ESTIMATION OF DOUBLE REDUCTION AND GENETIC PARAMETERS IN AUTOTETRAPLOIDS BASED ON $4X-2X$ AND $4X-4X$ MATINGS

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SUMMARY

A mating scheme is proposed for estimating double reduction coefficient and genetic parameters in an additive-dominance model for autotetraploids. The scheme uses three parents in two $4X-2X$ and four $4X-4X$ matings. The parents are a homozygous tetraploid ($AAAA$), a diploid hybrid (Aa) and its tetraploid ($AAaa$). The usefulness of the scheme is compared with the one proposed by Tai (1982).

1. INTRODUCTION

A METHOD was proposed by Tai (1982) for estimating double reduction and genetic parameters in an additive-dominance model for autotetraploids. It used a diploid hybrid Aa and its tetraploid in a series of seven crosses. The diploid hybrid produces $2n$ unreduced gametes by either first or second division restitution during meiosis. There are three types of crosses involved in the mating design, *i.e.*, diploid $\times$ diploid ($2X-2X$), diploid $\times$ tetraploid ($2X-4X$) and tetraploid $\times$ tetraploid ($4X-4X$). The use of $2X-2X$ cross in the mating system requires that the gametic output in $2n$ pollen is the same as that in $2n$ eggs. Experimental work in potato (Mendiburu and Peloquin 1971) indicates that there is no difficulty in obtaining $4X$ progenies from $2X-2X$ matings. Most cytogenetic and genetic studies on $2n$ gametes (*e.g.*, Bingham, 1968; Mok and Peloquin, 1975*a, b*; Ramanna, 1979) tend to concentrate on $2n$ pollen and its usefulness in plant breeding. No evidence is available to indicate whether the mechanisms of $2n$ pollen and egg production are identical in a diploid individual. Bias would be introduced into Tai's estimates of various parameters if the mechanism of $2n$ gamete production is somewhat different between male and female gametophytes.

The purpose of the present paper is to propose an alternative mating scheme for estimating the double reduction coefficient and genetic parameters of autotetraploids. It uses a homozygous tetraploid, a diploid hybrid and its tetraploid in a mating scheme involving six crosses. Only two types of crosses, *i.e.*, $4X-2X$ and $4X-4X$, are used in the system. The diploid parent can be solely used as male or female parent in the crosses. The problem of having identical gametic output in $2n$ pollen and egg is thus avoided.

2. MATING SCHEME

The mating scheme involves three parents: a diploid hybrid (Aa), its tetraploid ($AAaa$ or A_2a_2) and a homozygous tetraploid ($AAAA$ or A_4).

The diploid hybrid is obtained by crossing the haploid (AA) extracted from A_4 with a haploid derived from another tetraploid or diploid genotype from another species. The three parents are referred to as P_1 , P_2 and P_3 . Six crosses are made between them:

Type of crosses	Mating scheme	Symbol
$4X \times 2X$	$A_2a_2 \times Aa$	F_{12}
$4X \times 4X$	$A_2a_2 \times A_2a_2$	F_{22}
$4X \times 2X$	$A_4 \times Aa$	F_{13}
$4X \times 4X$	$A_4 \times A_2a_2$	F_{23}
$4X \times 4X$	$A_4 \times (A_4 \times Aa)$	$B_{3(13)}$
$4X \times 4X$	$A_4 \times (A_4 \times A_2a_2)$	$B_{3(23)}$

It is noted that the diploid parent (Aa) can be restricted as male(or female) parent in the two $4X-2X$ crosses if required. It produces $2n$ pollen by first (FDR) and/or second (SDR) division restitution during meiosis. The method of estimation using the FDR diploid parent will be described in the following section.

3. METHOD OF ESTIMATION

The additive-dominance model (Mather and Jinks, 1971) defines the five possible tetraploid genotypes as having different mean phenotypic deviations from m , the mid-homozygote value, as follows: A_4, d ; A_3a, h_3 ; A_2a_2, h_2 ; Aa_3, h_1 ; and $a_4, -d$. The expected mean of a cross can then be expressed as

$$\text{Mean} = m + c_1d + c_2h_3 + c_3h_2 + c_4h_1$$

where the c 's are coefficients associated with the genetic parameters d, h_3, h_2 and h_1 in a cross. To determine the sizes of the c 's we need to know the gametic output of the five tetraploid and FDR diploid (Aa) genotypes. Let α be the frequency of double reduction in the tetraploid (Fisher and Mather, 1943) and β that of single exchange tetrads in the diploid (Mendiburu and Peloquin, 1979; Tai, 1982). Also denote $u_1 = (2 + \alpha)/4$, $u_2 = (1 - \alpha)/2$, $u_3 = \alpha/4$, $u_4 = (1 + 2\alpha)/6$, $u_5 = (2 - 2\alpha)/3$, $v_1 = \beta/4$ and $v_2 = (2 - \beta)/2$. The gametic frequencies of five tetraploids and the FDR diploid can be expressed in terms of the u 's and v 's as shown in table 1. Using the information in table 1, the c coefficients in the expected means of P_2, P_3 and six crosses in the mating scheme are given in table 2.

TABLE 1
Gametic output of five autotetraploids and a FDR diploid

Parental genotype	Gametes		
	AA	Aa	aa
A_4	1	—	—
A_3a	u_1	u_2	u_3
A_2a_2	u_4	u_5	u_4
Aa_3	u_3	u_2	u_1
a_4	—	—	1
Aa (FDR)	v_1	v_2	v_1

TABLE 2

Coefficients associated with genetic parameters in the expressions of expected means of P_2 and P_3 and six crosses in the mating scheme

Means	Genetic parameters				
	m	d	h_3	h_2	h_1
$\bar{P}_2$	1	0	0	1	0
$\bar{P}_3$	1	1	0	0	0
$\bar{F}_{12}$	1	0	$u_4v_2 + u_5v_1$	$2u_4v_1 + u_5v_2$	$u_5v_1 + u_4v_2$
$\bar{F}_{22}$	1	0	$2u_4u_5$	$2u_4^2 + u_5^2$	$2u_4u_5$
$\bar{F}_{13}$	1	v_1	v_2	v_1	0
$\bar{F}_{23}$	1	u_4	u_5	u_4	0
$\bar{B}_{3(13)}$	1	$v_1 + u_1v_2 + u_4v_1$	$u_2v_2 + u_5v_1$	$u_3v_2 + u_4v_1$	0
$\bar{B}_{3(23)}$	1	$u_4 + u_1u_5 + u_4^2$	$u_2u_5 + u_4u_5$	$u_3u_5 + u_4^2$	0

The expected means of P_2 , P_3 , F_{12} , F_{13} , F_{22} and F_{23} can be easily obtained using table 1. Those of $B_{3(13)}$ and $B_{3(23)}$ cannot be readily derived. The detailed derivation of $\bar{B}_{3(13)}$ is given as follows:

- The cross $A_4 \times Aa$ produces the progenies A_4 , A_3a , A_2a_2 , Aa_3 and a_4 with frequencies v_1 , v_2 , v_1 , 0 and 0, respectively.
- The relative frequencies of AA , Aa and aa gametes produced by genotypes A_4 , A_3a and A_2a_2 are, respectively, 1:0:0; $u_1:u_2:u_3$; and $u_4:u_5:u_4$ (table 1).
- Backcrossing the progenies A_4 , A_3a and A_2a_2 to $P_3(A_4)$ produces the progenies A_4 , A_3a and A_2a_2 with relative frequencies: $v_1:0:0$; $u_1v_2:u_2v_2:u_3v_2$; and $u_4v_1:u_5v_1:u_4v_1$, respectively.
- The frequencies of A_4 , A_3a and A_2a_2 progenies in the cross $A_4 \times (A_4 \times Aa)$, i.e., $B_{3(13)}$, are consequently $v_1 + u_1v_2 + u_4v_1$, $u_2v_2 + u_5v_1$ and $u_3v_2 + u_4v_1$, respectively.
- The expected mean of $B_{3(13)}$ is then

$$\bar{B}_{3(13)} = m + (v_1 + u_1v_2 + u_4v_1)d + (u_2v_2 + u_5v_1)h_3 + (u_3v_2 + u_4v_1)h_2.$$

The following results can be obtained from table 2:

$$y_1 = \bar{F}_{13} - \bar{F}_{23} = \gamma(-d + 2h_3 - h_2)$$

$$y_2 = 6(\bar{B}_{3(13)} - \bar{B}_{3(23)}) = \gamma(1 - \alpha)(-d + 2h_3 - h_2)$$

$$y_3 = 3(\bar{F}_{23} - (\bar{P}_2 + \bar{P}_3)/2) = (1 - \alpha)(-d + 2h_3 - h_2)$$

where $\gamma = (2 + 4\alpha - 3\beta)/12 = u_4 - v_1 = (v_2 - u_5)/2$. Thus,

$$\hat{\alpha} = 1 - (y_2/y_1)$$

and $\hat{\gamma} = y_2/y_3$.

Also, $\hat{\beta} = (2 + 4\hat{\alpha} - 12\hat{\gamma})/3$. The $\hat{\alpha}$ and $\hat{\beta}$ values are then used to estimate the u 's and v 's in table 1 and the coefficients involving the u 's and v 's in table 2.

The genetic parameters m , d , h_3 , h_2 and h_1 are estimated by a weighted least squares procedure (Mather and Jinks, 1971). The weights are the reciprocal of the squared standard errors for $\bar{P}_2$, $\bar{P}_3$ and six cross means. Let V be the diagonal matrix of squared errors for the means, O the vector

of observed means, and $\hat{M}$ the vector of estimates of genetic parameters,

$$V = \text{diag} [V_{\bar{P}_2} \ V_{\bar{P}_3} \ V_{\bar{F}_{12}} \ V_{\bar{F}_{22}} \ V_{\bar{F}_{13}} \ V_{\bar{F}_{23}} \ V_{\bar{B}_{3(13)}} \ V_{\bar{B}_{3(23)}}]$$

$$O = \begin{bmatrix} \bar{P}_2 \\ \bar{P}_3 \\ \bar{F}_{12} \\ \bar{F}_{22} \\ \bar{F}_{13} \\ \bar{F}_{23} \\ \bar{B}_{3(13)} \\ \bar{B}_{3(23)} \end{bmatrix} \quad \hat{M} = \begin{bmatrix} \hat{m} \\ \hat{d} \\ \hat{h}_3 \\ \hat{h}_2 \\ \hat{h}_1 \end{bmatrix}$$

Also let C be the matrix of c coefficients as given in table 2. We have

$$M = (C'V^{-1}C)^{-1}C'V^{-1}O$$

where C' is the transpose of C .

The estimates of genetic parameters can then be used in a joint scaling test for goodness of fit of the additive-dominance model (Mather and Jinks, 1971). The χ^2 statistic has one degree of freedom since seven parameters (*i.e.*, m , α , β , d , h_3 , h_2 and h_1) are fitted out of eight observed means.

4. DISCUSSION

The mating scheme of Tai (1982) uses a diploid hybrid (Aa) and its tetraploid (A_2a_2) as parents. It does not need a homozygous tetraploid parent as required in the present system. It thus has advantages for investigating an asexually propagated species such as the potato since the available tetraploid clones are usually heterozygous. The present system, while requiring additional time and effort to self heterozygous tetraploids for parental material, is more reliable for use when no assurance can be given that the mechanisms of $2n$ sporogenesis in male and female gametophytes are the same in a diploid parent.

A faster way to obtain homozygous materials would be at the diploid rather than at the tetraploid level. Thus, an haploid population can be created at first from heterozygous tetraploid clones. Continuous selfing followed by chromosome doubling would give materials to start a mating scheme.

The mating scheme proposed here uses the minimum number of crosses required for estimating the various parameters. Precision of estimation can be increased when more generations are involved in the mating design. For example, the backcross generations $B_{1(12)}$, $B_{2(12)}$, $B_{1(22)}$ and $B_{2(22)}$ which are used in the mating scheme of Tai (1982) can be added to the present system.

The method of estimation is illustrated by using a FDR diploid parent. As indicated by Tai (1982), the same principle applies when a diploid parent produces $2n$ gametes by SDR or a mixture of FDR and SDR.

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5. REFERENCES

- BINGHAM, E. T. 1968. Transfer of diploid *medicago* spp. germplasm to tetraploid *M. sativa* L. in 4X-2X crosses. *Crop. Sci.*, 8, 760-762.
- FISHER, R. A., AND MATHER, K. 1943. The inheritance of style length in *Lythrum salicaria*. *Ann. Eugenics*, 12, 1-23.
- MATHER, K., AND JINKS, J. L. 1971. *Biometrical Genetics*. Second edition. Chapman Hall, London.
- MENDIBURU, A. O., AND PELOQUIN, S. J. 1971. High yielding tetraploids from 4X-2X and 2X-2X matings. *Am. Potato J.*, 48, 300-301.
- MENDIBURU, A. O., AND PELOQUIN, S. J. 1979. Gene-centrometre mapping by 4X-2X matings in potatoes. *Theor. Appl. Genet.*, 54, 177-180.
- MOK, D. W. S., AND PELOQUIN, S. J. 1975a. The mechanisms of $2n$ pollen formation in diploid potatoes. *Can. J. Genet. Cytol.*, 17, 217-212.
- MOK, D. W. S., AND PELOQUIN, S. J. 1975b. The inheritance of three mechanisms of diplan-droids ($2n$ pollen) formation in diploid potatoes. *Heredity*, 35, 295-302.
- RAMANNA, M. S. 1979. A re-examination of the mechanisms of $2n$ gamete formation in potato and its implications for breeding. *Euphytica*, 28, 537-561.
- TAI, G. C. C. 1982. Estimation of double reduction and genetic parameters in autotetraploids. *Heredity*, 49, 63-70.