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Recombination around the *Tm2a* and *Mi* resistance genes in different crosses of *Lycopersicon peruvianum*

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Abstract The amount of recombination in three different intraspecific crosses of the wild tomato species *Lycopersicon peruvianum* was investigated for the short arm of chromosome 6 that harbors the *Mi* nematode resistance gene and the centromeric region of chromosome 9 that contains the *Tm2a* virus resistance gene. These two genes have been introgressed into the cultivated tomato and are associated with a significant reduction in recombination in the respective region when crossed to other *L. esculentum* lines. For both regions and all crosses within *L. peruvianum* significantly more recombination (up to more than ten fold) was observed in the gametes derived from the female parent than in those from the male parent. In general, the differences were more pronounced for chromosome 6 than for chromosome 9. The amount of recombination in the three intraspecific *L. peruvianum* crosses was compared with the amount of recombination observed in the standard interspecific cross used for the construction of a saturated genetic map of tomato (*L. esculentum* × *L. pennellii*). In two of three cases for each region, more recombination was observed in the intraspecific crosses and in one case for each region significantly less recombination was found in the intraspecific cross when compared to the interspecific cross. Specifically for the *Mi*-carrying region, crosses within *L. peruvianum* exhibited up to 15-fold more recombination than crosses between resistant and susceptible *L. esculentum* lines, and such crosses will allow the fine mapping of this gene for the purpose of map-based cloning.

Key words RFLP mapping · Disease resistance · Plant breeding · Gametes · Tomato

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Introduction

Recombination in a given organism can vary considerably due to many factors. For example, it is known that the amount of recombination between marker loci can be increased or decreased by environmental factors such as temperature during gametogenesis. Furthermore, it has been shown that moderate doses of irradiation with X-rays or treatment with mutagenic chemical agents are able to increase the amount of recombination between marker loci. However, most frequently such differences have a genetic basis (Stadler 1926; Baker et al. 1976).

In many organisms, recombination during male and female gametogenesis occurs at different rates (Reeves 1990; Burt et al. 1991). For example, in humans and other mammalian species, the recombination rate during male gametogenesis is much lower than during female gametogenesis (Donis-Keller et al. 1987). In *Drosophila*, as an extreme case, no recombination at all is observed in male gametes. In plants, very little is known about different rates of recombination in male and female gametogenesis, and it has only been with the advent of genetic maps based on isoenzymes (Gadish and Zamir 1987) and restriction fragment length polymorphisms (RFLPs) that it has been possible to study this phenomenon in detail for many regions of a genome or even the entire genome. In tomato, data are now available that suggest a generally higher rate of recombination during female gametogenesis (de Vincente and Tanksley 1991; van Oijen et al., 1994). However, data from other plants such as potato and pearl millet suggest that this is not a general phenomenon (Busso et al. 1995; Gebhardt et al. 1991).

In some cases, it is known that the amount of recombination is controlled by specific genes. Again in *Drosophila*, it has been possible to breed strains with differing amounts of recombination for specific marker loci (Baker et al. 1976). The same has been found for certain plant species where specific genes affect recom-

bination. The genes with the most drastic effects in this context are the *ph* genes in hexaploid wheat that control the pairing of homeologous chromosomes and thus the occurrence of recombination between the different genomes.

Finally, it has been noted that interspecific hybrids often exhibit much less recombination than intraspecific hybrids. It is assumed that a lack of proper pairing during meiosis is the cause for this due to extensive differences in the DNA sequences between the two parents. This phenomenon is most pronounced in crosses between nearly isogenic lines of which one contains a segment from a distantly related species. In such cases, recombination can be highly suppressed (Rick 1969; 1972; Paterson et al. 1990). This situation is a major contributor to the phenomenon of 'linkage drag', which results in larger than expected segments being retained during backcross breeding (Young and Tanksley 1989). In tomato, examples for this are the *Mi* and the *Tm2a* genes that have been introgressed from the distantly related tomato species, *Lycopersicon peruvianum*. Here, a severely reduced amount of recombination over the entire introgressed region is observed in crosses between *L. esculentum* lines of which one carries the introgressed gene and the other does not (Messeguer et al. 1991). In the case of the *Tm2a* resistance gene, this results in a ratio of more than 4000 kb/cM for this region compared to the average ratio of approximately 700 kb/cM (Ganal et al. 1989).

In this study, we have investigated the amount of recombination in different crosses of the donor species of the *Tm2a* and *Mi* resistance genes, *L. peruvianum*, and compared these values among each other and with previously described genetic maps for these regions. Furthermore, these data allow conclusions to be drawn regarding the use of intraspecific crosses versus interspecific crosses for genetic mapping in tomato.

Material and methods

Plant material and segregating populations

All *Lycopersicon peruvianum* accessions used in this study were received from the USDA Genetic Resources Unit, Geneva, N.Y., USA. Crosses between *L. peruvianum* plants were performed without emasculation simply by applying pollen to the stigma. Table 1 gives a summary of the relevant data for each cross.

DNA extraction, blotting, and hybridization

DNA extraction, blotting and hybridization was performed as previously described (Bernatzky and Tanksley 1986; Messeguer et al. 1991; Tanksley et al. 1992). For the large populations, the published DNA extraction procedure was adapted to a smaller scale in the following way: 4–6 small leaves were harvested into an Eppendorf tube and directly homogenized in this tube using a fitting pistil on a mechanical drill. All further steps (chloroform extraction, precipitation) were performed directly in Eppendorf tubes. This procedure allows the extraction of 100–200 samples per day by a single person and yields approximately 10 µg DNA per sample, which is sufficient for digestions and analysis with two restriction enzymes.

RFLP markers

Most RFLP markers that were used in this study have been described in Tanksley et al. (1992). The hybridization probe for *Aps-1* was a cloned polymerase chain reaction (PCR) product derived with the primers described in Aarts et al. (1991). The probes CP 44 and GP 125 were kindly provided by C. Gebhardt (Gebhardt et al. 1991). The probes TG 415 and CT 119 were found during a screen of isogenic lines for *Mi* and *Tm2a*, respectively. RAPD 1 and 2 were isolated as polymorphic bands on isogenic lines carrying the *Mi* gene using the random amplified polymorphic DNA (RAPD) technique (Martin et al. 1991) and subsequently cloned.

Genetic mapping

Crosses from *L. peruvianum* (highly self-incompatible) are heterozygous for each parent and cannot be scored in precisely the same way as F_2 populations from inbreeding species such as the cultivated tomato. Usually for the purpose of this investigation clone/enzyme combinations were selected based on a survey with 6–12 restriction enzymes that resulted in three or four different alleles for the two parents taken together. Only these clone/enzyme combinations allow simultaneous mapping in both gametes (Ritter et al. 1990). The segregating bands were scored as presence and absence, and for each parent a separate map was constructed using the MAPMAKER program (Lander et al. 1987). All maps were constructed with a LOD threshold of > 3, and genetic distances were calculated in centiMorgans (cM) according to the Kosambi function of this program. Statistical analysis of the data was performed as previously described (de Vicente and Tanksley 1991).

Results

Genetic mapping of the *Mi* region on chromosome 6 in *Lycopersicon peruvianum*

Previous crosses used for the mapping of the *Mi* gene in tomato were between *L. esculentum* lines that contained an introgressed segment on chromosome 6 from *L.*

Table 1 Crosses analyzed for recombination on chromosome 6 and 9

Cross	Parents	Generation analyzed	Number of plants
128650	*L. peruvianum* PI 128650 × *L. peruvianum* PI 128650	F_1	324 plants
128650/128657	*L. peruvianum* PI 128650 × *L. peruvianum* PI 128657	F_1	177 plants
128660/128657	*L. peruvianum* PI 128660 × *L. peruvianum* PI 128657	F_2 (plant 4 × plant 1)	243 plants
128650/128660	*L. peruvianum* PI 128650 × *L. peruvianum* PI 128660	F_1	231 plants

peruvianum and *L. esculentum* lines that did not contain such a segment. When such crosses were compared to a standard interspecific cross in which the *Mi* gene was absent (*L. esculentum* × *L. pennellii*), a severe reduction in recombination between *L. esculentum* and *L. peruvianum* DNA was observed (Messeguer et al. 1991). Thus, we became interested in comparing the amount of recombination for the respective region obtained with this material to crosses within *L. peruvianum*.

The first cross analyzed was an F_2 population derived from a cross of a plant of *L. peruvianum* PI 128660 with a plant from the accession PI 128657, which is the original donor of the *Mi* gene. Two cross-compatible F_1 plants from this cross were crossed with each other to generate an F_2 mapping population (cross 128660/128657). Maps from both the male and the female gametes were collinear with previously published maps (Messeguer et al. 1991; Tanksley et al. 1992). However, there was a drastic difference in the total genetic distance of the two maps. Whereas the total distance between TG 297 and TG 232 was 1.6 cM in the male gametes, in the female gametes, the distance was 10.8 cM, which is 6.75 times greater (Fig. 1). The reduction in recombination was not localized to a single interval but was rather equally distributed over the entire segment analyzed.

In order to determine whether this observation was a general feature of crosses within *L. peruvianum* for this region, we analyzed two other crosses in the same way for the short arm of chromosome 6 (albeit with some different markers due to the lack of useful polymorphism for some of the previously used markers). The second mapping cross was an F_1 population between two plants of the accession PI 128650 (cross 128650). In this cross, the difference between male and female gametes was comparable to the first set of data. In the map derived from the female gametes, the total distance between TG 297 and *Aps-1* (as the most distal markers investigated) was 20.5 cM, whereas the map from the male gametes was only 4.2 cM, a 4.9-fold difference. As with the previous population, the reduction in recombination in the male is evenly spread over the entire region.

The third cross investigated, an F_1 population derived from a cross between an individual of PI 128650 with one of PI 128657 (cross 128650/128657), displayed an even more pronounced ratio for the short arm of chromosome 6. In the female parent, the total distance between CT 216 and *Aps-1* was 25 cM, while the total distance in the male parent was only 2.4 cM, a 10.4-fold difference. On the basis of the number of plants investigated the difference between male and female recombination are highly significant in all crosses ($P < 0.01$).

Comparisons with other crosses

It has been suggested that interspecific crosses generally display a significantly reduced amount of recombination compared to intraspecific crosses. To investigate this, we compared the maps derived from these intraspecific crosses with the data from our standard mapping population, which is an F_2 from an interspecific cross between *L. esculentum* and the distantly related species *L. pennellii* (Tanksley et al. 1992). This F_2 mapping population is of a relatively small size (67 F_2 individuals), but as far as comparable, does not show any significant differences in recombination percentage with a similar population of 400 plants (de Vincente and Tanksley 1991, 1993). For an accurate comparison, the data from the male and female gametes in the *L. peruvianum* crosses had to be combined and divided by 2 since it is not possible to discriminate recombination for male and female gametes in the *L. esculentum* × *L. pennellii* F_2 population. The results from this study are shown in Table 2. The *L. peruvianum* crosses 128650/128657 (1.43-fold) and 128650 (1.46-fold) showed higher recombination over the entire region analyzed than the *L. esculentum* × *L. pennellii* cross; in contrast the cross 128660/128657 resulted in a 1.85-fold lower recombination rate than the *L. esculentum* × *L. pennellii* cross. All crosses within *L. peruvianum* displayed a much higher level of recombination than crosses between *L. esculentum* lines, of which one of the latter carries the introgressed *Mi* gene and the other not (Fig. 1). In such interspecific crosses, this region of chromosome 6 shows a much reduced level of recombination (0.8 cM in total) (Messeguer et al. 1991; Ho et al. 1992). This is approximately 10- to 15-fold less than observed for the *L. peruvianum* crosses used in this study.

Genetic mapping of the centromeric region of chromosome 9 containing the *Tm2a* gene

Results for recombination on the short arm of chromosome 6 were compared to another region of the genome that contains the *Tm2a* virus resistance gene, which has also been introgressed from *L. peruvianum*. Due to lack of polymorphism (cross 128650), only two of the crosses studied above could be used. However, one additional F_1 population within *L. peruvianum* that was derived from the crossing of an individual from PI 128650 with one from PI 128660 (cross 128650/128660) that was available could be used instead. Figure 2 shows a comparison of the RFLP maps derived from the data of these three populations to the map derived from the interspecific control cross *L. esculentum* × *L. pennellii*. As for the short arm of chromosome 6, the alignment of markers was collinear with those of previously published maps for this region (Ganal et al. 1989; Tanksley et al. 1992). In this region, we can also observe differences in recombination derived from male and female gametes. However, the reduction in male gamete recombination was generally not as pronounced as for chromosome 6. In cross 128650, the total distance between the markers analyzed (CD 32 to TG 551) was found to be

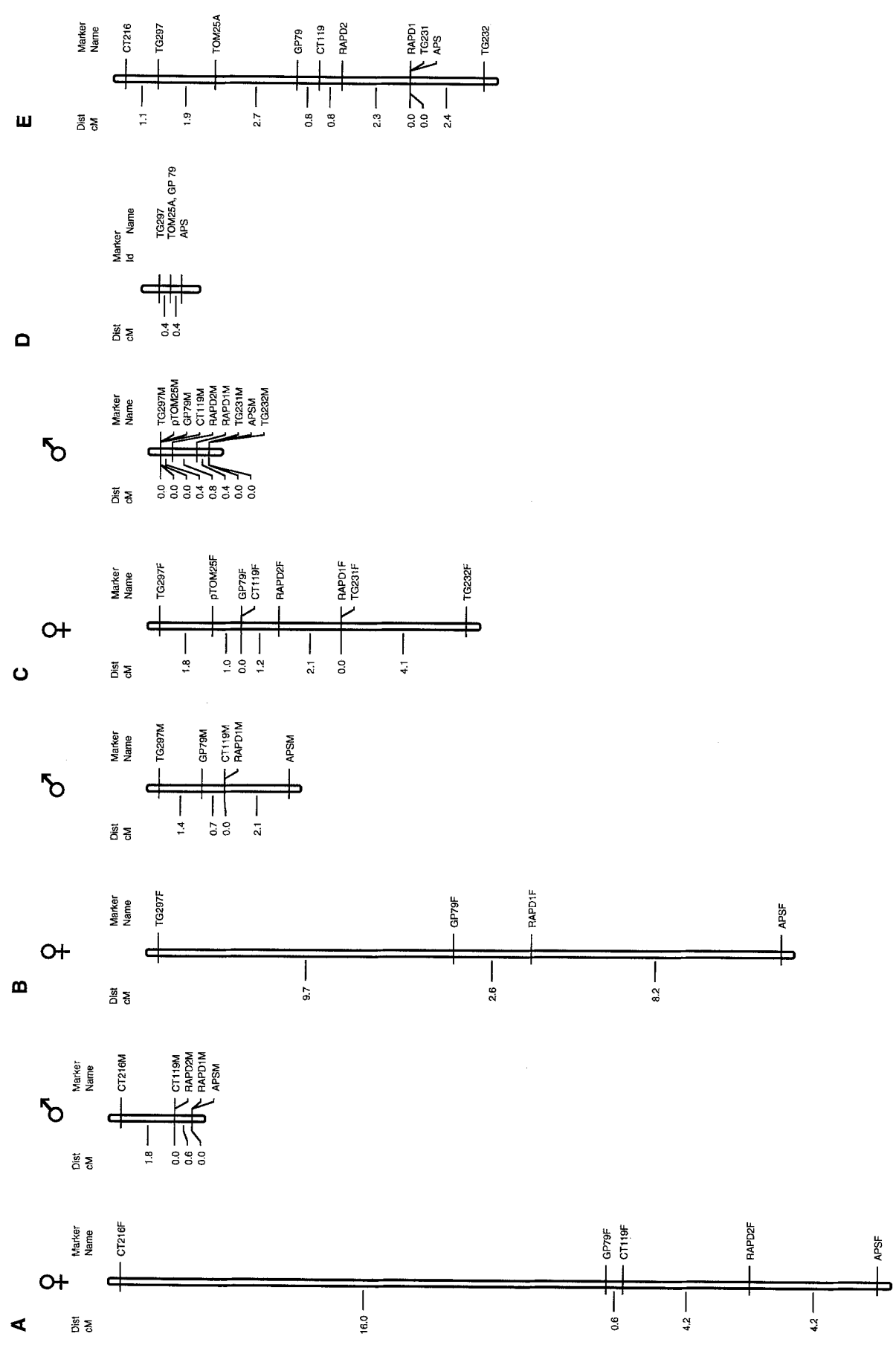
A
♀
Marker Name
CT216F
GP79F
CT119F
RAPD2F
APSF
Dist cM
16.0
0.6
4.2
4.2
♂
Marker Name
CT216M
CT119M
RAPD2M
RAPD1M
APSM
Dist cM
1.8
0.0
0.6
0.0
B
♀
Marker Name
TG297F
GP79F
RAPD1F
APSF
Dist cM
9.7
2.6
8.2
♂
Marker Name
TG297M
GP79M
CT119M
RAPD1M
APSM
Dist cM
1.4
0.7
0.0
2.1
C
♀
Marker Name
TG297F
pTOM25F
GP79F
CT119F
RAPD2F
RAPD1F
TG231F
TG232F
Dist cM
1.8
1.0
0.0
1.2
2.1
0.0
4.1
♂
Marker Name
TG297M
pTOM25M
GP79M
CT119M
RAPD2M
RAPD1M
TG231M
APSM
TG232M
Dist cM
0.0
0.0
0.0
0.4
0.8
0.4
0.0
0.0
D
Marker Id Name
TG297
TOM25A, GP 79
APS
Dist cM
0.4
0.4
E
Marker Name
CT216
TG297
TOM25A
GP79
CT119
RAPD2
RAPD1
TG231
APS
TG232
Dist cM
1.1
1.9
2.7
0.8
0.8
2.3
0.0
0.0
2.4

Fig. 1A–E Comparison of the different RFLP maps for the short arm of chromosome 6 of tomato. Maps drawn to scale are presented for the *L. peruvianum* cross 128650/128657 (**A**), cross 128650 (**B**), and cross 128660/128657 (**C**). The map derived from the female parent is always on the *left* (marker name labelled with *F*), and the map from the male parent (*M*) is on the *right*. For comparison, **D** shows the map derived from the cross *L. esculentum* cv 'Moneymaker' (*Mi* susceptible) × *L. esculentum* cv 'VFNT cherry' (*Mi* resistant) (Messeguer et al. 1991), and **E** shows the map derived from the cross *L. esculentum* cv 'TA 55' × *L. pennellii* LA716 (Tanksley et al. 1992). The *top* marker of each map is aligned to the standard map shown in **E**

30 cM for the female parent and 17.2 cM for the male parent, a 1.74-fold difference. For cross 128650/128657, a 1.77-fold reduction was observed for the male versus the female for the markers analyzed (CT32 to TG 390, female parent 13.5 cM versus male parent 7.8 cM). Both differences are highly significant ($P < 0.01$). In the third cross 128650/128660, a 1.21-fold reduction was observed for the region between CD 32 and CT 208 (female parent 8.1 cM versus male parent 6.7 cM). Interestingly, this population did not show the general reduction in recombination over the entire analyzed region as was observed for all other populations. Rather one interval (CD 32 to GP 125) was a little longer in the male parent than in the female parent, and the region between GP 125 and CT 208 did not show any recombination in the male parent. A *t*-test of the data revealed that the differences between male and female gametes for chromosome 9 of cross 128650/128660 were not highly significant ($P = 0.08$).

Comparison to an interspecific cross (*L. esculentum* × *L. pennellii*)

The comparison of the intraspecific maps from the *L. peruvianum* populations with the interspecific map derived from the *L. esculentum* × *L. pennellii* cross that contains all of the analyzed markers gave similar results as those found for chromosome 6 (Table 2). When analyzed in the same way as above, two of the intraspecific crosses 128660/128657 and 128650/128660 showed a higher amount of recombination than the interspecific cross (1.58-fold and 1.10-fold) while one (cross 128650/128657) showed a lower rate of recombination (1.66-fold).

Discussion

The data presented in this report give a detailed picture of recombination in two regions of the tomato genome (one on chromosome 6 and the other on chromosome 9) and allow a number of conclusions to be drawn. In both regions of the tomato genome, in the intra-specific *L. peruvianum* crosses, we observed an overall higher level of recombination in gametes derived from the female parent than in ones from the male parent. For the short arm of chromosome 6, male recombination was five- to ten-fold lower than female recombination. In the centromeric region of chromosome 9, recombination in the male gamete was also reduced with respect to that observed in female gametes (1.21- to 1.77-fold), in female. This reduction was less pronounced than on chromosome 6. These latter values are closer to those reported in

Table 2 Comparison of recombination frequencies in the different *L. peruvianum* crosses to the standard cross *L. esculentum* × *L. pennellii*

	L. esculentum × *L. pennellii*	Cross 128650	Cross 128650/128657	Cross 128660/128657	Cross 128650/128660
A) Chromosome 6:					
CT 216 to *Aps-1*	9.6 cM		25 cM female 2.4 cM male 13.7 cM (comb.)		
TG 297 to *Aps-1*	8.5 cM	20.5 cM female 4.2 cM male 12.4 cM (comb.)[a]			
TG 297 to TG 232	10.9 cM			10.2 cM female 1.6 cM male 5.9 cM (comb.)	
B) Chromosome 9:					
CT 32 to TG 390	17.8 cM		13.5 cM female 7.8 cM male 10.7 cM (comb.)		
CD 32 to TG 551	14.9 cM			30 cM female 17.2 cM male 23.6 cM (comb.)	
CD 32 to CT 208	6.7 cM				8.1 cM female 6.7 cM male 7.4 cM (comb.)

[a] Comb. = (female distance + male distance)/2

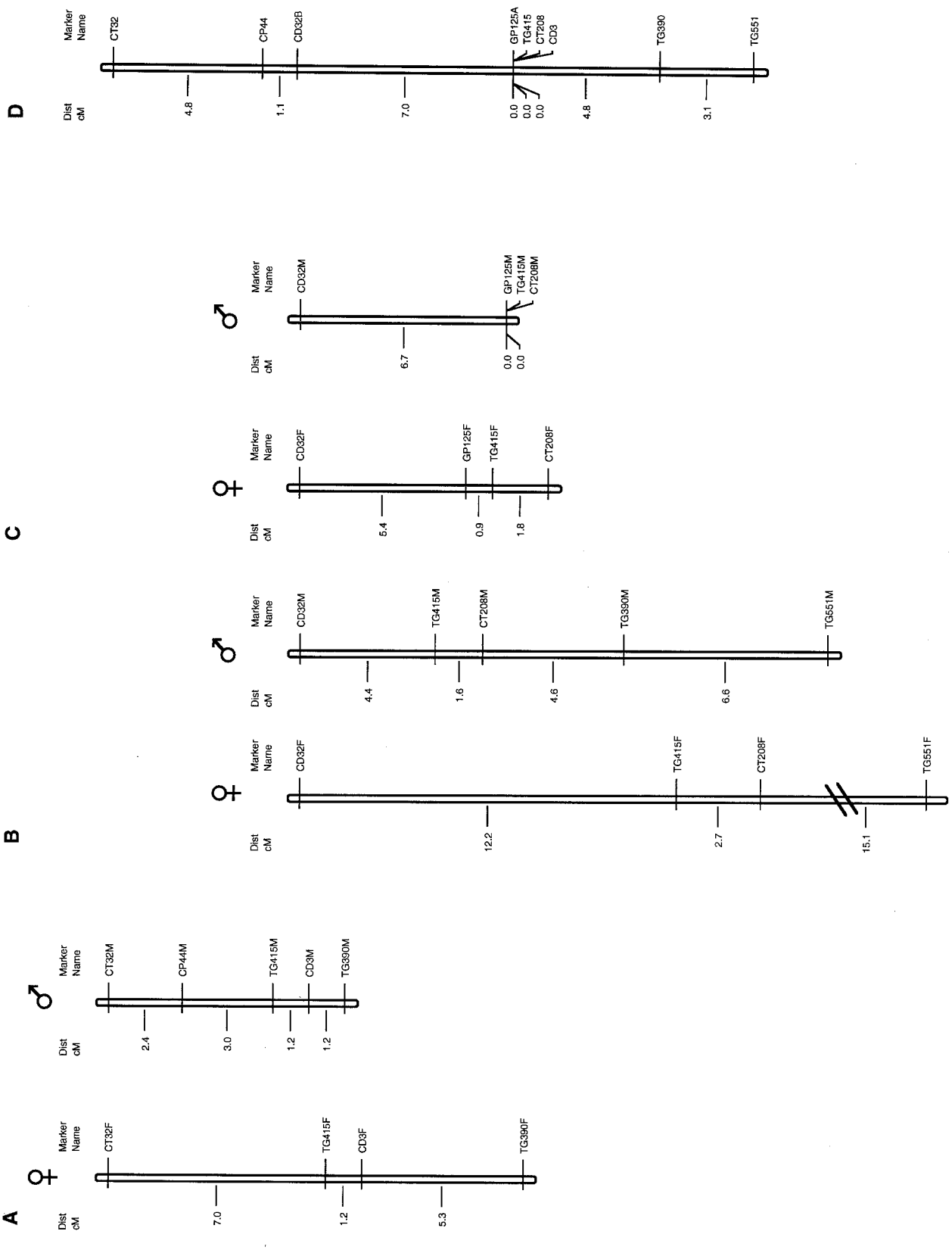
A
♀
Marker Name
CT32F
TG415F
CD3F
TG390F
Dist cM
7.0
1.2
5.3
B
♂
Marker Name
CT32M
CP44M
TG415M
CD3M
TG390M
Dist cM
2.4
3.0
1.2
1.2
C
♀
Marker Name
CD32F
TG415F
CT208F
TG551F
Dist cM
12.2
2.7
15.1
♂
Marker Name
CD32M
TG415M
CT208M
TG390M
TG551M
Dist cM
4.4
1.6
4.6
6.6
♀
Marker Name
CD32F
GP125F
TG415F
CT208F
Dist cM
5.4
0.9
1.8
♂
Marker Name
CD32M
GP125M
TG415M
CT208M
Dist cM
6.7
0.0
0.0
D
Marker Name
CT32
CP44
CD32B
GP125A
TG415
CT208
CD3
TG390
TG551
Dist cM
4.8
1.1
7.0
0.0
0.0
0.0
4.8
3.1

Fig. 2A–D Comparison of the different RFLP maps for the centromeric region of chromosome 9 of tomato. Maps drawn to scale are shown for the *L. peruvianum* cross 128650/128657 (**A**), cross 128660/128657 (**B**), and cross 128650/128660 (**C**). The map derived from the female parent is always on the *left* (marker name labelled with *F*), and the map from the male parent (*M*) is on the *right*. **D** shows the map derived from the standard cross *L. esculentum* cv 'TA 55' × *L. pennellii* LA716 (Tanksley et al. 1992). The *top* marker of each map is aligned to the standard map

studies with isozymes (Gadish and Zamir 1987) and RFLP markers (de Vicente and Tanksley 1991; van Oijen et al. 1994). The data presented by de Vicente and Tanksley (1991) regarding the use of an *L. esculentum/L. pennellii* hybrid as either the male or female parent show that over the entire genome there is an 1.18-fold difference in the genetic distance in maps derived from male and female gametes. A precise comparison of these data with the results presented in this study is, however, not possible for the short arm of chromosome 6 because no markers on this arm were used in the earlier study. With respect to the segment of chromosome 9, the two markers CD 32 and TG 390 were used in both studies, and comparable results were found. The genetic distance in female gametes of the *L. esculentum/L. pennellii* hybrid was calculated to be 15.8 cM compared to 4.5 cM in the male gametes (de Vicente and Tanksley 1991) and results in a 3.5-fold difference, which are even higher than what were found in the present study. The data of van Oijen et al. (1994), which are more comparable to the data from this study, were derived from reciprocal crosses between two *L. peruvianum* accessions. This study covered almost the entire tomato genome and female gametes displayed a 1.18-fold higher recombination than male gametes. As in the studies of de Vicente and Tanksley, (1991) however, the short arm of chromosome 6 was not covered, and no common markers were used for chromosome 9. Thus, direct comparisons are not possible. Nevertheless, the data show that in several different crosses of tomato, there is usually more recombination during female gametogenesis (van Oijen et al. 1994).

It is interesting to note that statistical analysis of the allele frequencies of male and female alleles of our studies indicate that there is no statistically significant deviation from a 1:1 segregation ratio ($P > 0.05$). Thus, gametophytic selection probably does not explain the fact that there is more recombination during female gametogenesis. Similar results have been described for other tomato crosses (Gadish and Zamir 1986).

The comparison of genetic distances in centiMorgans derived from intraspecific crosses with a standard interspecific cross (*L. esculentum* × *L. pennellii*) shows that it is not generally possible to state that intraspecific crosses have more recombination than interspecific crosses. For the regions on both chromosome 6 and chromosome 9, two of the three intraspecific crosses showed slightly more recombination (1.43 and 1.46-fold for chromosome 6 and 1.58 and 1.10-fold for chromosome 9) than the interspecific cross, but in both cases one intraspecific cross showed less recombination (1.85-fold for chromosome 6 and 1.66-fold for chromosome 9) than the interspecific cross *L. esculentum* × *L. pennellii*. Previous studies have shown that some other interspecific crosses, such as *L. esculentum* × *L. chmielewskii*, exhibit a significantly reduced level of recombination compared to *L. esculentum* × *L. pennellii* (Paterson et al. 1988), while again others have a similar level of recombination (*L. esculentum* × *L. cheesmanii*) (Paterson et al. 1991). There is certainly a tendency towards more recombination in intraspecific crosses, probably due to better chromosome pairing, but this has to be tested on a case by case basis. This is especially true in crosses within *L. peruvianum* where it appears to be important to analyze more than a single cross because the amount of recombination differs as much as three-fold in the crosses analyzed in this study. Recent data from additional crosses within *L. peruvianum* for the purpose of fine mapping disease resistance genes clearly indicate that the variation in recombination might be even more pronounced in different crosses (Ganal et al., unpublished results).

Finally, this study has implications for experiments such as the map-based cloning of genes in tomato that have been introgressed from distantly related wild species. For example, for the *Mi* gene on chromosome 6 it has been shown that crosses between *L. esculentum* lines that contain an introgressed *Mi* gene and lines that do not exhibit a much reduced level of recombination (Messeguer et al. 1990, Ho et al. 1992) in this region and that they can not be used for fine mapping this gene to a resolution that is necessary for map-based cloning (Tanksley et al. 1995). In this case, crosses within *L. peruvianum* offer a useful alternative for fine mapping since they do not show reduced recombination. A comparison of the data published in Messeguer et al. (1990) for the F_2 analysis of *L. esculentum* cv 'Moneymaker' (*Mi*-susceptible) × *L. esculentum* cv 'VFNT cherry' (*Mi*-resistant), which showed a distance between the markers TG 297 to *Aps-1* of 0.8 cM, with the data shown here (e.g. 12.4 cM for cross 128650) results in a more than 15-fold difference. With respect to fine mapping of the *Mi* gene, this means that the genetic analysis of 1000 plants from an *L. peruvianum* cross produces the same amount of recombinants as the analysis of 15 000 plants of a cross between a *Mi*-susceptible and *Mi*-resistant line. Recent data have shown that it is indeed possible to use populations of 1000–3000 plants derived from *L. peruvianum* crosses for a fine mapping of both the *Mi* and *Tm2a* gene that should be sufficient in resolution for map-based cloning (Ganal et al. unpublished results; Pillen et al., in preparation).

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