NOTES AND COMMENTS

SEGREGATION IN TETRAPLOID POTATOES

D. G. CATCHESIDE

Department of Microbiology, University of Birmingham

Estimates of the amount of double reduction in tomatoes (Mather, 1935, 1936) and in potatoes (Cadman, 1942) have given values that are larger when the segregating plant was duplex for the locus considered, than when it was simplex. This has been reported for one locus in the tomato (*r*) and for three in the potato (*nx*, *p* and *d*). However, in the potato examples the differences, though suggestively large in one case, are not at all significant statistically. The values are given in table 1,

TABLE 1

Indices of double reduction (α) calculated from simplex and duplex tomato (Mather, 1936) and potato (Cadman, 1942) data

Gene locus	Simplex index	Duplex index	Difference	P
Tomato *r* . .	0·106±0·040	0·272±0·014	0·166±0·042	0·0001
Potato *nx* . .	0·089±0·047	0·254±0·077	0·165±0·090	0·06-0·07
p . .	0·028±0·041	0·035±0·016	0·006±0·044	0·8-0·9
d . .	0·111±0·005	0·154±0·030	0·042±0·031	0·1-0·2

using the index of double reduction introduced by Fisher and Mather (1943) instead of the indices originally introduced by Mather; the latter are double the magnitude of the former.

It was at one time supposed (Mather, 1936) that a larger value for the index would be obtained from duplex data than from simplex data because of partner exchange between the chromosomes in a multivalent, but the fallacy in the argument leading to this conclusion was pointed out by Fisher and Mather (1943). Nevertheless the suggestion of a difference between the simplex and duplex indices remains and is capable of explanation in a different way, apart from misclassification and disturbed viability.

In tetraploid maize, it has been found (Catcheside, 1956) that numerically unbalanced gametes are quite frequent amongst those that function in zygote formation. Such numerically unbalanced gametes not only contribute to the class carrying only recessive genes, but do so to different extents when the gametes come from simplex, duplex and triplex heterozygotes respectively. The result is that numerical non-disjunction contributes differently to the quantities calculated above as purporting to be indices of double reduction respectively for the simplex and the duplex. In fact, if α is the true coefficient of double reduction and *x* is the coefficient of numerical non-disjunction, being the proportion of gametes having one or three instead of two of the particular chromosome concerned, the simplex

index is in fact $\alpha(1-x)$ while the duplex index is $\frac{1}{4}x+\alpha(1-x)$. Thus the duplex index should exceed the simplex index by an amount equal to a quarter of the frequency of numerical non-disjunction for the locus. Similarly, the triplex index, strictly $\frac{1}{2}x+\alpha(1-x)$, would exceed the simplex index by an amount equal to one-half of the rate of numerical non-disjunction.

TABLE 2

Segregation in tetraploid tomatoes and potatoes. Data of (1) Mather, 1936, (2) Cadman, 1942 and (3) Lunden, 1937. Note, $y = \alpha(1-x)$

Mating	Progeny class	Expectations	Tomato $r^{(1)}$	Potato $nx^{(2)}$	Potato $p^{(3)}$	Potato $d^{(3)}$
Duplex backcross .	Dom.	$\frac{1}{12}(10-x-4y)$	88	144	2588	668
	Rec.	$\frac{1}{12}(2+x+4y)$	20	38	577	205
			108	182	3165	783
Duplex self .	Dom.	$1-\frac{1}{144}(2+x+4y)^2$	885	122	3414	889
	Rec.	$\frac{1}{144}(2+x+4y)^2$	68	10	104	34
			953	132	3518	923
Simplex backcross	Dom.	$\frac{1}{4}(2-y)$	...	762	1122	494
	Rec.	$\frac{1}{4}(2+y)$	...	842	1151	570
				1604	2273	1064
Simplex self .	Dom.	$1-\frac{1}{16}(2+y)^2$	605	122		
	Rec.	$\frac{1}{16}(2+y)^2$	221	41		
			826	163		
Simplex backcross	Duplex	$\frac{1}{4}y$	3			
	Simplex	$\frac{1}{2}(1-y)$	45			
	Nulliplex	$\frac{1}{4}(2+y)$	68			
			116			

The differences between the simplex and duplex indices therefore yield estimates of the rates of non-disjunction. However, these are not efficient estimates, because they pay no regard to the unequal amounts of information about x and α contributed by different classes of data and do not weight the data. Nevertheless they are useful as starting points in the computation of efficient estimates.

Efficient estimates of both α and x may be obtained by joint estimation using a maximum likelihood method, which has been applied to similar data obtained for the sugary locus in maize (Catcheside, 1956). The data available in the tomato and potato and expectations for different classes of segregation are given in table 2. The estimates computed from them are given in table 3. The rates of non-disjunction for p and d agree very well with one another, but that for nx seems to be exceptionally large. The

mean value of the rate of non-disjunction, $\bar{x}$, in the potato is $0 \cdot 0961 \pm 0 \cdot 1364$. These estimates represent very good fits to the observed data with a general absence of heterogeneity between the different classes of data. Thus the heterogeneity $\chi^2_{[2]}$ is $2 \cdot 4107$ in the case of nx; for p, $\chi^2_{[1]}$ is $0 \cdot 9148$ and for d $\chi^2_{[1]}$ is $3 \cdot 7803$.

The data for r in the tomato differ in that the dominant progeny of the simplex backcross had been further classified as to whether they were duplex or simplex (table 2). Though little credence can be placed in the large values of x and α found (table 3) in the tomato, the various classes of the data are in fair agreement with one another. The heterogeneity $\chi^2_{[3]}$ is only $5 \cdot 424$.

The cytological data, with which these deductions should be reconciled, are as scanty as the genetic parameters are lacking in precision. There is no information available for any particular recognisable chromosome nor is it known whether there is an equal or unequal incidence of quadrivalent

TABLE 3

Estimates of coefficients of numerical non-disjunction (x) and of double reduction (α) in tetraploid tomatoes and potatoes

Gene				x	α
Tomato r	.	.	.	$0 \cdot 665 \pm 0 \cdot 168$	$0 \cdot 316 \pm 0 \cdot 236$
Potato nx	.	.	.	$0 \cdot 450 \pm 0 \cdot 356$	$0 \cdot 161 \pm 0 \cdot 094$
d	.	.	.	$0 \cdot 033 \pm 0 \cdot 267$	$0 \cdot 148 \pm 0 \cdot 032$
p	.	.	.	$0 \cdot 036 \pm 0 \cdot 179$	$0 \cdot 027 \pm 0 \cdot 039$

formation and numerical non-disjunction amongst the chromosomes. The available evidence will therefore have to be treated as though it were averaged over all chromosomes.

The occurrence of chromatid segregation, measured genetically as α, is dependent upon the formation of multivalents, particularly quadrivalents. Its value is related to a number of genetical and cytological factors approximately by the formula $\alpha = c.q.p.d.$, where c is the amount of crossing-over between the centromere and the locus, q is the frequency of quadrivalent formation per set of four homologues, p the frequency of adjacent (or parallel) co-orientation and disjunction of quadrivalents and d is the frequency with which adjacent disjunction of the quadrivalent results in non-disjunction of the gene locus concerned. It has been thought useful to separate p and d in this way, rather than to combine them into one statistic, say a, which expresses the probability of adjacent disjunction for a given locus in a quadrivalent. The statistic p can be derived relatively easily from cytological observations, but d is much harder to determine owing to the rarity with which the two different arms of a chromosome may be separately distinguished in a quadrivalent. There is, of course, no independent evidence about the value of c in the potato and tomato.

In the potato, the frequency of quadrivalents is rather low. The data gathered by Lamm (1945), Bains (1951) and Swaminathan (1954a, b) shows an average of about $2 \cdot 1$ quadrivalents per cell. If every one of the twelve sets of four chromosomes had an equal chance of forming a quadrivalent, the value of q would be $0 \cdot 175$. The few illustrations of metaphase I

that have been published suggest that p may be about 0·5. Likewise, since the centromeres are approximately median in potato chromosomes d may be taken as 0·5. The maximum value of c is probably 0·5. Hence the maximum value that α would be expected to take is about 0·022, on the assumption that all chromosomes have an equal chance of entering into quadrivalents. Cadman (1943) recorded a much larger rate of quadrivalent formation in Flourball, namely 5·24 per cell. This would give an average value of $q = 0·437$ and a maximum value of $\alpha = 0·055$.

The observed values of α (table 3) for the genes nx and p can be considered reconcilable with the maximum values theoretically possible in the light of cytological considerations. However, the value for the gene d is much greater even than the value admitted by Cadman's Flourball data, which are generally considered to be exceptional. If the arguments and inferences are reliable, it should be concluded that the probability of quadrivalent formation falls unequally upon the twelve sets of chromosomes in the potato. It would then follow that the values of α for different unlinked loci would not necessarily reflect the relative amount of recombination with the centromere shown by each locus, apart from the possible complexities due to more than a single chiasma occurring between the centromere and a locus. The value of α might be small because quadrivalents were seldom formed or because adjacent orientation of quadrivalents occurred only rarely, altogether apart from the relative amount of recombination with the centromere.

The available cytological data have been scrutinised for evidence of non-random distribution of quadrivalent formation amongst the twelve sets of homologous chromosomes. On the whole, there appears to be no appreciable departure from randomness, the observed distributions agreeing very well with expectations based on this assumption. For example, in the case of Chippewa (Swaminathan, 1954), the 50 pollen mother cells have an average of 4·8 quadrivalents each. Cells were observed to have as few as two or as many as nine quadrivalents. The χ^2 value, on the basis of equal probability (0·4) for all twelve sets of chromosomes, is only 3·9687. The assumption of various patterns of unequal distribution of probabilities generally results in worse agreement. Concentration of all quadrivalent formation into fewer than nine of the twelve sets is excluded as, also, is the occurrence of unit probability in more than two sets. As an example of the effect of unequal probabilities of quadrivalent formation, the assumption of equal probabilities of 0·8 for 4 sets and of 0·2 for 8 sets raises the value of χ^2 to 12·3111, a value which is still not unreasonably large. Obviously, some patterns of unequal distribution of quadrivalent formation could be compatible with the cytological data, but there is no compelling evidence for either view.

As regards the tomato, Upcott (1935) observed an average of 3·84 quadrivalents per cell. Hence $q = 0·32$ and, with p, q and c each a half, the maximum value of α would be 0·04.

An indication of the upper limit of x may be derived from consideration of the frequency of numerically unbalanced sets at metaphase II of meiosis. For the potato, Lamm's (1945) data yield a value of 0·049 while Swaminathan's (1954) data give 0·026. These values agree with two of the genetical estimates, those for d and p. For the tomato, Upcott's (1935) data yield x not greater than 0·029. This is greatly different from the large

and uncertain estimate obtained by genetic means. Unfortunately none of our genetical estimations have sufficient precision for a satisfactory comparison.

1. SUMMARY

The values of double reduction previously made for various loci in the tomato and potato showed systematic differences according to whether the estimates were made from duplex or simplex data. The differences may be accounted for by the complicating effects of numerical non-disjunction.

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