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RFLP maps of potato and their alignment with the homoeologous tomato genome

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Summary. An RFLP linkage map of the potato is presented which comprises 304 loci derived from 230 DNA probes and one morphological marker (tuber skin color). The self-incompatibility locus of potato was mapped to chromosome I, which is homoeologous to tomato chromosome I. By mapping chromosome-specific tomato RFLP markers in potato and, vice versa, potato markers in tomato, the different potato and tomato RFLP maps were aligned to each other and the similarity of the potato and tomato genome was confirmed. The numbers given to the 12 potato chromosomes are now in accordance with the established tomato nomenclature. Comparisons between potato RFLP maps derived from different genetic backgrounds revealed conservation of marker order but differences in chromosome and total map length. In particular, significant reduction of map length was observed in interspecific compared to intraspecific crosses. The distribution of regions with distorted segregation ratios in the genome was analyzed for four potato parents. The most prominent distortion of recombination was found to be caused by the self-incompatibility locus.

Key words: RFLP – Potato – Tomato – Genetic maps

Introduction

Restriction fragment length polymorphisms (RFLPs) provide a new tool for genetics and plant breeding (recently reviewed for plants in Tanksley et al. 1989). RFLP linkage maps are now available for many plant species (Helentjaris et al. 1986; Bernatzky and Tanksley 1986; Landry et al. 1987; McCouch et al. 1988; Tanksley et al. 1988; Chang et al. 1988; Bonierbale et al. 1988; Gebhardt et al. 1989; Nam et al. 1989; Slocum et al. 1990), including two important members of the *Solanaceae*, potato (*Solanum tuberosum* ssp. *tuberosum*) and tomato (*Lycopersicon esculentum*). Their genomes are similar, differing only by a small number of inversions, as shown by mapping of RFLP loci in an interspecific cross involving *S. phureja* and a hybrid between *S. tuberosum* ssp. *tuberosum* and *S. chacoense* with tomato probes (Bonierbale et al. 1988). A second potato RFLP map was developed independently, using potato markers and an intraspecific backcross population derived from diploid potato breeding lines (Gebhardt et al. 1989).

To this potato map a substantial number of markers has now been added, including a set of tomato probes of known location, which make the alignment of homoeologous potato and tomato chromosomes possible. Moreover, in mapping disease resistance loci in a new potato cross (Barone et al. 1990; Ritter et al 1991), a further potato map has been obtained in a different genetic background. The comparison of the tomato and potato maps makes it possible to discuss structural differences, map lengths and, genomic distribution of chromosomal regions where markers show distorted segregation.

The RFLP data thus far obtained for tomato and potato are complementary in their capacity to provide a better description of genomes in the family of *Solanaceae*. This complementarity has already been useful in mapping an RFLP locus closely linked to the resistance gene against the root knot nematode *Meloidogyne incognita* in tomato using the potato marker GP79 (Klein-Lankhorst et al. 1990).

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Materials and methods

Plant material

Two segregating populations from crosses betwen diploid potato breeding lines were used in linkage analysis. The presented RFLP map (Fig. 1) was based on a population of 67 tuber-propagated lines originating from the backcross (H81.691/1 × H82.309/5) × H82.309/5 (Gebhardt et al. 1989). The recurrent parent H82.309/5 was the pollen donor and not the pistillate parent, as stated by Gebhardt et al. (1989). H82.309/5 is referred to in this paper as P16, H81.691/1 as P9, the F_1 parent as FP916, and the backcross progeny as BC916[2].

The second population consisted of 100 F_1 individuals obtained by crossing line H82.337/49 (P18, female parent) with H80.696/4 (P40, male parent), and is referred to as F1840. Line H80.696/4 was a hybrid between *S. tuberosum* ssp. *tuberosum* and *S. spegazzinii* (Barone et al. 1990).

RFLP markers

The following were used as RFLP markers: 211 cloned potato sequences (137 genomic and 74 cDNA clones), one genomic fragment of the sucrose synthase gene of maize (*ShM*, 3.3-kb *Bgl*II fragment) (Werr et al. 1985), and 26 genomic sequences of tomato. The cDNA clone coding for *Sr*1, a self-incompatibility allele of *S. tuberosum*, is described in Kaufmann et al. (1991). Potato cDNA clones coding for two wound-inducible genes (*WUN*1, *WUN*2) (Logemann et al. 1988) and for 1,3-β-glucanase, EC 3.2.1.6 (*β-Gluc*, E. Kombrink, L. Beerhues, unpublished results) were obtained from J. Logemann and E. Kombrink, respectively (MPI für Züchtungsforschung, Köln). The tomato markers (TG markers) were originally isolated and mapped at Cornell University, Ithaca/NY. The nomenclature for anonymous genomic (GP) and cDNA (CP) markers of potato is given in Gebhardt et al. (1989). Markers with numbers between 1 and 100 were already present in the map of Gebhardt et al. (1989).

RFLP analysis

DNA extraction, restriction digests, electrophoresis, blotting, probe preparation, and hybridization procedures were as described previously (Gebhardt et al. 1989). Essentially, genomic potato DNA was restricted with 4-bp recognition site enzymes. Restriction fragments between 250 and 2,000 bp in length were separated on 4% denaturing polyacrylamide gels and transferred onto Nylon membranes by electroblotting. The membranes were hybridized (10–20 times) to ^{32}P-labelled probes. With a probe length in the range of 500 to 2,000 bp, in many cases two or more restriction fragments were found to be associated with the same RFLP allele, because they cosegregated (in coupling) in the progeny. Therefore, they were scored as one single fragment in the data analysis.

Data and linkage analysis

As an allogamous species, two types of segregation patterns occur in the potato. A restriction fragment representing an RFLP allele (or part of it, see above) that is heterozygous and present in only one or the other parent (=parent specific) is expected to segregate at a 1 : 1 ratio (presence versus absence) in the progeny (model A). A fragment representing an RFLP allele that is heterozygous and present in both parents segregates at a 3 : 1 ratio (presence versus absence, model B). Data analysis was based on scoring presence versus absence of single RFLP alleles according to the two models. An RFLP locus was defined by a single RFLP allele in all those cases in which the fragments representing the putative other alleles of the same locus were homozygous or not detectable experimentally. In the backcross BC916[2], it was possible to score up to three RFLP alleles per RFLP locus, two parent specific (model A) and one in common (model B), the latter forming an "allelic bridge" as discussed in Ritter et al. (1990). In the F_1 cross F1840, up to four RFLP alleles (all four model A) were scored per locus.

Linkage analysis between RFLP alleles, estimation of recombination frequencies between RFLP loci, and determination of the linear order of linked loci, including multipoint linkage analysis and the EM algorithm for handling missing data, were performed as described by Ritter et al. (1990) and Barone et al. (1990). SAS software (Statistical Analysis System, Cary/NC) was used to perform *t*-tests.

The approximate positions on the BC916[2] map of loci polymorphic only in cross F1840 were determined as follows: the relative genetic distance between a marker A on map 1 and a marker N on map 2 ($=r_{A1N1}$) was calculated using the formula

$$r_{A1N1} = r_{A2N2} \cdot r_{A1B1}/r_{A2B2} ,$$

with r_{A2N2} being the distance between A and N on map 2 and r_{A1B1} and r_{A2B2} being the intervals between two neighboring markers A and B mapped in both populations 1 and 2.

The estimate of the total map length of BC916[2] was obtained by plotting the increase in map length per unit of mapped loci versus the total map length, and extrapolating onto an increase of zero.

Mapping of potato markers in tomato

RFLP analysis of 38 potato markers was performed in an F_2 population of an interspecific cross between *Lycopersicon esculentum* and *L. pennellii*, as described by Bernatzky and Tanksley (1986). The map position of these markers was determined by placing them onto a framework map of approximately 250 RFLP markers using Mapmaker (Lander et al. 1987). The detailed map position with respect to all mapped loci in tomato (<1,000) will be reported (M. W. Ganal, S. D. Tanksley, in preparation).

Results and discussion

RFLP mapping in BC916[2] and F1840

RFLP analysis of the backcross progeny BC916[2] has been carried out with a total of 230 RFLP markers and one morphological marker (PSC=purple skin color) (Gebhardt et al. 1989). A total of 508 segregating restriction fragments (=RFLP alleles) also containing the data of the markers mapped by Gebhardt et al. (1989) have been included in this data set. Recombination frequencies between RFLP alleles were calculated, and linkage groups were established according to Ritter et al. (1990). The order of linked loci was determined by multipoint estimates. Of all fragments analyzed, 492 or 97% were mapped to 304 loci on the 12 linkage groups shown in Fig. 1. The total length of the map was 1,034 cM (units defined as in Kosambi 1944). Increasing the number of mapped loci by 117% (from 140 to 304) extended the map length from 690 (Gebhardt et al. 1989) to 1,034 cM, corresponding to a 50% increase. These values lead to an approximate total map length of 1,200–1,300 cM estimated for the BC916[2] population (see "Materials and methods"). The present map covers, therefore, approxi-

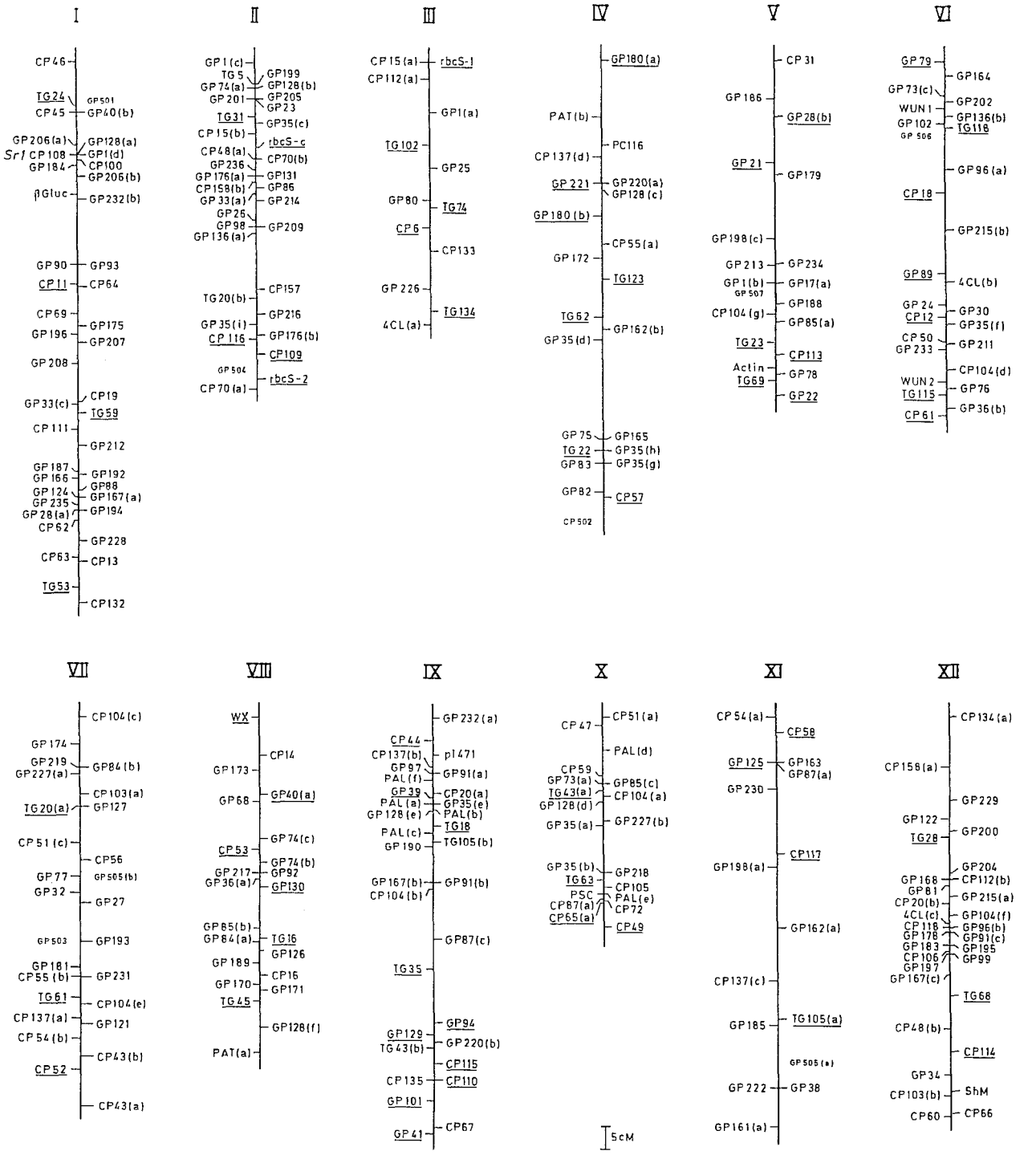

Fig. 1. RFLP linkage map of potato as derived from the backcross BC916[2]. Map distances are given in centimorgans (Kosambi units). Loci detected by random genomic clones of potato and tomato carry the letters GP and TG, respectively, loci detected by random potato cDNA clones are labelled CP, and loci marked by clones of known or specified functions are designated by their specific names. The letters in parentheses indicate that more than one locus is detected with the same probe. Potato and tomato markers mapping to homoeologous positions in both genomes are *underlined*. The orientation of chromosomes is the same as in Bonierbale et al. (1988). Markers with numbers 501–507 and *Sr1* were mapped only in the F_1 cross F1840

mately 80% of the potato genome. The loci represented by single, parent-specific RFLP alleles (expected to segregate with a 1 : 1 ratio, "Materials and methods") were 79 for parent P16 and 77 for F_1 parent FP916, respectively. A total of 38 loci was allocated to common RFLP alleles, heterozygous in both parents and therefore segregating with a 3 : 1 ratio. The remaining 109 loci were defined on the basis of the segregation of two to three RFLP alleles. The map intervals among those loci were calculated as the mean values of the recombination frequency estimates between the individual alleles and had the highest precision.

A total of 221 (43.5%) segregating fragments was inherited from both parents, 144 (28.3%) from P16 and 143 (28.1%) from FP916. This balanced contribution of polymorphisms by the recurrent and the F_1 parent indicates that in an allogamous species like potato, the already high heterozygosity of diploid lines is sufficient for mapping. The higher proportion of fragments segregating from both parents in our backcross population (43.5% in $BC916^2$ versus 20% in F1840) was, however, an advantage for connecting the independent linkage subgroups formed on the basis of segregations of single fragment loci via "allelic bridges" (Ritter et al. 1990).

A second potato RFLP map was based on the F_1 population F1840 tested with 83 selected RFLP markers covering most of the map previously described. Linkage groups and the order of loci were the same as in $BC916^2$, with the exception of two pairs of closely linked loci: *CP51 (a)* and *CP47* on chromosome X and *TG74* and *CP6* on chromosome III (see Fig. 1), which were found in an inverted order in F1840 (data not shown). Rather than being attributed to chromosomal rearrangements, however, the apparent inversions can be attributed to interactions between the method of mapping (model A or model B), sampling error, and the distorted segregation ratios found in the same two chromosomal regions of F1840. Twelve loci were mapped in F1840 using eight probes (CP55, CP65, GP73, GP84, GP128, GP161, GP17, and GP40; data not shown) which reveal a multiple banding pattern in potato. These loci remained undetected in $BC916^2$ because the fragments associated with them did not segregate. Eight additional markers that did not segregate in $BC916^2$ defined nine loci in F1840, which are included in Fig. 1 (marker numbers 501 to 507 and *Sr1*). Their approximate positions on the $BC916^2$ map were calculated as described in "Materials and methods." From a total of 211 RFLP alleles segregating in F1840, 78% were inherited either from parent P40 or P18 and 22% were inherited from both parents. The higher amount of parent specific alleles of the F_1 population compared to the backcross population is in part explained by the possibility of finding up to four alleles per locus in an F_1 (compared to a maximum of three in a backcross), but in part also by the intentional selection of putatively heterozygous markers for mapping disease resistance genes (see Barone et al. 1990; Ritter et al. 1991).

Out of 239 molecular probes so far tested in either of the two populations, 189 (78%) mapped at a single locus and 50 (22%) at two or more loci. The percentage of single loci, however, is likely to be overestimated because in several cases a probe, which showed polymorphism, detected additional monomorphic fragments which could not be analyzed. They could either be monomorphic parts of the segregating alleles or parts of independent, nonsegregating loci hybridizing to the same probe. The duplication of adjacent loci to other genomic positions, which suggests duplication of large chromosomal segments during evolution, was reported to occur rather frequently in maize (Helentjaris et al. 1988) and *Brassica* (Slocum et al. 1990). It was observed only once for the potato map: the two *rbcS* loci on chromosome II have conserved their linkage to two duplicated loci revealed by markers CP70 and GP176 [*rbcS-c, CP70 (b), GP176 (a)* within ca. 10 cM and *rbcS-2, CP70 (a), GP176 (b)* within ca. 15 cM].

Map position of the self-incompatibility locus

A cDNA clone, *Sr1* (Kaufmann et al. 1991), coding for one allele of the *S*-locus in potato was also hybridized to DNAs of the F1840 population. This locus was located on chromosome I and mapped without recombination with loci *CP100* and *GP128 (a)*. These two loci were 1.2 cM apart in $BC916^2$ and located in a proximal position with respect to *TG24*, from which they were separated by 12.8 and 11.6 cM, respectively. The position is indicated in Fig. 1. Also, the *S*-locus of *Lycopersicon peruvianum* has been mapped previously to the homoeologous chromosome I (see below) 11.1 cM proximal to *Idh-1* and distal to *Skdh-1* (Tanksley and Loaiza-Figueroa 1985). Both isoenzyme loci are grouped together with *TG24* in one of the distal ends of chromosome I in the potato/tomato map of Bonierbale et al. (1988). As indicated by the reference marker TG24, which was mapped in tomato and potato, the self-incompatibility locus therefore has a similar chromosomal position in *Lycopersicon* and *Solanum* species.

Alignment of homoeologous potato and tomato chromosomes

Based on a segregating progeny from an interspecific potato cross involving *S. phureja*, *S. tuberosum*, and *S. chacoense*, Bonierbale et al. (1988) have shown that the chromosomes of potato and tomato are largely homoeologous using tomato markers. By mapping 26 tomato markers of known chromosomal position in our potato maps and 38 potato markers in tomato, we have aligned the potato and tomato maps. The numbers given in Fig. 1 to potato chromosomes are in accordance with

Table 1. Chromosome numbering in potato and tomato

Tomato/potato chromosome number according to [a]	Linkage group number according to [b]
I	I
II	II
III	III
IV	XI
V	V
VI	VIII
VII	IX
VIII	VII
IX	VI
X	IV
XI	XII
XII	X

[a] Rick (1974); Bonierbale et al. (1988); this paper
[b] Gebhardt et al. (1989)

the genetic map of tomato (Rick 1974; Bonierbale et al. 1988). The reference markers of tomato (TG) and potato (GP, CP) mapping to homoeologous positions, as well as the previously mapped ribulose-bisphosphate carboxylase (small subunit) loci used as reference markers by Gebhardt et al. (1989), are indicated in Fig. 1. Chromosome numbers of the potato are now in accordance with the establishment nomenclature of the tomato (Table 1).

Overall, the order of the mapped potato and tomato markers on the potato and tomato RFLP maps agreed with each other when taking into account the known inversions of potato compared with tomato. The orientation of markers to each other was not completely unambiguous for only a limited number of markers. These were regions where markers were very close together or cosegregating in tomato. Specifically, these markers were CP116 and CP109 on chromosome II, TG22 and CP57 on chromosome IV, GP130 and TG16 on chromosome VIII, GP39 and TG18 on chromosome IX, GP125 and CP58 on chromosome XI, and TG68 and CP114 on chromosome XII. These regions might reflect parts of the genome in which the rate of recombination in potato is higher than in tomato. The addition of more markers in these regions in tomato and potato is in progress and might resolve these ambiguities. Furthermore, the map presented here is an expansion of the existing potato maps (Bonierbale et al. 1988; Gebhardt et al. 1989), and it therefore cannot be completely excluded that it reveals additional minor rearrangements between potato and tomato. These regions are at the moment subject to further investigations.

Out of 26 tomato markers, 3 mapped to duplicate loci in potato: TG20 (located on tomato chromosome VII) revealed two loci on potato chromosomes VII and II, TG43 (X) on X and IX, and TG105 (XI) on XI and IX (TG105 is also duplicated in tomato). Conversely, for 6 potato markers out of 38, additional loci were found in tomato: on chromosomes XI and V for CP58 (XI), on IX and I for GP94 (IX), on II and III for CP116 (II), on IV and V for GP180 (IV), on XI and IX for GP125 (XI), and on chromosomes IV, II, IX, and X for pC116 (IV). However, these cases should not be taken as proof that a duplicated locus in one species is present in only one copy in the other. In most cases where we have observed duplicated loci in potato or tomato, it was not possible to decide whether a duplication remained undetected due to absence of fragment segregation or whether the two species differed by gene copy numbers for some of the markers. However, an example for the existence of species-specific duplications is revealed by marker pC116. All restriction fragments detected by this probe segregated and mapped at a single locus in potato, whereas in tomato four independent loci were identified. Similar observations with respect to different copy numbers and mapping positions of homologous sequences in the two species were made by Bonierbale et al. (1988) and Ganal et al. (1991).

Of the 64 markers analyzed in potato and tomato, 3 did not map to homoeologous positions. The single-copy marker TG5 mapping to chromosome VII in tomato was assigned in both potato populations to chromosome II. TG5 gave one strong hybridization signal only in some potato genotypes and not in others (data not shown). This explains why Bonierbale et al. (1988) did not detect it in their potato cross. TG5 combines two features of a putative transposable element: the insertion/deletion phenotype and a variable genomic location in two homoeologous genomes. Two potato markers were assigned to different positions in tomato: GP102 of potato chromosome VI defined a locus on chromosome II in tomato. GP17, mapping at two loci on potato chromosomes V and VI [GP17 (b) was mapped only in F1840 and the locus is not reported in Fig. 1], was associated with tomato chromosomes X and XI. In conclusion, it can be stated that reciprocal RFLP mapping in potato and tomato revealed only a few structural differences between the two genomes.

Length of potato and tomato RFLP linkage maps

The potato RFLP map derived from the intraspecific cross BC916[2], if further saturated, could reach at its completion a total length of 1,200–1,300 cM. The total value of 1,034 cM obtained by mapping 304 RFLP loci is not much lower than that of the highly saturated RFLP map of tomato with 400 loci (>1,400 cM), and is very similar to the less saturated classical linkage map of this species, as based on morphological and isozyme markers (Tanksley and Mutschler 1990) (Table 2A). It should be pointed out that the tomato RFLP map was derived from an interspecific cross, due to the difficulties of ob-

Table 2. Comparison of chromosome and map lengths (given in Kosambi units) between potato and tomato maps (A) and as derived from homologous intervals in the potato crosses $BC916^2$ and F1840 (B)

A	Tomato		Potato	
Chromosome no.	Intraspecific (classical)[b]	Interspecific RFLP[a]	Intraspecific $BC916^2$ RFLP	Interspecific RFLP[c]
I	161	>186	127	63
II	74	166	76	46
III	111	105	62	47
IV	89	108	102	55
V	55	130	78	47
VI	113	115	83	59
VII	71	94	92	55
VIII	67	95	79	64
IX	62	104	97	50
X	132	105	49	53
XI	97	110	96	21
XII	31	102	93	46
Total	1,063	>1,420	1,034	606

B	Potato		
	$BC916^2$	F1840	$BC916^2$–F1840
I	116	61	55
II	51	59	−8
III	39	27	12
IV	101	58	43
V	50	49	1
VI	76	74	2
VII	70	67	3
VIII	55	39	16
IX	85	62	23
X	36	30	6
XI	69	27	42
XII	74	83	−9
Total	822	636	186

[a] As derived from a tomato framework map based on a total of 400 markers (Ganal et al., unpublished results)
[b] As derived from Tanksley and Mutschler (1990)
[c] As derived from Bonierbale et al. (1988)

taining intraspecific RFLP maps in this species. When the map derived from the intraspecific cross $BC916^2$ was compared to the potato map from an interspecific cross involving *S. phureja* and *S. chacoense*, in addition to *S. tuberosum*, a 65% increase ($P<0.001$, as judged from a paired *t*-test with sets of corresponding chromosomes) in map length was observed (1,034 versus 606 cM; Table 2A). Moreover, by summing up the differences between homologous intervals of $BC916^2$ and F1840, a significant ($P<0.05$) reduction of 23% in the map length of F1840 versus $BC916^2$ was also found (Table 2B). The reduction could be attributed specifically to a reduced frequency of recombination in P40, which was the interspecific hybrid staminate parent in the cross. This was shown by comparing homologous intervals between parent-specific alleles of crosses $BC916^2$ and F1840. Summing up 27 intervals of P16 and FP916 covering ca. 220 cM, no significant difference in recombination was found between the two *S. tuberosum* parents. When 20 homologous intervals of P40 and P18 were compared, a significant reduction of 14% in recombination ($P<0.05$, one-tailed, paired *t*-test) was found for P40 compared to P18 (the sum of the intervals was 302 cM for P18 and 259 cM for P40, with a difference of 43 cM).

The reduced map length of F1840 compared to $BC916^2$ was accounted for mainly by six chromosomes (I, III, IV, VIII, IX, and XI; Table 2B). Reasons for random variability of genetic distances between the same markers may be experimental, such as different population sizes, sampling and/or evaluation errors, or large standard errors of marker positions due to distorted segregation ratios (Bailey 1961; Kinzer et al. 1990). However, the differences in lengths observed in maps obtained for intra- and interspecific crosses can be clearly associated to a non-random reduction of the recombination frequency due to interspecific hybridity. Similar observations were made in tomato by Rick (1969) and in potato by Douches and Quiros (1988), with experiments based on a few map intervals. Such a reduction was even more pronounced in the map of Bonierbale et al. (1988) derived from intercrossing three *Solanum* species. The size of the reductions in recombination might also have been influenced by the fact that recombination frequencies were derived in the latter case and in P40 from male gametes. Sex-specific differences in recombination were reported in corn (Robertson 1984) and in tomato for introgressed material, but not for pure *L. esculentum* backcross lines used as controls (Rick 1969). Similarly, we did not observe significant differences in recombination rates averaged over 27 intervals between male and female gametes of the intraspecific backcross $BC916^2$. In contrast to the finding of reduced recombination, cytogenetic observations of tomato and potato indicate similar or even increased chiasmata frequencies in pollen meiosis of interspecific hybrids compared to their parents (Khush and Rick 1963; Singh et al. 1989).

The hypothesis that in interspecific crosses a reduced recombination in some parts of the genome is counteracted by an increase in others, which could not be ruled out by Rick (1969) by reason of the incomplete genome coverage with the markers tested, seems unlikely in the light of our results: these show that the total map length decreases when different species are involved in a cross. The alternative hypothesis, favored by Rick (1969), seems more likely: recombination itself may not be impaired, but recombinant gametes as such or their zygotes may be preferentially eliminated (see also the results on distorted segregation ratios).

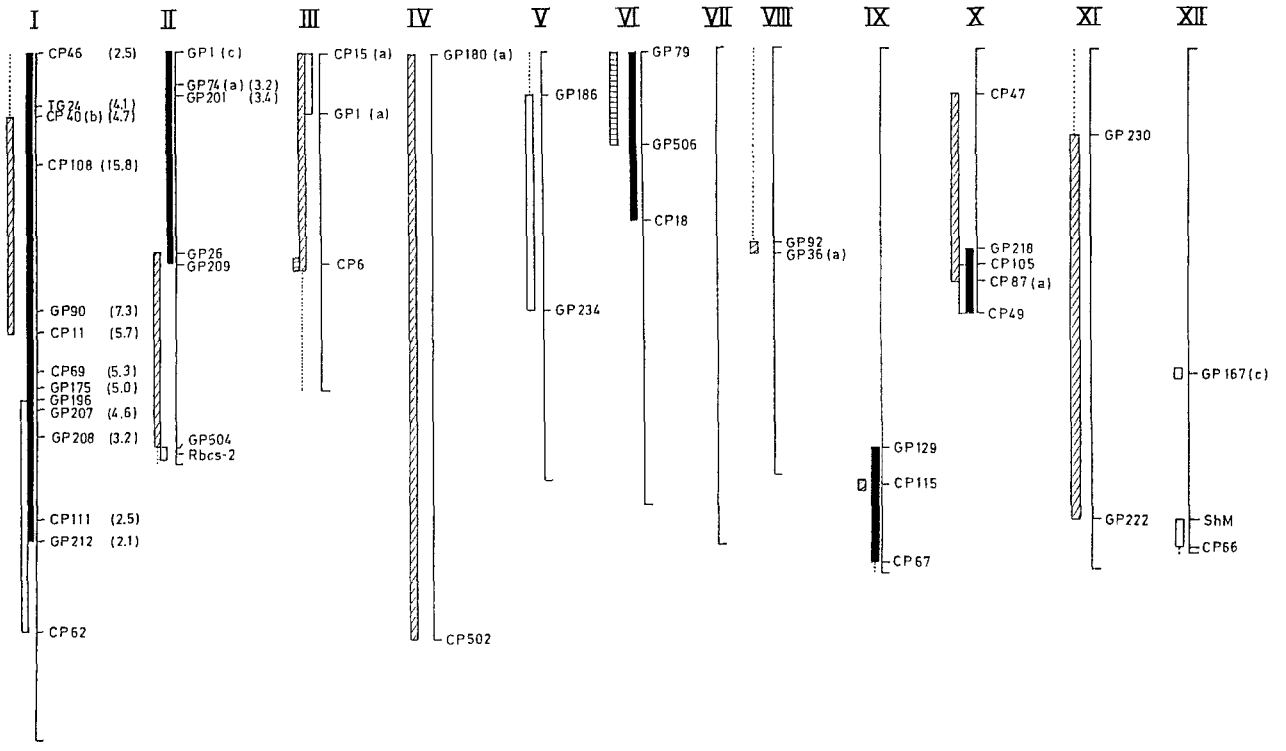

Fig. 2. Chromosomal distribution of regions with distorted segregation ratios in parents P16, FP916, P40, and P18 of map populations BC916[2] and F1840. Numbers in parentheses on chromosomes I and II are the observed segregation ratios for the preferentially transmitted allele. The map scale is derived from cross BC916[2]. The borders of the chromosomal regions with distorted segregation ratios are indicated by the bordering marker loci. Solid black bars: distortions descending from P16; open bars: aberrant segregation ratios descending from FP916; horizontally hatched bars: distortions descending from parent P18; diagonally hatched bars: aberrant segregation ratios descending from P40

Genomic distribution of distorted segregation ratios

In the backcross BC916[2], alleles at 82 loci (27%) segregated with distorted segregation ratios. Most of these loci were located on chromosomes I and II. The significance of the deviations from the expected ratios of 1:1 and 3:1, respectively (models A and B; see "Materials and methods"), was assessed with the χ^2 test. For cross F1840, aberrant segregations were found for 40 (40%) loci mapped. Most of the alleles with distorted segregation ratios could be attributed to P40, the interspecific hybrid between *S. tuberosum* ssp. *tuberosum* and *S. spegazzinii* (Barone et al. 1990). The interspecific parent P40 is therefore characterized not only by a decreased recombination, but also by a higher amount of distortions in transmission of its gametes. The distribution of loci with alleles segregating with abnormal ratios of the four parents P16, FP916, P18, and P40 was deducted from the inheritance of parent-specific alleles and is shown in Fig. 2. Chromosomal regions were found on chromosomes I, II, III, VI, IX, and X, for which alleles of two or three of the parental lines of the two crosses, BC916[2] and F1840, segregated with distorted ratios, although to a different extent.

With the exception of chromosome IX, the same chromosomes exhibited an anomalous transmission of markers in the experiment of Bonierbale et al. (1988). Additional regions with cross-specific, distorted segregation ratios were found for parent FP916 on chromosomes V and XII and for parent P40 on IV, VIII, and XI. The only chromosome not showing any distortions in both populations was chromosome VII. The degree of distortion of the segregation ratio 1:1 varied between 1.5:1 and 2.5:1 (for the preferentially transmitted allele). A higher degree of segregation distortion was found on the distal end of chromosome II for the closely linked loci *GP74(a)* and *GP201* (3.2:1 and 3.4:1). On chromosome I, parent P16 exhibited highly distorted segregation ratios, which increased from the distal end towards marker *CP108* (15.8:1) and then decreased towards marker *GP212* (Fig. 2). As P16 was the pollen parent in the backcross BC916[2], the distortions could be mostly explained as being induced by the self-incompatibility locus mapping very close to marker CP108 (Fig. 1). Similar observations, although not as pronounced as for P16, were made for P40, which was the pollen parent of the cross F1840. The self-incompatibility allele *Sr1* mapped in this cross was inherited from P18 and segregated with the expected 1:1 ratio.

Aberrant Mendelian segregation ratios are the result of selection processes taking place during sporogenesis, gametogenesis, fertilization, seed development, seed germination, and plant growth (Grant 1975). Until now, the genetic analysis of the phenomenon made use of morphological mutants and isozyme loci (Butler 1977; Zamir and Tadmor 1986; Gadish and Zamir 1987). The availability of dense RFLP maps provides a better knowledge about the detailed chromosomal distribution of groups of linked alleles transmitted with distorted ratios. This type of mapping might lead to the identification of genetic factors responsible for local aberrations. The presence of the self-incompatibility locus on chromosome I, for example, explains clearly one such group of loci with prominent Mendelian disturbances in their transmission. Structural chromosomal differences might be a second reason for skewed segregations. Such structural differences were reported for the 45 S ribosomal RNA locus in tomato, which has been mapped to the distal end of chromosome II (Vallejos et al. 1986; Bonierbale et al. 1988). The aberrant ratios observed for P16 in the homologous region on our potato maps might have been caused by the presence of this locus. Other more moderate and cross-specific distortions of segregation ratios could be the result of selection for or against particular allelic combinations, or the result of statistical effects due to the small population sizes. This will affect not only the transmission of particular chromosomes, but also the differential survival of recombinant gametes and zygotes, as indicated by reduced recombination frequencies. In fact, reduced recombination frequencies in cross F1840 versus BC916[2] coincided with extended regions of skewed segregation ratios observed for alleles of P40 on chromosomes I, III, IV, and XI but not on VIII and IX (Table 2B and Fig. 2; see also Rick 1969).

Conclusions

The results reported in this paper show that extensive RFLP mapping in potato has within a few years, filled in the gaps with respect to genetic information available for this species.

The genomes of potato and tomato are surprisingly similar. A relatively small number of genes, differences in gene copy number or DNA sequences not considered for RFLP analysis, such as highly repeated sequences, might be responsible for the distinct morphological differences between the two species.

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