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Heterozygosity in 2n gametes of potato evaluated by RFLP markers

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Abstract The heterozygosity transmitted through 2n gametes in potato was evaluated by following the segregation of RFLP markers in tetraploid progeny from bilateral sexual polyploidization in a cross between two diploid (2x) interspecific hybrids which produce 2n SDR eggs or 2n FDR pollen. Out of 84 probe/enzyme combinations tested, 23 revealed polymorphism between the parents and were heterozygous in at least one of the parents. These probes characterized 13 loci distributed on five different chromosomes of the potato RFLP map. The heterozygosity transmitted through SDR and FDR gametes was estimated to be 31.8% and 71.4%, respectively. Two different indices (LH and RHI) were used to select plants showing a high level of heterozygosity in the tetraploid progeny. The recombination events and the centromere positions were estimated for chromosomes I, VI and VII, following the segregation ratios of SDR or FDR gametes produced by the parents. A different recombination rate was observed between the two interspecific hybrids.

Key words Bilateral sexual polyploidization · FDR · SDR · Recombination rate

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Introduction

The occurrence of 2n gametes in diploid potatoes makes possible the production of 4x progenies from either unilateral (4x × 2x, 2x × 4x) or bilateral (2x × 2x) sexual polyploidization (Mendiburu et al. 1974; Peloquin 1982; Hermsen 1984a). This allows the exploitation in potato breeding of wild and cultivated relatives of the species, with the aim of increasing the allelic diversity of new 4x cultivars (Peloquin et al. 1989). In potato 2n gametes are formed as a result of either a first division (FDR) or a second division restitution mechanism (SDR). FDR 2n gametes derive from an equational division of the entire chromosome complement and they thus include "non-sister chromatids", whereas SDR 2n gametes result from chromosome doubling following reductional chromosome division and thus comprise "sister chromatids".

The mode of 2n gamete formation in diploid clones is important, since FDR and SDR differ in their genetic consequences. It has been estimated theoretically that FDR 2n gametes transmit 80% of the parental heterozygosity to 4x progenies whereas SDR 2n gametes transmit about 40% heterozygosity (Peloquin 1983; Hermsen 1984b). In 2x × 4x crosses Douches and Quiros (1988a) and Jongedijk et al. (1991) confirmed these estimates using several isozyme markers having known gene-centromere map distances. RFLP (restriction fragment length polymorphism) markers offers the opportunity to easily identify heterozygous loci in a single plant (Landry and Michelmore 1987; Tanksley et al. 1989), thus allowing one to test the level of heterozygosity transmitted through 2n gametes. The segregation analysis of 2–3 RFLP markers, already mapped on a potato chromosome by Gebhardt et al. (1991), could also help to localize the centromere positions on the map.

In the present paper RFLP markers are used to follow the segregation of heterozygous loci in tetraploid progeny produced through bilateral sexual polyploidi-

zation (2x × 2x) between two interspecific potato hybrids which produce 2n SDR or FDR gametes.

Materials and methods

Crosses between two haploid-species hybrids (2n = 2x = 24) were performed in 1991 at Camigliatello Silano (Cs). The female parent was a *tuberosum* haploid × *chacoense* hybrid (UP88C75) producing 30–35% of 2n eggs through SDR, whereas the male parent was a *phureja* × *tuberosum* haploid hybrid (US-W5295-7) which produces 50% 2n pollen through FDR (Conicella et al. 1992). The clone UP88C75 was selected in Portici, while the clone US-W5295-7 was kindly provided by S.J. Peloquin (University of Wisconsin, Madison, Wis.).

In 1992, seedlings from 2x × 2x crosses were analyzed for ploidy level by counting the chloroplasts in stomatal guard cells (Frandsen 1968). Diploid progeny from parental n gametes, and tetraploid progeny from 2n gametes of the same parents were isolated. The two groups of genotypes were made up by 15 (diploid) and 30 (tetraploid) clones. Total genomic DNA was extracted from 0.5 g of freeze-dried leaf material of each genotype, including the two parental clones. DNA extraction, restriction digests, electrophoresis, blotting and hybridization methods were as described by Gebhardt et al. (1989). Fifteen cDNA probes and 13 genomic probes from the potato RFLP map (Gebhardt et al. 1991), distributed on the 12 chromosomes of potato, were used with the restriction enzymes *Alu*I, *Rsa*I and *Taq*I. Probes revealing a polymorphism between parents, and in one or both parents, were screened on the diploid progeny. In what follows we will define those probes revealing a polymorphism between parents as polymorphic probes and those identifying loci in the heterozygous state in one or both parents as heterozygous probes. Such informative probes were tested on the tetraploid progeny to estimate the heterozygosity transmitted to the tetraploid plants through 2n gametes. The relative level of heterozygosity (LH) (Gebhardt et al. 1989) was estimated in % from the number of probe/enzyme combinations showing heterogosity per total number of probe/enzyme combinations. A relative heterozygosity index (RHI) (Gebhardt et al. 1989) was also calculated for each genotype by dividing the number of polymorphic fragments present at heterozygous loci in each individual by the total number of scorable fragment positions (251 in total).

Results

Selection of informative probes

Informative probes were selected by screening the RFLP pattern of 84 probe/enzyme combinations on 15 diploid clones. Forty-four (23 + 21) probe/enzyme combinations revealed a polymorphism between the parental clones (52.4%, Table 1), and 59 (23 + 36) probe/enzyme combinations identified intraparental heterozygous loci (70.2%), *Taq*I being the most useful enzyme for detecting both polymorphism and heterozygosity. Most of the heterozygous probes (36 out of 59) were not polymorphic between the parents since they identified segregating fragment alleles common to UP88C75 and US-W5295-7 (*ab* × *ab*); only 23 probe/enzyme combinations were polymorphic and heterozygous in at least one parent (27.4%). Finally, 21 combinations were polymorphic but homozygous (*aa* × *bb*) and four combinations were not polymorphic and homozygous (*aa* × *aa*).

The only informative probes were the polymorphic and heterozygous ones and the possible parental genotypes revealed through these probes are reported in Table 1. In most cases not all alleles at each locus were identified and therefore it was impossible to clearly determine the parental genotypes. In fact, none of the 23 probe/enzyme combinations identified two alleles per heterozygous loci for both parents (*ab* × *cd*), but in 13% of the cases two alleles for one parent, and one segregating allele for the other parent, were identified (*ab* × *c*-), the fourth being a null allele (absence of band). In other cases only two alleles (17.4% of -*b* × *c*- and 8.7% of *ab* × --) or even only one allele (34.6% of -*b* × --) per locus were identified. Therefore, it was often impossible to follow the segregation of FDR and SDR gametes at the same locus. Finally, in 26.1% of the cases one allele for each parent was identified, the third being a common allele (*ab* × *ac*).

Level of heterozygosity in tetraploid plants

The RFLP pattern of the 23 most-informative probe/enzyme combinations was determined in the tetraploid progeny to estimate the relative level of heterozygosity (LH) and the relative heterozygosity index (RHI, Table 2) in each plant. The highest LH value (90.8%) was found in plants 28 and 43 and the lowest one (14.3%) in plant 49. The RHI varied from a minimum of 0.08 for plant 49 to a maximum of 0.54 for plant 82; plants 43 and 89 also had high values of RHI, 0.51 and 0.49 respectively. In most cases LH and RHI were highly correlated. The RHI index was previously used to estimate heterozygosity by Gebhardt et al. (1989) and by Bonierbale et al. (1993). In the present study it underestimated the level of heterozygosity since in many cases null alleles were evidenced. Therefore, we cannot exclude the possibility that a fraction of plants with a low RHI index are more heterozygous than was revealed by the RHI values.

Out of 23 polymorphic and heterozygous probe/enzyme combinations, only eight were able to identify three alleles per locus, and the plants having triallelic loci with all eight combinations are marked (+) in Table 2. In some cases the presence of triallelic loci was correlated with a higher RHI value (plants 43, 82 and 89), whereas in other cases the presence of triallelic loci was associated with a lower RHI value (plants 3, 50 and 85).

Segregations in the tetraploid progeny

The 23 probe/enzyme combinations which were both polymorphic and heterozygous identified 13 loci; three on chromosome I, four on chromosome VI, four on chromosome VII, and one on both of chromosomes X and XI (Table 3). Following the segregation of the alleles revealed by these probes in the tetraploid progeny (Fig. 1), it was possible to determine the type of gametes produced by UP88C75 and US-W5295-7. Out of the 13 loci, only six were heterozygous in both parents whereas the other seven loci were heterozygous only in UP88C75 or in US-W5295-7.

Table 1 Results of screening the RFLP patterns of 28 × 3 probe/enzyme combinations on 15 diploid F_1-plants and on both diploid parents, and detection of informative probes. The last column gives the possible parental genotypes; *a*, *b*, *c*, and *d* are symbols of alleles (same symbols used for simplicity sake for alleles at different loci)

Probe/enzyme combinations[a]	28 Probes combined with			Total	Possible parental genotypes in the diploid × diploid cross (no. of common parental alleles)	
	*Alu*I	*Rsa*I	*Taq*I			
Polymorphic, heterozygous	4	9	10	23	*ab* × *cd* (0) *ab* × *cc* (0) *cc* × *ab* (0)	*ab* × *ac* (1) *ab* × *aa* (1) *aa* × *ab* (1)
Not polymorphic, heterozygous	9	12	15	36	*ab* × *ab* (2)	
Polymorphic, homozygous	3	8	10	21	*aa* × *bb* (0)	
Not polymorphic, homozygous	1	1	2	4	*aa* × *aa* (1)	
Total	17	30	37	84		

[a] Polymorphic combinations reveal polymorphism between parents; heterozygous combinations reveal heterozygosity in at least one parent

Table 2 Value of the LH and RHI indices and the presence of triallelic loci (+) in the 30 tetraploid plants considered using the 23 most-informative probe/enzyme combinations

Plant	LH %	RHI	Triallelic loci
3	28.6	0.19	+
4	57.1	0.30	
7	37.5	0.14	
8	71.4	0.30	
17	75.0	0.31	
24	75.0	0.34	+
25	71.4	0.25	+
28	90.8	0.38	+
29	72.4	0.28	
30	77.8	0.35	+
33	42.8	0.16	
36	74.2	0.30	
38	87.5	0.38	
43	90.8	0.51	+
44	28.6	0.12	
49	14.3	0.08	
50	71.4	0.22	+
52	68.3	0.16	
53	71.4	0.34	+
58	55.6	0.32	
62	57.1	0.16	
66	85.6	0.31	+
76	83.2	0.28	
77	42.8	0.12	
78	28.9	0.12	
81	57.1	0.22	
82	77.8	0.54	+
84	71.4	0.25	+
85	55.5	0.22	+
89	79.1	0.49	+

Gametes produced by UP88C75 were not uniform (No in Table 3) for 10 out of 11 loci, with only probe CP62 (chromosome I) revealing no polymorphism. Considering only the fragments contributed by UP88C75, the RFLP patterns at loci revealed by one probe of chromosome I, three of VI, and one of X, segregated in the tetraploid population according to a ratio approaching 1:1, the two contrasting RFLP phenotypes being homozygous for both alleles of the UP88C75 parent. A similar ratio is expected (Table 4) when, in the absence of crossing over between the centromere and the polymorphic locus, an SDR mechanism is active in originating 2n spores homozygous at that locus but genetically different (Table 4). When one crossover takes always place because of the distance between the polymorphic locus and the centromere, all loci affected will reveal heterozygosity in SDR gametes (Table 4): this was the case for probe CP62 on chromosome I, for which no segregation of an RFLP fragment was observed. Loci revealed by probe GP127 on chromosomes VII and GP125 on XI segregated with ratios near 3:1 or 2:1, and hence intermediate between the extremes 1:1 and 1:0. It can be assumed that in such cases the crossover between the centromere and the polymorphic locus did not always occur, resulting in the formation of a mixture of heterozygous and homozygous gametes.

A similar analysis for parental clone US-W5295-7 revealed that in some cases it produced uniform gametes, as was the case for loci revealed by probe CP64 on chromosome I, and CP51 and GP77 on chromosome VII. The uniformity of FDR 2n gametes is expected when no crossover takes place between the locus and the centromere, leading to the formation of only heterozygous gametes at that locus (Table 4). When segregation was observed (CP46 on chromosome I, CP18 and GP79 on chromosome VI, CP52 on chromosome VII), this always fitted a 3:1 ratio, as expected with FDR for loci affected by one crossover leading to 50% homozygous and 50% heterozygous dyads (Table 4). It should be noted that in one case (CP46) the segregation of FDR gametes should be 1:2:1 (cross *ab* × *cd*), but heterozygous plants have the same RFLP pattern as plants which are homozygous for one of the contrasting

Table 3 Uniformity and segregation ratios (χ^2 calculated with Yates' correction of continuity) of 2n gametes produced by UP88C75 and US-W5295-7 evaluated by the RFLP patterns of their tetraploid progeny

Probe	Polymorphic locus mapping on chromosome	Parental clone									
		UP88C75 (SDR)					US-W5295-7 (FDR)				
		Uniformity of gametes	Observed segregation ratio	χ^2 1:1	χ^2 2:1	χ^2 3:1	Uniformity of gametes	Observed segregation ratio	χ^2 1:1	χ^2 2:1	χ^2 3:1
CP46	I	No	15:15	0.00ns	3.04ns	8.71**	No	19:11	1.63ns	0.04ns	1.60ns
CP62	I	Yes	—	—	—	—	nd				
CP64	I	nd					Yes	—	—	—	—
CP12	VI	No	14:14	0.00ns	2.84ns	8.05**	nd				
CP18	VI	No	15:15	0.00ns	3.04ns	8.71**	No	18:7	4.00*	0.11ns	0.01ns
GP76	VI	No	18:12	0.83ns	0.34ns	2.84ns	nd				
GP79	VI	No	15:13	0.03ns	1.65ns	5.76*	No	20:8	4.32*	0.10ns	0.05ns
CP51	VII	nd					Yes	—	—	—	—
CP52	VII	No	20:10	2.70ns	0.00ns	0.71ns	No	23:7	7.50**	0.94ns	0.00ns
GP77	VII	No	19:11	1.63ns	0.04ns	1.60ns	Yes	—	—	—	—
GP127	VII	No	23:7	7.50**	0.94ns	0.00ns	No	15:15	0.00ns	3.04ns	8.71**
CP105	X	No	15:13	0.03ns	1.65ns	5.76*	nd				
GP125	XI	No	22:8	5.63*	0.34ns	0.00ns	nd				

nd = not determined
ns = not significant

* = significant; $P < 0.05$
** = significant; $P < 0.01$

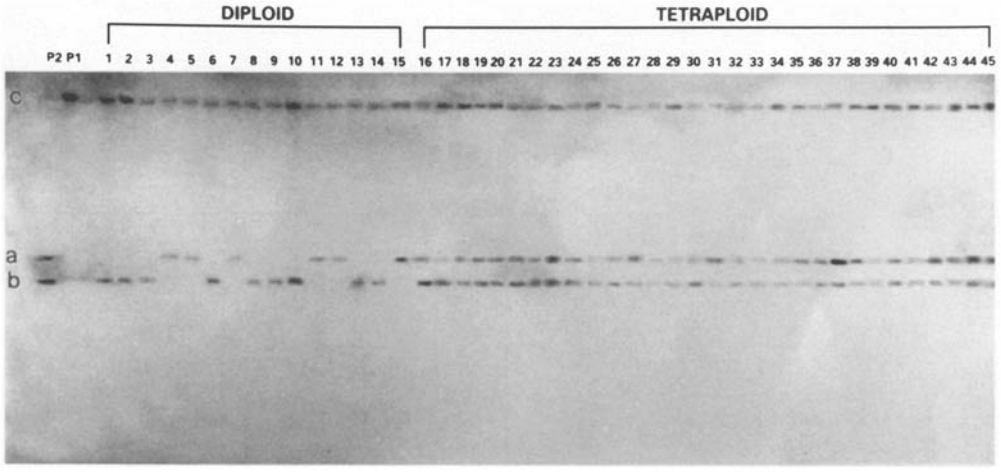

Fig. 1 Segregation of probe CP62 in the diploid and tetraploid progenies of the cross UP88C75 × US-W5295-7. The DNA was digested with *Taq*I. P2 = UP88C75 (*ab*); P1 = US-W5295-7 (*cc*); *lanes 1–15* = diploid plants; *lanes 16–45* = tetraploid plants

alleles of the segregating locus, since this probe could identify only one allele the other being a null (absence of band). In this case it was not possible to discriminate between one homozygous genotype (*abcc*) and the heterozygous genotype (*abc-*) produced by the FDR parent, thus explaining the 3:1 ratio observed (3 *abc-*:1*ab--*). For probe GP127 on chromosome VII an unexplained segregation approaching 1:1 was observed.

For the 13 loci sampled, the overall fraction of heterozygosity transmitted by UP88C75 was estimated to be 31.8%, considering as heterozygous 50% of the gametes of loci segregating 3:1; in the same way, the heterozygosity transmitted by US-W5295-7 was estimated to be 71.4%.

Recombination events and localization of the centromere

Considering the segregation ratios of SDR and FDR gametes together, it is possible to estimate the number of crossovers and the position of the centromere on chromosomes for which the segregation of a sufficient number of RFLP probes was followed.

On chromosome I the centromere should be located between loci defined by probes CP46 and CP64; such loci recombine freely (Fig. 2). This is based on the fact that UP88C75 produced 100% homozygous gametes for locus CP46 (1:1 ratio) and 100% heterozygous gametes for locus CP62, showing that the first locus did

Table 4 Genotypes and ratios in tetraploid progeny from the crosses of Table 1 last column assuming no crossover and one crossover respectively between locus and centromere. Ratios based on the absence of allelic dosage effects. In each tetraploid genotype the left two alleles are from the female, the right ones from the male

Crosses (of Table 1 last column)	Relevant mechanisms		Tetraploid progeny						
			Locus proximal to centromere (no crossover)			Locus distal to centromere (one crossover)			
♀ ♂	♀	♂	Genotypes		Ratio	Genotypes			Ratio
ab × *cd*	SDR	FDR	1/2 *aacd*	1/2 *bbcd*	1:1	1/4 *abcc*	1/2 *abcd*	1/4 *abdd*	1:2:1
ab × *cc*	SDR	—	1/2 *aacc*	1/2 *bbcc*	1:1	1 *abcc*			1:0
cc × *ab*	—	FDR	1 *ccab*		1:0	1/4 *ccaa*	1/2 *ccab*	1/4 *ccbb*	1:2:1
ab × *ac*	SDR	FDR	1/2 *aaac*	1/2 *bbac*	1:1	1/4 *abaa*	1/2 *abac*	1/4 *abcc*	1:3
ab × *aa*	SDR	—	1/2 *aaaa*	1/2 *bbaa*	1:1	1 *abaa*			1:0
aa × *ab*	—	FDR	1 *aaab*		1:0	1/4 *aaaa*	1/2 *aaab*	1/4 *aabb*	1:3
ab × *ab*	SDR	FDR	1/2 *aabb*	1/2 *bbab*	1:0	1/4 *abaa*	1/2 *abab*	1/4 *abbb*	1:0
aa × *bb*	—	—	1 *aabb*		1:0	1 *aabb*			1:0
aa × *aa*	—	—	1 *aaaa*		1:0	1 *aaaa*			1:0

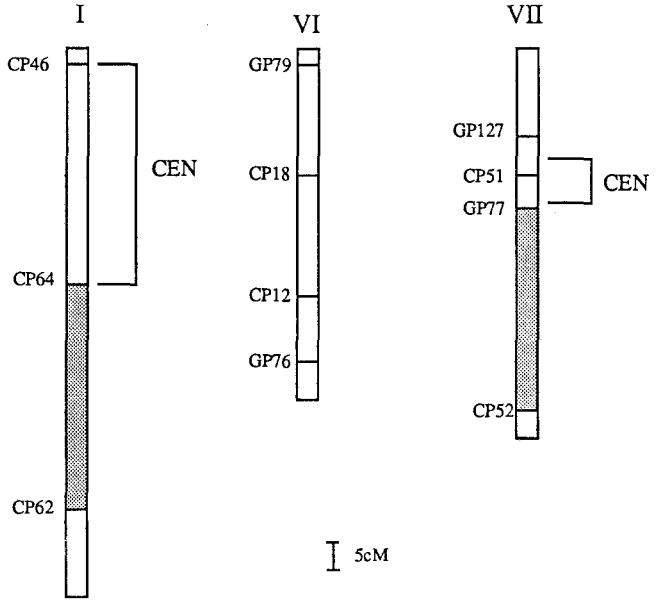

Fig. 2 Chromosomes I, VI and VII with the position of 3, 4 and 4 RFLP markers, respectively. Centromere position (*CEN*) and regions where a crossover occurs (*dotted area*) on chromosomes I and VII of the potato RFLP map. The map scale is derived from the mapping population BC916[2] (Gebhardt et al. 1991)

not recombine with the centromere whereas the other did. On the other hand, the FDR parent US-W5295-7 produced both homozygous and heterozygous gametes for the locus CP46 (3:1 or 2:1 ratio) and 100% heterozygous gametes for the locus CP64. Therefore, it can be assumed that locus CP64 is in the centromeric region, since it is not affected by crossovers in FDR gametes. Unfortunately, segregation data for the same locus are not available for SDR gametes. A different recombination rate between UP88C75 and US-W5295-7 is evident for locus CP46, which recombines with the centromere in US-W5295-7 but does not in UP88C75.

The segregation of four RFLP probes on chromosome VI was not informative in respect of the position of the centromere. In fact, SDR gametes of UP88C75 were 100% homozygous for different alleles in all four loci, as if all of them were linked to the centromere without recombination; this held even if a certain degree of recombination could be supposed for the locus GP76, since the segregation ratio also fitted a 2:1. It is worth pointing out that these loci are uniformly distributed and cover the whole chromosome. The segregation of contrasting alleles in FDR gametes of US-W5295-7 was available only for loci CP18 and GP79, both of which recombine freely with the centromere.

The three loci segregating in UP88C75 and mapping on chromosome VII were linked but with a certain degree of recombination with the centromere, as revealed by the finding of a mixture of heterozygous and homozygous gametes. The segregation of alleles at loci defined by probes CP52, GP77 and GP127 fitted both a 2:1 and a 3:1 ratio. The 2:1 ratio would imply a lower percentage of recombination between these loci and the centromere as expected for loci that are proximal to the centromere. The FDR parent produced 100% heterozygous gametes for loci CP51 and GP77, showing that they do not recombine with the centromere (Fig. 2). The 50% homozygous and 50% heterozygous gametes observed at the locus CP52 indicate that loci GP77 and CP52 recombine freely. The segregation ratio (1:1) observed for locus GP127 implies a distorted segregation when referred to FDR gametes.

Discussion

Tetraploid potatoes may have four different alleles at each locus, thus greatly increasing the intra- and inter-locus interactions. Such interactions are believed to be important in exploiting heterosis (Mendoza and Haynes 1974). It is thus important to maximize potato heterozygosity by using suitable breeding methods. One of these is based on the production of 4x progenies from 2x × 2x crosses, where 2x parents are hybrids between unrelated genetic materials, one of which produces 2n eggs (SDR) and the other 2n pollen (FDR). This breeding scheme exploits the possible complementation of FDR and SDR gametes in transmitting parental heterozygosity and in maximizing allelic interactions (more than two alleles per locus) (Peloquin et al. 1989). The highly heterotic 4x progenies recovered following 2x × 2x crosses (SDR × FDR) support the theoretical expectations (Mendiburu et al. 1974; Chujoy 1985; Werner and Peloquin 1991).

The diploid clones UP88C75 and US-W5295-7 have been generated starting from unrelated genetic backgrounds. However, only 52.4% of the probe/enzyme combinations tested were able to detect polymorphism between them. In fact, they often shared at least one fragment, indicating they had a common allele, probably due to their *tuberosum* haploid complement. Moreover, several RFLP probes identified null alleles which did not allow the identification of tri- and tetra-allelic loci. Since we could not verify the allelic condition at the loci examined we cannot confirm the existence in our 4x progeny of only tri- and tetra-allelic conditions, as predicted from SDR and FDR complementation in 2x × 2x crosses (Peloquin et al. 1989). We could only identify plants for which triallelic loci were found and which simultaneously showed a high level of heterozygosity as measured by LH and RHI indices. Experimental trials to test yield are needed to confirm the validity of the association between LH and RHI and heterosis in this material.

The degree of recombination between loci mapping on chromosomes I, VI and VII, based on the assumption that the genetic consequences of FDR and SDR mechanisms differ depending on the distance between locus and centromere (Hermsen 1984b), was estimated. Following FDR, 100% of parental heterozygosity from the centromere to the first crossover and 50% from the first to the second crossover is transmitted to 4x progeny; with SDR, 0% of heterozygosity from the centromere to the first crossover and 100% from the first to the second crossover is transmitted to 4x progeny. The observed values of 71.4% and 31.8% heterozygosity transmitted by FDR and SDR gametes, respectively, are similar to the values reported by Jongedijk et al. (1991) and by Douches and Quiros (1988a).

Assuming that double, or higher-order, crossing over does not occur in potato (Howard 1970), we could position the centromere on chromosomes I and VII on the basis of the segregation ratios we observed between heterozygous and homozygous gametes produced by UP88C75 (SDR) and US-W5295-7 (FDR). Our data are particularly clear for chromosome VII where the difference in heterozygosity transmitted by SDR and FDR gametes was expected to be larger for loci near the centromere and to rapidly decrease with increasing gene centromere map distances. This is especially true if we consider the 2:1 segregation ratio observed for probes GP77 and GP127 from UP88C75, which indicated that these loci did not always recombine in the SDR gametes depending on their proximity to the centromere.

The 1:1 segregation observed for all loci of UP88C75 on chromosome VI could be due to the lack of crossing over. However, for US-W5295-7 two loci of the same chromosome recombined with the centromere, and this could be explained by a different recombination level in the two sexes. Sex-specific differences in recombination have been reported in plants (Robertson 1984) as well as animals (Andersson and Sandberg 1984; Johnston et al. 1987; Graf 1989), where males normally show less crossing-over than females. However, in some cases females show less recombination than males (Madea 1939).

In backcrosses of F_1 hybrids between *Lycopersicon esculentum* and *Solanum pennellii*, Rick (1969) observed that recombination values were considerably higher than in reciprocals when the F_1 hybrids were used as female parents. These data were confirmed following the segregation of isozymes in two linkage groups in crosses between *L. esculentum* and *L. pennellii* (Gadish and Zamir 1987). Using RFLP markers, which covered the whole tomato genome, de Vincente and Tanksley (1991) determined that meiotic recombination differs between male and female gametes derived from the same F_1 plant (*L. esculentum* × *L. pennellii*), being significantly lower in the progeny derived from male gametes.

In contrast with the finding of reduced recombination, cytogenetic observations on tomato and potato indicate similar, or even increased, chiasma frequencies in the pollen meiosis of interspecific hybrids compared to their parent (Khush and Rick 1963; Singh et al. 1989). Rick (1969) suggested that recombination itself may not be impaired in males and females but that recombinant gametes or zygotes may be preferentially eliminated. In such cases, selection may favor parental genotypes in progeny from interspecific crosses giving rise to skewed segregation ratios in favor of parental alleles. Mechanisms such as balanced lethal alleles, which ensure that neither of the two alternate chromosome groups can produce viable homozygous combinations at fertilization, or pollen lethals, which ensure that pollen can only fertilize eggs containing the opposite chromosome groups, have been observed in plants of the genus *Oenothera*, where they allow the maintenance of permanent translocation heterozygosity (Cleland 1972). Skewed segregation ratios have been observed in interspecific crosses in tomato (Rick 1969), pepper (Tanksley 1983), and cotton (Stephens 1949). Bonierbale et al. (1988), as well as Gebhardt et al. (1989), revealed reduced

recombination in interspecific diploid *Solanum* crosses. Douches and Quiros (1988b) suggested that genomic differentiation between *S. tuberosum* and *S. chacoense* could account for the reduced recombination levels found in the species hybrid, as could also be the case for UP88C75. The segregation data for UP88C75 reported in the present paper may supply evidence to further support this proposal of genomic differentiation. A more detailed RFLP analysis of chromosome VI would provide further information about the different recombination levels observed in gametes produced by the two diploid *Solanum* parents.

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