ESTIMATION OF DOUBLE REDUCTION AND GENETIC PARAMETERS OF AUTOTETRAPLOIDS

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SUMMARY

A method is proposed for estimating double reduction and genetic parameters in an additive-dominance model for autotetraploids. It uses a mating scheme involving a diploid hybrid and its tetraploid in a series of seven crosses. The diploid produces $2n$ unreduced gametes by first and/or second division restitution during meiosis.

1. INTRODUCTION

Two major factors complicate the study of polygenic variation of autotetraploids. There are four alleles at a locus. This gives a complex pattern of genic interactions as compared to that of diploids. The situation can, however, be somewhat simplified by considering only two alleles per locus. A more troublesome problem is the phenomenon of double reduction, which was elucidated by Mather (1936). Most theoretical work, for example, Kempthorne (1955), Li (1957), Dessureaux (1959), Levings and Dudley (1963), Hill (1971) and Gallais (1974), consider a random mating population having chromosomal segregation. Killick (1971) and Tan (1976) investigated generations derived from a cross between two pure lines with allowance for double reduction. The complexity produced by the double reduction can be verified by the expressions for generation means in Killick's paper.

The discovery by Peloquin and his colleagues (Mendiburu, Peloquin and Mok, 1974) that certain interspecific diploids in potato produce $2n$ unreduced gametes provides a new tool for genetic studies of autotetraploids. The $2n$ gametes are produced by either first (FDR) or second (SDR) division restitution during meiosis (Mendiburu and Peloquin, 1979). As exemplified by many experiments (*e.g.*, Hanneman and Peloquin, 1969; Mendiburu and Peloquin, 1971; De Jong and Tai, 1977; McHale and Laurer, 1981), there seems no difficulty in obtaining tetraploid progenies from diploid-diploid ($2x \times 2x$) and diploid-tetraploid ($2x \times 4x$) matings.

In the present paper a procedure is proposed for estimating the double reduction coefficient and genetic parameters in an "additive-dominance" model for autotetraploids. It is based on a mating system involving a series of crosses between diploids and tetraploids.

2. BASIC CONSIDERATIONS

The additive-dominance model considers two alleles per locus with the five possible tetraploid genotypes taking the following values:

AAAA	or	A_4	$m + d$
AAAa	or	A_3a	$m + h_3$
AAaa	or	A_2a_2	$m + h_2$
Aaaa	or	Aa_3	$m + h_1$
aaaa	or	a_4	$m - d$

This is the model developed by Mather and Jinks (1971) and Killick (1971).

A feature of the proposed procedure is the use of a diploid genotype Aa and its tetraploid A_2a_2 in a series of seven crosses. The diploid produces unreduced $2n$ gametes by either FDR or SDR during meiosis. We shall, however, concentrate on the FDR diploid since the principle of using the SDR diploid is exactly the same. It is necessary to know the gametic output of the above five tetraploids and the FDR diploid, and the frequencies of progeny genotypes when they are crossed with two parents Aa (FDR) and A_2a_2 , before we proceed with the mating scheme. Table 1 gives the gametic output of the tetraploids (Fisher and Mather, 1943) and FDR diploid (Mendiburu and Peloquin, 1979). Different sizes are allowed for the frequencies of double reduction (α) in the tetraploid and single exchange tetrads (β) in the diploid genotypes.

TABLE 1
Gametic output of five autotetraploids and a FDR diploid

Parental genotype	Gametes			Divisor
	AA	Aa	aa	
A_4	1	—	—	1
A_3a	$2 + \alpha$	$2 - 2\alpha$	α	4
A_2a_2	$1 + 2\alpha$	$4 - 4\alpha$	$1 + 2\alpha$	6
Aa_3	α	$2 - 2\alpha$	$2 + \alpha$	4
a_4	—	—	1	1
Aa (FDR)	β	$4 - 2\beta$	β	4

There are again five possible genotypes in the progenies when any one of the five tetraploids (A_4 , A_3a , A_2a_2 , Aa_3 and a_4) or FDR diploid (Aa) is crossed with Aa or A_2a_2 . The frequencies of five genotypes in the progenies of $Aa \times A_3a$ and $A_2a_2 \times A_3a$, for example, are given in table 2. The expressions of the frequencies, as shown in the second and third columns in table 2, appear to be complicated. The difference between pairs of frequencies for each of the progeny genotypes from the two crosses, which are given in the fourth column in table 2, assume rather simpler forms. This is generally true for the other four tetraploids and the FDR diploid crossed with Aa and A_2a_2 . The results for all the differences are shown in table 3.

The differences between mean genotypic values of the crosses $Aa \times A_3a$ and $A_2a_2 \times A_3a$ can be easily obtained by using the results in table 2, i.e.,

$$\begin{aligned}
 & \overline{(Aa \times A_3a)} - \overline{(A_2a_2 \times A_3a)} \\
 &= \gamma \left[-\left(\frac{2+\alpha}{4}\right)d + \left(\frac{2+4\alpha}{4}\right)h_3 + \left(\frac{2-6\alpha}{4}\right)h_2 - \left(\frac{2-4\alpha}{4}\right)h_1 - \left(\frac{\alpha}{4}\right)(-d) \right] \\
 &= \frac{\gamma}{2} [-d + (1+2\alpha)h_3 + (1-3\alpha)h_2 - (1-2\alpha)h_1]
 \end{aligned}$$

in which $\gamma = (2+4\alpha-3\beta)/12$.

TABLE 2

Frequencies of five autotetraploid genotypes in the progenies of $Aa \times A_3a$ and $A_2a_2 \times A_3a$ crosses and differences in frequencies between the two crosses

Progeny genotype	Crosses		Difference
	$Aa \times A_3a$	$A_2a_2 \times A_3a$	
A_4	$\left(\frac{\beta}{4}\right)\left(\frac{2+\alpha}{4}\right)$	$\left(\frac{1+2\alpha}{6}\right)\left(\frac{2+\alpha}{4}\right)$	$-\gamma^*\left(\frac{2+\alpha}{4}\right)$
A_3a	$\left(\frac{\beta}{4}\right)\left(\frac{2-2\alpha}{4}\right) + \left(\frac{4-2\beta}{4}\right)\left(\frac{2+\alpha}{4}\right)$	$\left(\frac{1+2\alpha}{6}\right)\left(\frac{2-2\alpha}{4}\right) + \left(\frac{4-4\alpha}{6}\right)\left(\frac{2+\alpha}{4}\right)$	$\gamma\left(\frac{2+4\alpha}{4}\right)$
A_2a_2	$\left(\frac{\beta}{4}\right)\left(\frac{\alpha}{4}\right) + \left(\frac{\beta}{4}\right)\left(\frac{2+\alpha}{4}\right) + \left(\frac{4-2\beta}{4}\right)\left(\frac{2-2\alpha}{4}\right)$	$\left(\frac{1+2\alpha}{6}\right)\left(\frac{\alpha}{4}\right) + \left(\frac{1+2\alpha}{6}\right)\left(\frac{2+\alpha}{4}\right) + \left(\frac{4-4\alpha}{6}\right)\left(\frac{2-2\alpha}{4}\right)$	$\gamma\left(\frac{2-6\alpha}{4}\right)$
Aa_3	$\left(\frac{4-2\beta}{4}\right)\left(\frac{\alpha}{4}\right) + \left(\frac{\beta}{4}\right)\left(\frac{2-2\alpha}{4}\right)$	$\left(\frac{4-4\alpha}{6}\right)\left(\frac{\alpha}{4}\right) + \left(\frac{1+2\alpha}{6}\right)\left(\frac{2-2\alpha}{4}\right)$	$-\gamma\left(\frac{2-4\alpha}{4}\right)$
a_4	$\left(\frac{\beta}{4}\right)\left(\frac{\alpha}{4}\right)$	$\left(\frac{1+2\alpha}{6}\right)\left(\frac{\alpha}{4}\right)$	$-\gamma\left(\frac{\alpha}{4}\right)$

* $\gamma = (2 + 4\alpha - 3\beta)/12$.

TABLE 3

Differences in genotypic frequencies between two crosses

Comparison	Progeny genotypes					Multiplier
	A_4	A_3a	A_2a_2	Aa_3	a_4	
$(Aa \times A_4) - (A_2a_2 \times A_4)$	-1	2	-1	—	—	γ
$(Aa \times A_3a) - (A_2a_2 \times A_3a)$	$-(2+\alpha)$	$2+4\alpha$	$2-6\alpha$	$-(2-4\alpha)$	$-\alpha$	$\gamma/4$
$(Aa \times A_2a_2) - (A_2a_2 \times A_2a_2)$	$-(1+2\alpha)$	$-(2-8\alpha)$	$6-12\alpha$	$-(2-8\alpha)$	$-(1+2\alpha)$	$\gamma/6$
$(Aa \times Aa_3) - (A_2a_2 \times Aa_3)$	$-\alpha$	$-(2-4\alpha)$	$2-6\alpha$	$2+4\alpha$	$-(2+\alpha)$	$\gamma/4$
$(Aa \times a_4) - (A_2a_2 \times a_4)$	—	—	-1	2	-1	γ
$(Aa \times Aa) - (A_2a_2 \times Aa)$	$-\beta$	$-(4-4\beta)$	$8-6\beta$	$-(4-4\beta)$	$-\beta$	$\gamma/4$

TABLE 4

Differences between genotypic means of two crosses

Comparison	Difference	Symbol
$(Aa \times A_4) - (A_2a_2 \times A_4)$	$\gamma[-d + 2h_3 - h_2]$	d'_1
$(Aa \times A_3a) - (A_2a_2 \times A_3a)$	$\frac{\gamma}{2}[-d + (1 + 2\alpha)h_3 + (1 - 3\alpha)h_2 - (1 - 2\alpha)h_1]$	h'_3
$(Aa \times A_2a_2) - (A_2a_2 \times A_2a_2)$	$\frac{\gamma}{3}[-(1 - 4\alpha)(h_3 + h_1) + (3 - 6\alpha)h_2]$	h'_2
$(Aa \times Aa_3) - (A_2a_2 \times Aa_3)$	$\frac{\gamma}{2}[d - (1 - 2\alpha)h_3 + (1 - 3\alpha)h_2 + (1 + 2\alpha)h_1]$	h'_1
$(Aa \times a_4) - (A_2a_2 \times a_4)$	$\gamma[d - h_2 + 2h_1]$	d'_2
$(Aa \times Aa) - (A_2a_2 \times Aa)$	$\frac{\gamma}{2}[-(2 - 2\beta)(h_3 + h_1) + (4 - 3\beta)h_2]$	—

Table 4 gives the differences between pairs of mean genotypic values of progenies obtained from crossing Aa and A_2a_2 with each of the five tetraploids and the FDR diploid. The expressions of all six differences, again, are relatively simple.

3. METHOD OF ESTIMATION

We may now propose a mating scheme using Aa and A_2a_2 as parents for estimating the frequencies of double reduction (α) and single exchange tetrads (β) and genetic parameters (m , h_3 , h_2 and h_1). We assume that Aa produces FDR $2n$ gametes and there is no difficulty in extracting tetraploid progenies from such crosses as $Aa \times Aa$, $Aa \times A_2a_2$, etc. Let $P_1 = Aa$ and $P_2 = A_2a_2$. A series of seven crosses are made as follows:

Type of crosses	Mating scheme	Symbols
$2x \times 2x$	$Aa \times Aa$	F_{11}
$2x \times 4x$	$Aa \times A_2a_2$	F_{12}
$4x \times 4x$	$A_2a_2 \times A_2a_2$	F_{22}
$2x \times 4x$	$Aa \times (Aa \times A_2a_2)$	$B_{1(12)}$
$4x \times 4x$	$A_2a_2 \times (Aa \times A_2a_2)$	$B_{2(12)}$
$2x \times 4x$	$Aa \times (A_2a_2 \times A_2a_2)$	$B_{1(22)}$
$4x \times 4x$	$A_2a_2 \times (A_2a_2 \times A_2a_2)$	$B_{2(22)}$

The mean values of the seven crosses, together with that of P_2 , are combined to simplify the procedure of estimation. Using results in table 4,

$$\bar{F}_{12} - \bar{F}_{22} = \frac{\gamma}{3}[-(1 - 4\alpha)(h_3 + h_1) + (3 - 6\alpha)h_2] \quad (1)$$

$$\bar{F}_{11} + \bar{F}_{22} - 2\bar{F}_{12} = 2\gamma^2[-2(h_3 + h_1) + 3h_2]. \quad (2)$$

Also,

$$\begin{aligned}
 & (\bar{B}_{1(12)} - \bar{B}_{2(12)}) - (\bar{B}_{1(22)} - \bar{B}_{2(22)}) \\
 &= \frac{\gamma}{3}[-(1 + 2\alpha)(d'_1 + d'_2) - (1 - 4\alpha)(h'_3 + h'_1) + (3 - 6\alpha)h'_2] \\
 &= \frac{\gamma^2}{3}[-(2 - 2\alpha)(h_3 + h_1) + (3 - 3\alpha)h_2] \quad (3)
 \end{aligned}$$

where the compositions of d'_1 , d'_2 , h'_3 , h'_2 and h'_1 are as given in table 4. The derivation of (3) is more complex. Using information from tables 1 and 4, a step-by-step illustration of the contribution of the genotype A_3a to (3) is given as follows:

- (i) The $(Aa \times A_2a_2)$ cross produces the progeny A_3a with the frequency

$$\left[\left(\frac{\beta}{4} \right) \left(\frac{4-4\alpha}{6} \right) + \left(\frac{2-\beta}{2} \right) \left(\frac{1+2\alpha}{6} \right) \right].$$

- (ii) The $(A_2a_2 \times A_2a_2)$ cross produces the progeny A_3a with the frequency

$$\left[2 \left(\frac{4-4\alpha}{6} \right) \left(\frac{1+2\alpha}{6} \right) \right].$$

- (iii) The progeny A_3a is crossed with P_1 (Aa) and P_2 (A_2a_2). The difference between mean values of the crosses $(Aa \times A_3a)$ and $(A_2a_2 \times A_3a)$ is h'_3 .

- (iv) The contribution of A_3a to the difference $(\bar{B}_{1(12)} - \bar{B}_{2(12)})$ is then

$$\left[\left(\frac{\beta}{4} \right) \left(\frac{4-4\alpha}{6} \right) + \left(\frac{2-\beta}{2} \right) \left(\frac{1+2\alpha}{6} \right) \right] h'_3$$

whereas that to the difference $(B_{1(22)} - B_{2(22)})$ is

$$\left[2 \left(\frac{4-4\alpha}{6} \right) \left(\frac{1+2\alpha}{6} \right) \right] h'_3.$$

- (v) Therefore, the contribution of A_3a to the difference in (3) is

$$\left[\left(\frac{\beta}{4} \right) \left(\frac{4-4\alpha}{6} \right) + \left(\frac{2-\beta}{2} \right) \left(\frac{1+2\alpha}{6} \right) - 2 \left(\frac{4-4\alpha}{6} \right) \left(\frac{1+2\alpha}{6} \right) \right] h'_3 = -\frac{\gamma}{3} (1-4\alpha) h'_3.$$

The contributions of progeny genotypes A_4 , A_2a_2 , Aa_3 and a_4 are similarly worked out as $-(\gamma/6)(1+2\alpha)d'_1$, $\gamma(1-2\alpha)h'_2$, $-(\gamma/3)(1-4\alpha)h'_1$, and $-(\gamma/6)(1+2\alpha)d'_2$, respectively. Adding them together we obtain (3).

Let

$$w_1 = \bar{F}_{12} - \bar{F}_{22}$$

$$w_2 = \bar{F}_{11} + \bar{F}_{22} - 2\bar{F}_{12}$$

$$w_3 = \bar{B}_{1(12)} - \bar{B}_{2(12)} - \bar{B}_{1(22)} + \bar{B}_{2(22)}.$$

Substituting these expressions in (1), (2) and (3),

$$-(1-4\alpha)(h_3 + h_1) + (3-6\alpha)h_2 = \frac{3w_1}{\gamma} \quad (4)$$

$$-2(h_3 + h_1) + 3h_2 = \frac{w_2}{2\gamma^2} \quad (5)$$

$$-(2-2\alpha)(h_3 + h_1) + (3-3\alpha)h_2 = \frac{3w_3}{\gamma^2} \quad (6)$$

α can be solved from (5) and (6), i.e.,

$$\alpha = 1 - \frac{6w_3}{w_2}.$$

Also, h_2 and $(h_3 + h_1)$ can be expressed in terms of γ :

$$h_2 = \frac{2w_1}{\gamma} + (4\alpha - 1) \frac{w_2}{6\gamma^2}$$

$$(h_3 + h_1) = \frac{3w_1}{\gamma} + (2\alpha - 1) \frac{w_2}{2\gamma^2}.$$

Solutions of $(h_3 + h_1)$, h_2 , α and m are obtained by using the difference between $\bar{F}_{22}$ and $\bar{P}_2$, i.e.,

$$\bar{F}_{22} - \bar{P}_2 = \frac{1}{36} \{ 2(1 + 2\alpha)(4 - 4\alpha)(h_3 + h_1) + [2(1 + 2\alpha)^2 + (4 - 4\alpha)^2]h_2 \} - h_2. \quad (7)$$

Let $w_4 = \bar{F}_{22} - \bar{P}_2$ and express (7) in terms of γ ,

$$\gamma^2 + \left(\frac{w_1 w_2 - 4w_1 w_3}{w_2 w_4} \right) \gamma + \frac{(w_2 - 4w_3)^2}{4w_2 w_4} = 0.$$

We can then solve this equation for γ . This leads to estimates of h_2 , $(h_3 + h_1)$, β and m . The component d cannot be estimated and h_3 and h_1 cannot be separated.

The estimation procedure involving SDR diploid (Aa) is exactly the same as the one described above. The only difference is the structure of γ which is $(2\alpha + 3\beta - 2)/6$. This is derived from the gametic output of the SDR diploid Aa , i.e., $AA : Aa : aa = (1 - \beta)/2 : \beta : (1 - \beta)/2$ (Mendiburu and Peloquin, 1979).

4. DISCUSSION

The estimation procedure depends on the simplicity of the differences between specific crosses (table 4). It is interesting to note the development bears a close resemblance to the method used by Kearsey and Jinks (1968) for the triple test cross.

In potatoes, the diploid hybrids are often obtained by crossing a haploid ($2n = 24$) extracted from the cultivated species *Solanum tuberosum* ($2n = 48$) with a diploid species such as *S. phureja* ($2n = 24$) (Hanneman and Peloquin, 1969). All the various parameters that can be estimated by the present method apply to the specific series of crosses derived from a diploid hybrid, rather than to either of the original species. The analytical method is in fact a useful tool for analysing variation within an autotetraploid species so long as the extracted haploids from the tetraploids will themselves produce $2n$ unreduced gametes.

Because of the symmetrical distributions of the gametic frequencies in all seven crosses in the proposed mating scheme, d is inestimable. Also, h_3 and h_1 can only be jointly estimated. A possibility for estimating d , h_3 and h_1 separately is to extract a homozygous haploid from a tetraploid pure line (e.g., A_4). The haploid (AA) is then crossed with another extracted haploid genotype or diploid species to produce the diploid parent (P_1) used

in the mating scheme. In this case, data from the tetraploid pure line itself can be used for obtaining an estimate of d . It can also be used to cross with P_1 (i.e., $Aa \times A_4$) and P_2 (i.e., $A_2a_2 \times A_4$). Hybrids produced by the two extra crosses will give an estimate of d'_1 (see table 4) which in turn provides information for separate estimates of h_3 and h_1 .

The method works when the $2n$ gametes are produced by either the FDR or SDR mechanisms. It is in fact also valid when the pool of $2n$ gametes are contributed by both FDR and SDR. The gametic output of the diploid hybrid in this generalized situation is

$$AA : Aa : aa = \frac{2 - 2(\beta + \delta) + 3\beta\delta}{4} : \frac{2(\beta + \delta) - 3\beta\delta}{2} : \frac{2 - 2(\beta + \delta) + 3\beta\delta}{4}$$

where $0 \leq \delta \leq 1$ (Mendiburu and Peloquin, 1979). The variable in (1)–(7) is then expressed as

$$\gamma = \frac{4 + 6(\beta + \delta) - 9\beta\delta - 4}{12}.$$

The gametic ratios and γ of FDR and SDR are derived by putting $\delta = 1$ and $\delta = 0$ in the above formulae respectively. It is clear that the parameter β cannot be estimated when the mechanism of $2n$ gamete production is neither FDR nor SDR but a mixture of both. The other three parameters (α , h_2 and $h_3 + h_1$) can be estimated without difficulty. The parameter β , however, is less important than others in the study of tetrasomic inheritance.

The estimates of h_2 and $(h_3 + h_1)$ in a polygenic system represent a summation over all heterozygous loci affecting the character under study. For the estimate of the summed effect of h_2 (or $h_3 + h_1$) to be unbiased, it must be assumed that the size of an individual h_2 is not associated with those of α over all loci. In other words, the magnitude of a genic effect has nothing to do with the gene's location on the chromosome. In general, such an assumption appears genetically reasonable. The estimates of α and β then represent the average values over all loci.

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