n)\,[(2^{n-1} - 1)\,\bar{x}(A) + 2\bar{x}(AB)\,F_1 + (2^{n-1} - 1)\,\bar{x}(B)] = \delta_1 \qquad (21)$$

can be used to detect epistasis. Thus, $\delta_1 \neq 0$ denotes the presence of epistasis, and $\delta_1 = 0$ implies either the absence of epistasis or balanced epistatic effects. Furthermore, the crosses $[(AB)\,A]$, $[A(AB)]$ and $[A(BA)]$ are the same both plasmatypically and genotypically and, therefore, are expected to have equal means. Consequently, in the absence of both the plasmatypic and the gene-dosis effects the following comparison is also supposed to detect epistasis:

$$\bar{x}(AB)\,F_n - \left(\frac{1}{6}\right)\{\bar{x}\,[(AB)\,A]\,F_{n-1} + \bar{x}\,[A(AB)]\,F_{n-1} + \bar{x}\,[A(BA)]\,F_{n-1} + 3\bar{x}\,[(AB)\,B]\,F_{n-1}\} = \delta_2 . \qquad (22)$$

If $\delta_1 = 0$ because there is no epistasis, then $\delta_2 \neq 0$ may be attributed to differential gene-dosis effects. Obviously $\delta_2 = 0$ may imply either the absence of gene-dosis effects or the equality of opposing effects of equal doses of $\cup_k\{a\}_k$ and $\cup_k\{b\}_k$ allelic sets, i.e., balanced gene-dosis effects. The following comparisons show the magnitude of the dosis effects of $\cup_k\{a\}_k$ and $\cup_k\{b\}_k$, respectively:

$$\left(\frac{1}{3}\right)\{\bar{x}\,[(AB)\,A]\,F_n + \bar{x}\,[A(AB)]\,F_n + \bar{x}\,[A(BA)]\,F_n\} - \left(\frac{1}{2}\right)[\bar{x}(A) + \bar{x}(AB)\,F_n] = \delta_{(3\alpha\div\beta)} \qquad (23)$$

and

$$\bar{x}\,[(AB)\,B]\,F_n - \left(\frac{1}{2}\right)[\bar{x}(B) + \bar{x}(BA)\,F_n = \delta_{(\alpha\div 3\beta)} \qquad (24)$$

where α and β in the subscripts of δ refer to allelic sets $\cup_k\{a\}_k$ and $\cup_k\{b\}_k$, in that order. If the effects of equal doses of $\cup_k\{a\}_k$ and $\cup_k\{b\}_k$ are of the same magnitude then $\delta_{(3\alpha\div\beta)} = (-1)\,\delta_{(\alpha\div 3\beta)}$; otherwise $\delta_{(3\alpha\div\beta)} \neq (-1)\,\delta_{(\alpha\div 3\beta)}$. Note that the comparisons (21), (22), (23) and (24) are basically Mather's (1949) scaling test formulae.

The effect of the dosis of paternal set of alleles and that of maternal plasmatype can be in opposition or reinforcement, depending upon the inheritance being quasi-matroclinous or quasi-patroclinous. Similarly, the dosis of maternal set of alleles and the maternal plasmatype may have effects either reinforcing or opposing one another, or they may act in a manner similar to that of duplicate genes with dominance of both. In the latter case they would be expected to have equal effects and the parameters $\Delta_{[h]}$ and $\Delta_{[d]}$ as components of means of the backcross families with maternal plasmatype would refer either to the plasmatypic or the gene-dosis effect but not to both.

The comparison (24), i.e., $\delta_{(3\alpha\div\beta)}$ shows the effect of three doses of $\cup_k\{a\}_k$ upon one dosis of its allelic set $\cup_k\{b\}_k$. Since $\cup_k\{b\}_k$ occurs in both the heterozygous and the homozygous states $\delta_{(3\alpha\div\beta)} = \delta_{[h]}, \delta_{[d]}$. In particular when $\delta_{(3\alpha\div\beta)} = (-1)\,\delta_{(\alpha\div 3\beta)}$, $(-1)\,\delta_{(\alpha\div 3\beta)} = (-1)\,(\delta_{[h]}, \delta_{[d]})$. Generally, in the equations estimating the backcross-means the parameters $\delta_{[h]}$ and $\delta_{[d]}$ will have their sign determined by the gene-set with higher dosis and their coefficients by the frequencies with which its allelic set is expected to be in heterozygous and homozygous states, respectively.

When the cause of the nonequivalence of reciprocal crosses is both plasmatic and nuclear, $\pi(A)$ and $\cup_k\{a\}_k$ are either complementary or supplementary in their effect upon $\cup_k\{b\}_k$. If $\pi(A)$ supplements $\cup_k\{a\}_k$, and not *vice versa*, then the effect of $\cup_k\{a\}_k$ on the expressivity of $\cup_k\{b\}_k$ is expected to manifest itself also in the $\{\pi(B), \cup_k\{a, b\}\}$ families provided that $\cup_k\{a\}_k$ is not sensitive to $\pi(B)$. In the absence of $\pi(A)$ to supplement it, the effect of $\cup_k\{a\}_k$ on $\cup_k\{b\}_k$ in the $\{\pi(B), \cup_k\{a, b\}_k\}$ families as compared to its effect in the $\{\pi(A), \cup_k\{a, b\}_k\}$ families, is expected to be less pronounced and, possibly, its manifestation delayed for one generation. In the absence of gene-dosis effects the parametric formulation of the expected means of families implied by $\{\pi(B), \cup_k\{a, b\}_k\}$ will be quasi-patroclinous.

The idiotypically $\{\pi(B), {}_k\{a, b\}_k\}$ crosses are (BA), $[(BA)\,A]$, $[B(AB)]$, $[B(BA)]$ and $[(BA)\,B]$. The first three of these crosses obtain their female and male gametes from $\pi(B)$ and $\pi(A)$ parents, respectively, whereas the last two obtain them from parents both of which have $\pi(B)$. If the paternal plasmatype does not affect the faculty of $\cup_k\{a\}_k$ to affect the expressivity of $\cup_k\{b\}_k \subset \{\pi(B), \cup_k\{a, b\}_k\}$, then $\Delta_{[h]}$ and $\Delta_{[d]}$ will be different from zero for all the crosses implied. On the contrary, if the necessary condition for $\cup_k\{b\}_k \subset \{\pi(B), \cup_k\{a, b\}_k\}$ to be affected in its expressivity by $\cup_k\{a\}_k$ is that $\cup_k\{a\}_k$ has to be contributed by a $\pi(A)$ male, then the means of families $(BA)\,F_n$, $[(BA)\,A]\,F_n$ and $[B(AB)]\,F_n$ imply $\Delta_{[h]} \neq 0$ and $\Delta_{[d]} \neq 0$ and those of $[(BA)\,B]\,F_n$ and $[B(BA)]\,F_n$ imply $\Delta_{[h]} = \Delta_{[d]} = 0$. Consequently, assuming $\cup_k\{a\}_k$ to operate in a manner similar to that of $\pi(A)$ or $\{\pi(A), \cup_k\{a\}_k\}$ in $\{\pi(A), \cup_k\{a, b\}_k\}$ as implied by

assumption 6a or 6b, and assuming $\delta_{(3\alpha \div \beta)} = -(-1)\,\delta_{(3\alpha \div \beta)} \neq 0$, the parametric constitution of the estimates of means of the families considered will be as follows:

$$E\bar{x}(BA)\,F_n = m + (1/2^{n-1})\,[h] - (1/2^{n-1})\,\Delta_{[h]} - (1/2)\,(1 - 1/2^{n-1})\,\Delta_{[d]}\,, \tag{25}$$

$$\bar{x}\,[(BA)\,A]\,F_n = m - (1/2)\,[d] + (1/2^n)\,[h] - (1/2^n)\,\Delta_{[h]} - (1/4)\,(1 - 1/2^{n-1})\,\Delta_{[d]} - (1/2^n)\,\delta_{[h]} - (1/4)\,(1 - 1/2^{n-1})\,\delta_{[d]}\,, \tag{26}$$

$$E\bar{x}\,[B(AB)]\,F_n = m + (1/2)\,[d] + (1/2^n)\,[h] - (1/2^n)\,\Delta_{[h]} - (1/4)\,(3 - 1/2^{n-1})\,\Delta_{[d]} + (1/2^n)\,\delta_{[h]} + (1/4)\,(1 - 1/2^{n-1})\,\delta_{[d]} \tag{27}$$

and

$$E\bar{x}\,[(BA)\,B]\,F_n = E\bar{x}\,[B(BA)]\,F_n = m + (1/2)\,[d] + (1/2^n)\,[h] + (1/2^n)\,\delta_{[h]} + (1/4)\,(1 - 1/2^{n-1})\,\delta_{[d]} \tag{28}$$

where, as before, it is assumed that $\bar{x}(A) < \bar{x}(B)$ and, implicitly, the allelic sets $\cup_k\{a\}_k$ and $\cup_k\{b\}_k$ when homozygous have genotypic values $-[d]$ and $[d]$, respectively. If the allelic set $\cup_k\{a\}_k$ in $\{\pi(B), \cup_k\{a, b\}_k\}$ is supposed to operate in a manner similar to that implied by assumption 6c for $\{\pi(A), \cup_k\{a, b\}_k\}$ then the only change is that $-(1/4)\,(3 - 1/2^{n-1})\,\Delta_{[d]}$ in (27) becomes $-(1/4)\,(1 - 1/2^{n-1})\,\Delta_{[d]}$.

Summary of the Procedure

1. Compare $\bar{x}(AB)\,F_1$ and $\bar{x}(AB)\,F_2$ with $\bar{x}(BA)\,F_1$ and $\bar{x}(BA)\,F_2$, respectively, and $\bar{x}(AB)\,F_3$ with $\bar{x}(BA)\,F_3$ if available. If they are significantly different from one another and all the differences have the same sign, then the reciprocal crosses are not equivalent with respect to the character considered. In some cases the difference between the reciprocals may appear beginning with the F_2 or the F_3 generation (Hiorth, 1963, p. 85).

2. Use equation (21) on both the reciprocal sets of families. When reciprocal differences manifest themselves beginning with the F_1 generation the nonsignificance of δ_1 for both sets of families denotes the absence of epistasis. When reciprocal differences manifest themselves beginning with the F_2 generation, $\delta_1 \neq 0$ either for one or for both sets of families. In the latter case the two δ_1's will have opposing signs. The significance of only one of δ_1's most likely implies that only one of the parents contains plasma sensitive genes, and the significance of both of them means that both parents contain plasma sensitive genes.

3. When reciprocal differences manifest themselves beginning with F_2 and only one of δ_1's is significantly different from zero, use equations (23) and (24) to test for the presence and the magnitude of genedoses effects in the set of families for which $\delta_1 = 0$.

4. Formulate in terms of appropriate parameters the expectations of family means for the two sets of families. Solve the two systems of linear equations thus obtained for the parameter estimates using, preferably, the method of weighted least squares. Test the assumed genetic model for adequacy (chi-square test). Discuss and interpret the experimental results obtained.

Zusammenfassung

Die in der vorliegenden Arbeit beschriebene Analyse der Mittelwerte ist auf zwei reine Linien einer autogamen Pflanzenart und ihre reziproken Kreuzungen und Rückkreuzungen anwendbar. Die Analyse beruht auf einer Reihe von Annahmen hinsichtlich der Eltern, der Gendosiseffekte und der Expressivität der Allele an den unterschiedlichen Loci, die durch die Kreuzung in einen anderen Plasmotyp überführt werden. Die beobachteten Familienmittel bilden zusammen mit den auf Grund der Annahmen formulierten Erwartungsparametern zwei unabhängige lineare Gleichungssysteme. Die Auflösung dieser Systeme mit Hilfe der Methode der kleinsten Quadrate führt zu den Parameterschätzungen und ihren Standardfehlern. Die Angemessenheit des genetischen Modells kann mit Hilfe der χ^2-Methode geprüft werden.

Literature

Aksel, R.: Quantitative-genetic analysis of characters in wheat using crosses of chromosome substitution lines. Genetics **57**, 195–211 (1967).

Bhat, B. K., Dhavan, N. L.: Threshold concentration of plasmonsensitive polygenes in the expression of quantitative characters of maize (*Zea mays* L.). Theor. Appl. Genet. **40**, 347–350 (1970).

Caspari, E.: Cytoplasmic inheritance. Advances in Genetics **II**, 1–66 (1948).

Chandraratna, M. F., Sakai, Kan-Ichi: A biometrical analysis of matroclinous inheritance of grain weight in rice. Heredity **14**, 365–373 (1960).

Durrant, A.: Analysis of reciprocal differences in diallel crosses. Heredity **20**, 573–607 (1965).

Durrant, A.: Genetic control of environmentally induced changes in Linum. Heredity **30**, 369–379 (1973).

Fleming, A. A., Kozelnicky, G. M., Brown, E. B.: Cytoplasmic effect on agronomic characters in a double-cross maize hybrid. Agron. J. **52**, 112–115 (1960).

Hagemann, R.: Plasmatische Vererbung. Jena: Gustav Fischer Verlag 1964.

Hiorth, G. E.: Quantitative Genetik. Berlin: Springer-Verlag 1963.

Jinks, J. L.: Extrachromosomal inheritance. Englewood Cliffs: Prentice-Hall 1964.

Jinks, J. L., Perkins, J. M., Gregory, S. R.: The analysis and interpretation of differences between reciprocal crosses of *Nicotiana rustica* varieties. Heredity **28**, 363–377 (1972).

Mather, K.: Biometrical Genetics. London: Methuen & Co. 1949.

Mather, K., Jinks, J. L.: Biometrical Genetics. Ithaca, New York: Cornell University Press 1971.

Michaelis, P.: Cytoplasmic inheritance in *Epilobium* and its theoretical significance. Advances in Genetics **VI**, 287—401 (1954).

Nečas, J.: Inheritance of kernel size in barley (Czechoslovakian, with summaries in Russian and German). Sbornik CSAZV, Rostl. vyroba **7**, 1607—1634 (1961).

Nečas, J.: Inheritance of spike length in barley (Czechoslovakian, with summaries in Russian and English). Biologia **17**, 401—414 (1962).

Nečas, J.: Inheritance of spike length in barley (Czechoslovakian, with summaries in Russian and English). Biologia **18**, 195—209 (1963).

Nečas, J.: Unequality of reciprocal crosses of barley (English, with German summary). Z. Pflanzenzücht. **55**, 260—275 (1966).

Richey, F. D.: The inequality in reciprocal corn crosses. J. Amer. Soc. Agron. **12**, 185—196 (1920).

Sakai, K. S. Iyama, Narise, T.: Biometrical approach to cytoplasmic inheritance in autogamous plants. Bull. International Stat. Instit. **38**, 249—257 (1961).

Sirks, M. J.: Plasmatic influences upon the inheritance of *Vicia faba*, cited after S. Wright, Evolution and Genetics of Populations, Vol. I. Chicago: The Univ. of Chicago Press 1968.

Smith, W. E., Fitzsimmons, J. E.: Maternal Inheritance of seed weight in flax (*Linum usitatissimum* L.) Can. J. Genet. Cytol. **VI**, 244 (1964).

Smith, W. E., Fitzsimmons, J. E.: Maternal inheritance of seed weight in flax (*Linum usitatissimum* L.). Can. J. Genet. Cytol. **VII**, 658—662 (1965).

St. John, R. R.: A comparison of reciprocal top crosses in corn. J. Amer. Soc. Agron. **26**, 721—724 (1934).

Tyson, H.: Cytoplasmic effects on plant weight in crosses between flax genotypes and genotrophs. Heredity **30**, 327—340 (1973).

Received March 11, 1974

Communicated by H. Stubbe/W. Seyffert

Dr. Rustem Aksel
Professor of Genetics
Department of Genetics
University of Alberta
Edmonton (Canada T6G 2E9)