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Estimation of the coefficient of double reduction in the cultivated tetraploid potato

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Summary. Theoretical models to estimate the coefficient of double reduction in tetraploid organisms and the standard error of this estimate are derived. Using these models, we were able to estimate the coefficient of double reduction for several loci in tetraploid potatoes, *Solanum tuberosum* L., through examination of segregating isozyme loci in a series of 4x–2x crosses and in haploid progeny derived from six cultivated tetraploid potatoes. Tetraploid × diploid crosses are useful for estimating the frequency of double reduction because of the availability of homozygous diploid tester lines and the large number of tetraploid progeny generated via the functioning of 2n pollen. The strength of haploid analysis is the examination of diploid progeny. However, it is frequently difficult to obtain large numbers of progeny for testing. Based on our results, we conclude that double reduction occurs sporadically in tetraploid potatoes.

Key words: Chromosomal segregation – Chromatid segregation – Haploids – Map distance – Isozyme loci

Introduction

Meiosis is a complex process in an autotetraploid organism. Three types of segregations are recognized. Muller (1914) and Haldane (1930) described chromosome segregation, and the mathematical genetics of chromosome segregation for a single locus was considered by Geiringer (1948). Haldane (1930) also proposed random chromatid segregation and Geiringer (1949) subsequently presented the mathematical consequences of this segregation for a single locus. Mather (1935, 1936) reviewed the cytological behavior of chromosomes for an autotetraploid organism during meiosis and proposed maximum equational segregation.

Autopolyploids (i.e., autotetraploids or autotriploids) can undergo double reduction that results in (the segments of) two sister chromatids being recovered in a single gamete. For this to occur, multivalent pairing must take place with a cross-over between a locus and its centromere followed by the two pairs of chromatids passing to the same pole in anaphase I (adjacent segregation). Mather (1935, 1936) also demonstrated that the coefficient of double reduction (α) is a product of the mean frequency of equational separation (e) and the frequency with which equationally separating chromosomes pass to the same poles in anaphase I (a). If quadrivalents are always formed in a tetraploid and an effective cross-over occurs between the locus and its centromere, the maximum frequency of double reduction is 1/6. Since the amount of double reduction for a given gene is a function of the cross-over distance between the locus and the centromere, segregation ratios in an autotetraploid will vary from gene to gene.

Double reduction is readily detectable in any cross in which an allele of a locus is present in a single dose in a parental clone. It can also be detected through non-chromosomal type segregation ratios in crosses in which at least two copies of each allele are present. The cultivated potato, *Solanum tuberosum* L. ($2n = 4x = 48$) is a polysomic tetraploid and presents two opportunities to estimate the coefficient of double reduction. Typically, an asymmetric heterozygote ($x_1x_1x_1x_2$ or $x_1x_2x_2x_2$) or a symmetric heterozygote

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($x_1x_1x_2x_2$) can be crossed to a homozygous tester (i.e., 4x–4x or 4x–2x crosses). Alternatively, haploids ($2n=2x=24$) can be extracted from tetraploid potatoes that have a non-homozygous locus to detect double reduction. Provided there is no selection associated with this process, the haploids express the gametophytic output of the parental tetraploids. Our ability to estimate double reduction in potato has been enhanced because: (1) the process of extracting haploids has become routine using the haploid pollinator technique (Hougas and Peloquin 1958) and has resulted in large numbers of haploids (Kotch and Peloquin 1987), and (2) researchers have developed codominant potato isozyme loci with the resolution to detect allelic dosage within a tetraploid locus (Staub et al. 1984; Martinez-Zapater and Olivier 1984; Quiros and McHale 1985; Douches and Quiros 1988).

We know that if there is chromosomal segregation ($\alpha=0$), gametophytes with genotypes x_1x_2, x_1x_3, x_1x_4, x_2x_3, x_2x_4, and x_3x_4 should occur with frequencies of 1/6 from a tetraploid of genotype x_1x_2-x_3x_4. Furthermore, we know that if there is chromatid segregation we would expect four homozygous gametophytic genotypes each with frequencies of 1/28 and six heterozygous gametophytic genotypes each with frequencies of 1/7. From these, it is easy to deduce that for $0\leq\alpha\leq 1/7$ the expected gametophytic genotypes and their frequencies are: x_1x_1, x_2x_2, x_3x_3, and x_4x_4 with a frequency of $(1/4)\alpha$, and x_1x_2, x_1x_3, x_1x_4, x_2x_3, x_2x_4, and x_3x_4 with a frequency of $(1/6)(1-\alpha)$.

The purposes of this paper are to: (1) derive a theoretical estimate of the coefficient of double reduction and the standard error of this estimate, and (2) examine the segregation of isozyme loci in a series of 4x–2x crosses and in haploid progeny derived from six cultivated tetraploid potatoes to obtain an estimate of the coefficient of double reduction and its standard error. In addition, we will compare the estimates of double reduction with previously estimated gene-centromere map distances for these loci.

Materials and methods

Model

In developing a general model we will assume that there are four different alleles at the locus under consideration: x_1, x_2, x_3, and x_4. Thus, in the absence of any selection pressure, we would expect a tetraploid plant of genotype $x_1x_2x_3x_4$ to produce gametophytes of x_1x_1, x_2x_2, x_3x_3, and x_4x_4 with a frequency of $(1/4)\alpha$, and x_1x_2, x_1x_3, x_1x_4, x_2x_3, x_2x_4, and x_3x_4 with a frequency of $(1/6)(1-\alpha)$.

We know that x_1x_1, x_2x_2, x_3x_3, and x_4x_4 could be produced only if in fact double reduction was occurring. We will call these four genotypes the chromatid types. The remaining six possible genotypes of the gametophyte are chromosomal segregation types. We will call these six genotypes the chromosomal types.

The proportion of gametophytes of the chromosomal types is $(6)(1/6)(1-\alpha)=(1-\alpha)$. Let n individual plants (either haploids of *S. tuberosum* or progeny from tetraploid × homozygous tester crosses) be scored as being of the chromosomal type ($x_i=1$) or of the chromatid type ($x_i=0$). Given the genetic assumptions developed earlier, $\sum_{i=1}^{n} x_i$ has a binomial distribution with parameters n and p, i.e., the probability that $x_i=1$ is p. The uniform minimum variance unbiased estimate of p is:

$$\bar{x}=(1/n)\sum_{i=1}^{n} x_i.$$

The variance of $\bar{x}$ is:

$$\mathrm{Var}(\bar{x})=p(1-p)/n.$$

By setting the proportion (p) of gametophytes of the chromosomal types equal to $(1-\alpha)$ and solving for α:

$$\alpha=1-p.$$

The uniform minimum variance unbiased estimator of $1-p$ is $1-\bar{x}$, and the variance of $(1-\bar{x})$ is $p(1-p)/n$. The maximum likelihood estimate of the variance of $(1-\bar{x})$ is $\bar{x}(1-\bar{x})/n$. Thus, the standard error (SE) of $(1-\bar{x})$ is:

$$\widehat{SE}(1-\bar{x})=[\bar{x}(1-\bar{x})/n]^{\frac{1}{2}}$$

From this an approximate 95% confidence interval for $(1-\bar{x})$ is:

$$(1-\bar{x})\pm z_{0.025}\cdot\widehat{SE}(1-\bar{x}).$$

From these derivations it is easy to show that if there are four different alleles ($x_1x_2x_3x_4$) at the locus in question in the tetraploid parent the estimate of α for the chromosomal types is:

$$\hat{\alpha}=1-\bar{x}$$

and the standard error of this estimate is:

$$\widehat{SE}(\hat{\alpha})=[\bar{x}(1-\bar{x})/n]^{\frac{1}{2}}.$$

In this case, the frequency of individual plants of the chromosomal types is: $6/7\leq p\leq 1$.

If there are three different alleles ($x_1x_2x_3x_3$) at the locus in question in the tetraploid parent we know that the homozygous gametophytes x_1x_1 and x_2x_2 can only arise by chromatid-type segregation. All other gametophytes arise through a mixture of chromosomal and chromatid segregation. Let p be the proportion of gametophytes of this mixture. Thus, the estimate of α for a mixture of these chromosomal and chromatid types is:

$$\hat{\alpha}=2(1-\bar{x})$$

and the standard error of this estimate is:

$$\widehat{SE}(\hat{\alpha})=[4\bar{x}(1-\bar{x})/n]^{\frac{1}{2}}.$$

In this case, the frequency of individuals of this mixture type is: $13/14\leq p\leq 1$.

If there are two different alleles at the locus in question in the tetraploid parent of the form $x_1x_1x_1x_2$, we know that the homozygous gametophyte x_2x_2 can arise only by chromatid-type segregation. All other gametophytes arise through a mixture of chromosomal and chromatid-type segregation. Let p be the proportion of gametophytes of this mixture. Thus, the estimate of α for a mixture of these chromosomal and chromatid types is:

$$\hat{\alpha}=4(1-\bar{x})$$

and the standard error of this estimate is:

$\widehat{SE}(\hat{\alpha})=[16\bar{x}(1-\bar{x})/n]^{\frac{1}{2}}$.

In this case, the frequency of individuals of the mixture types is: $27/28 \leq p \leq 1$.

If there are two different alleles at the locus in question in the tetraploid parent of the form $x_1x_1x_2x_2$, we know that the heterozygous gametophyte can arise only by chromosomal-type segregation. Let p be the proportion of these gametophytes. Thus, the estimate of α from these heterozygous gametophytes is:

$\hat{\alpha}=1-(3/2)\bar{x}$

and the standard error of this estimate is:

$\widehat{SE}(\hat{\alpha})=[9\bar{x}(1-\bar{x})/4n]^{\frac{1}{2}}$.

In this case, the frequency of individuals of this heterozygous type is: $12/21 \leq p \leq 2/3$.

Plant material

Tubers of haploid families from Atlantic (182), Chippewa (56), Katahdin (20), Merrimack (98), Superior (12) and W231 (95) were generously supplied by Drs. S. J. Peloquin (University of Wisconsin, Madison) and R. E. Hanneman, Jr. (USDA/ARS University of Wisconsin, Madison). The eyes of these dormant tubers (150 mg) were sampled for electrophoretic analysis.

Tetraploid × diploid crosses were made to estimate the coefficient of double reduction (Table 1). In general, the tetraploid parent was a simplex heterozygote for the locus of interest and was crossed with a diploid parent that was homozygous for that locus producing 2n pollen. Double reduction products were detected as either duplex heterozygotes or nulliplex genotypic classes, depending upon the cross.

All crosses were made in the greenhouse with the tetraploid as the pistillate parent. Seed was harvested from mature fruit, dried, treated with 1500 ppm of gibberellic acid for 24 h, and then sowed in the greenhouse. Leaf samples (150 mg) were taken from each of the 4- to 6-week-old seedlings for electrophoretic analysis.

Electrophoresis

Horizontal starch electrophoresis was employed to resolve the isozyme loci. The procedure regarding tissue processing, electrophoresis, staining, and nomenclature is described by Douches and Quiros (1988); however, a Tris-borate buffer, pH 8.3 and gel system (Stuber et al. 1988) was substituted for the Tris-citrate buffer, pH 7.8. The MDH, PGI, 6-PGDH and IDH enzyme systems were resolved in the histidine-citrate, pH 5.7 buffer system, while the PRX and PGM enzyme staining was reserved for the Tris-borate, pH 8.3 system.

Table 1. 4x–2x crosses used to detect double reduction

Locus	4x parent	Locus genotype[b]	2x tester genotype	Detectable double reduction product
Mdh-1	Tejon	1222	22	1122
6-Pgdh-3	Nooksack	1222	11	1111
Pgi-1	MS005	2224	22	2244
Idh-1	ND0277-2	1222	11	1111
Mdh-2[a]	A66133-2	1222	22	1122

[a] From Douches and Quiros (1988)

[b] $1222=1^1 1^2 1^2 1^2$

Results

The 4x–2x segregation data are summarized in Table 2 for the five isozyme loci. The estimates of α and the standard error of the estimates are also calculated along with the gene-centromere map distance based upon half-tetrad analysis (Douches and Quiros 1987). In all cases the estimates of α were within the theoretical limits proposed by Mather (1935, 1936), although only two of these estimates were significantly greater than zero. The largest estimate of α was not found for the locus that is farthest from the centromere; however, the smallest estimate of α was associated with the most proximal locus studied.

Table 3 summarizes the potential to use the haploid family data to estimate the coefficient of double reduction. Six haploid families were electrophoretically analyzed, and a total of 42 segregating loci were examined. Of these, in only 28 locus/haploid family combinations were the tetraploid parents asymmetric

Table 2. Estimation of coefficients of double reduction in 4x–2x crosses

Locus	Total progeny	Double reduction products	$\bar{x}$	$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$	Gene centromere map distance[a]
Mdh-1	283	7	0.9753	0.099*	0.037	33.5 cM
6-Pgdh-3	214	7	0.9673	0.131*	0.049	30.1 cM
Pgi-1	122	3	0.9754	0.098 ns	0.057	26.0 cM
Idh-1	314	2	0.9936	0.025 ns	0.018	18.4 cM
Mdh-2	144	2	0.9861	0.063 ns	0.044	n/a

n/a, Not available

* Estimates of α significantly greater than zero at the 5% level of significance; ns, estimates of α not significantly greater than zero at the 5% level of significance

[a] From Douches and Quiros (1988)

Table 3. The haploid families that were electrophoretically analyzed to determine coefficient of double reduction

Haploid families	Family size	Number of segregating loci	Potential number of loci in which double reduction could be detected[a]	Actual loci in which double reduction was observed
Atlantic	71	10	6	1 (*Prx-3*)
Merrimack	98	7	4	1 (*Pgm-1*)
Superior	12	8	5	0
Katahdin	20	7	5	1 (*Pgm-1*)
Chippewa	56	5	4	1 (*Prx-3*)
W231	95	5	4	0

[a] Double reduction could be directly detected in asymmetric or simplex heterozygous tetraploids

or simplex heterozygotes, and double reduction, as determined by the presence of a haploid homozygous for a given isozyme that was derived from a tetraploid parent with only one of the isozymes in question, was detected in only 4 instances. The haploid-family segregation data for these loci are summarized in Table 4. The estimates of α and the standard error of these estimates are also given. At the *Pgm-1* locus both estimates of α in the Merrimack and Katahdin haploid families exceeded the theoretical limit, and in both cases there were fewer haploids of the genotype *Pgm-1*^{3}*1*^{3} than expected. In addition, there were more Merrimack haploids with the *Pgm-1*^{1}*1*^{1} genotype than expected. For the *Prx-3* locus (18.4 cM gene-centromere map distance), the Atlantic and Chippewa haploid-family α estimates that were obtained were within the theoretically allowable range; however, the standard errors of these estimates were of the same order of magnitude as the estimates themselves.

Table 5 summarizes the use of haploid family data from symmetric heterozygous tetraploid parents to estimate the coefficient of double reduction. Only 6 locus/haploid family combinations were examined: in 4 of these, the estimate of α was not significantly different from zero. At the *6-Pgdh-3* locus in Atlantic, the estimate of α was significantly greater than zero. At the *Idh-1* locus in Merrimack, a significant negative estimate of α was obtained. There were more heterozygous haploids than expected.

Table 4. Estimates of α, the coefficient of double reduction, and the standard error (SE) of these estimates for haploids extracted from four asymmetric or simplex heterozygous potato varieties. The variety and the genotype of that variety for the isozyme system investigated are indicated. The genotype of the haploids and the number of individuals observed with that genotype are also indicated

				Atlantic *Prx* $3^13^13^23^3$				
Total	3^13^1	3^13^2	3^13^3	3^23^2	3^23^3	3^33^3	$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
71	12	21	26	2	10	0	0.056	0.039
				Chippewa *Prx* $3^13^13^13^3$				
Total	3^13^1	3^13^3	3^33^3				$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
56	26	29	1				0.071	0.071
				Katahdin *Pgm* $1^11^31^31^3$				
Total	1^11^1	1^11^3	1^31^3				$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
20	1	11	8				0.200	0.195
				Merrimack *Pgm* $1^11^21^31^3$				
Total	1^11^1	1^11^2	1^11^3	1^21^2	1^21^3	1^31^3	$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
98	9	17	28	1	23	20	0.204	0.061

Table 5. Estimates of α, the coefficient of double reduction, and the standard error (SE) of these estimates for haploids extracted from four symmetric heterozygous potato varieties. The variety and genotype of that variety for the isozyme system investigated are indicated. The genotype of the haploids and the number of individuals observed with that genotype are also indicated

				Atlantic *6-Pgdh* $3^13^13^23^2$		
Total	3^13^1	3^13^2	3^23^2		$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
100	17	57	26		0.145	0.074
				Atlantic *Pgm* $2^22^22^32^3$		
Total	2^22^2	2^22^3	2^32^3		$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
182	26	121	35		0.003	0.052
				Merrimack *Idh* $1^11^11^21^2$		
Total	1^11^1	1^11^2	1^21^2		$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
96	7	77	16		−0.203	0.061
				Superior *Idh* $1^11^11^21^2$		
Total	1^11^1	1^11^2	1^21^2		$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
12	3	8	1		0	0.204
				Superior *Got* $2^32^32^52^5$		
Total	2^32^3	2^32^5	2^52^5		$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
12	3	7	2		0.125	0.213
				Katahdin *Idh* $1^11^11^21^2$		
Total	1^11^1	1^11^2	1^21^2		$\hat{\alpha}$	$\widehat{SE}(\hat{\alpha})$
20	2	14	4		−0.050	0.154

Discussion

Detection of a double reduction product is conclusive evidence of quadrivalent formation, followed by crossing-over, and tetrasomic segregation. A cross between a simplex or asymmetric heterozygote to a nulliplex individual can be analyzed for evidence of double reduction. The ability to detect double reduction depends upon: (1) the sample size of the progeny, (2) the frequency of quadrivalent formation, (3) the types and relative frequencies of centromere segregation that occur in the quadrivalents, and (4) the map distance between the gene and centromere (Burnham 1962). Various frequencies of quadrivalents have been found in potato cultivars with mean quadrivalent frequencies ranging from 1.52–4.4 per cell (Swaminathan 1954). In addition, we know the gene-centromere relationships for ten isozyme loci in potato (Douches and Quiros 1987). Estimates of α for *Mdh-2* and *Pgm-1* suggest distal positions on their chromosome arm.

All of the 4x–2x crosses used to estimate α were based upon diallelic locus conditions (Table 1). These crosses are useful for estimating double reduction frequency because it is easy to (1) identify diploid clones that can act as the homozygous tester, and (2) generate large numbers of 4x progeny (>200) via the functioning of 2n pollen.

Enzyme electrophoresis allowed us to detect multiple codominant alleles at two loci in the haploid families (Table 4). With a greater number of alleles at a locus we are able to reduce the size of the standard error of the α estimate. The strength of haploid analysis is the examination of diploid progeny; therefore, dosage differences do not need to be considered in the interpretation of locus. The difficulty in analyzing haploid families is the inability to obtain large enough family numbers to generate a reasonably small standard error of the α estimate.

Table 3 summarizes our ability to detect double reduction in the six haploid families we examined from asymmetric or simplex heterozygous tetraploid parents. Twenty-eight loci/haploid family combinations were in the proper allelic state to detect double reduction; however, double reduction was detected in only 4 of these combinations. These results may indicate that double reduction occurs sporadically. If we look at the individual locus/family combinations, we find that in 4 cases the isozyme patterns were too complex to clearly identify a double reduction event. In another 4 cases we can attribute the lack of double reduction to the proximal location of the isozyme loci. The small sizes of the Superior and Katahdin families may have been the limitation of another 9 locus/family combinations. Lastly, double reduction was not detected for the *Got-2* locus in 2 instances. We do not know the gene-centromere relationship for this locus, and it could also be closely linked to its centromere. In total, double reduction was detected in 4 of 9 possible locus/haploid family combinations.

Our ability to detect double reduction in the haploid families from symmetric heterozygous tetraploid parents was limited in 3 of the locus/haploid family combinations by the small sizes of the Superior and Katahdin families. The excess number of heterozygous haploids at the *Idh-1* locus in Merrimack may be due to random sampling error or to some selection pressure on the gametophyte favoring heterozygosity at this locus or a closely linked locus. In 1 of the 6 locus/haploid family combinations, a significant and meaningful estimate of α was obtained.

The estimates of α and the standard errors of these estimates emphasize the importance of observing large numbers of individuals in a population. The closer the estimate of α is to zero, i.e., the closer the locus is to the centromere, the more critical population size becomes in obtaining a meaningful estimate of α.

Different polyploidization mechanisms have been suggested for the origin of the cultivated tetraploid potato, such as autopolyploidy (Hawkes 1956), intervarietal autoploidy (Stebbins 1957), segmental allopploidy (Matsubayashi 1960), and amphidiploidy (Brucher 1964; Hawkes 1967; Howard 1973). Cytogenetic data such as frequency of multivalents have not provided sufficient evidence to differentiate between these mechanisms. Howard (1970) and Swaminathan and Magoon (1961) established tetrasomic ratios for morphological characters and disease resistance, but these segregation ratios can also be supported by a monogenic model. Martinez-Zapater and Oliver (1984) observed tetrasomic inheritance chromosomal-type at four isozyme loci in two Group Tuberosum cultivars and one Andigena cultivar. Quiros and McHale (1985) also have found evidence of tetrasomic segregation for three isozyme loci in potato. In these analyses the dosage effects due to asymmetric heterozygotes were disregarded. Our data, which identify the occurrence of double reduction at 5 isozyme loci/family, support the existence of tetrasomic segregation in the cultivated potato and can be accounted for either by autoploidy or by amphiploidy with a lack of chromosome differentiation between the putative ancestors.

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