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Tomato chromosome 6: a high resolution map of the long arm and construction of a composite integrated marker-order map

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Abstract Integration of molecular and classical genetic maps is an essential requirement for marker-assisted breeding, quantitative trait locus mapping and map-based cloning. With respects to tomato, such maps are only available for the top part of chromosome 1, for chromosome 3 and for the short arm and the centromere proximal part of the long arm of chromosome 6. Employing an *L. esculentum* line carrying an *L. hirsutum* introgression we constructed an integrated linkage map for the telomere proximal part of the long arm of tomato chromosome 6, thereby completing the integrated map published previously. With an average map distance of only 0.6 cM the map provides detailed information on the relative position of molecular markers and several traits of economical importance, such as the fruit color marker *B*. Furthermore, two additional crosses using lines containing *L. pennellii* introgressions were performed to address the question as to how the recombination frequency in a marked interval on the long arm of chromosome 6 is affected by introgressed segments from different origins. It is concluded that recombination is not merely affected by the local level of homology but also by surrounding sequences. Combination of all the linkage data generated in various crosses described in this and other studies enabled the construction of the first integrated map of an entire tomato chromosome. This map carries 42 loci and shows the position of 15 classical genes relative to 59 molecular markers.

Key words Genetic linkage map · *Lycopersicon esculentum* · Fruit colour · Marker order map · Recombination

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Introduction

Marker-assisted breeding, quantitative trait locus (QTL) mapping and map-based cloning require the availability of an accurate genetic linkage map showing the position of the trait of interest relative to molecular markers. In tomato, virtually all morphological markers have been mapped in intraspecific *L. esculentum* crosses. On the other hand, because of the low level of sequence polymorphism within the species *L. esculentum* (Miller and Tanksley 1990; Van der Beek et al. 1992), map positions of molecular markers had to be determined in an *L. esculentum* × *L. pennellii* cross (Tanksley et al. 1992). As the distribution of recombination events differs largely among these two types of crosses, the respective maps are not compatible. Proper integration of the molecular and classical maps requires the mapping of both types of markers in the same segregating population. To date, this has been accomplished for the top part of chromosome 1 (Balint-Kurti et al. 1995), for chromosome 3 (Koornneef et al. 1993; Van der Biezen et al. 1994) and for chromosome 6 (Weide et al. 1993). With respect to the latter, simultaneous mapping of classical and molecular markers was conducted by employing a *L. esculentum* line (WSL6), containing an introgressed chromosome 6 from *L. pennellii*, in crosses to a variety of *L. esculentum* marker lines. Thus, an integrated map could be constructed that covered a large part of the chromosome. More recently, this map was extended with further details on the short arm and the position of the centromere (Van Wordragen et al. 1994). However, no integration could be achieved for the distal part of the long arm since the *L. pennellii* substitution in WSL6 did not cover this region.

The distal end of the long arm of chromosome 6 carries significant QTL effects for fruit weight, soluble solids content and seed weight (Paterson et al. 1988, 1990; Goldman et al. 1995) and several genes that affect the growth habit of the plant and the quality of the fruits, including *gibberelin-1* (*gib-1*), *potato leaf* (*c*), *self pruning* (*sp*) and *β-carotene* (*B*). In the (orange) fruits from plants with the *B* allele β-carotene accounts for up to 90% of the total carotene content; in red fruits (*bb*) this is only about 10% (Stevens and Rick 1986). As vitamin A, a principal nutrient of tomato, is directly related to the β-carotene content, the *B* locus is of obvious importance in breeding for nutritional value.

Thus far, information on the relative positions of these morphological markers on the molecular linkage map has remained very limited. *B* and *sp* have both been assigned to a 35 cM interval that is flanked by molecular markers (Paterson et al. 1988, 1990; Paran et al. 1995). Unlike *sp* that was mapped recently in more detail (Weide et al. 1993), the position of *B* relative to molecular markers has never been established at a higher resolution. A major obstacle in mapping *B* is that in a *L. pennellii* × *L. esculentum* cross, traits segregate that obscure the identification of the *B* phenotype, such as *r* (yellow flesh). As for *gib-1*, the most distal locus on the genetic linkage map of tomato chromosome 6 (Weide et al. 1993), there is also no information available on its position relative to molecular markers.

The significance of the telomere proximal section of chromosome 6 warranted the effort of a different approach to permit the inclusion of this section in the integrated linkage map. To this end we applied a *L. esculentum* introgression line (LA316) in which the distal part of chromosome 6 is replaced by the homoeologous region from *L. hirsutum*. By analysing segregating populations from crosses of this line with an *L. esculentum* tester line we were able to fill in the lacuna in the integrated linkage map. Analysis of these crosses also revealed severe suppression of recombination at the site of the introgressed DNA. Suppression of recombination is a problem often met in applying substitution or introgression lines (Rick et al. 1969; Messeguer et al. 1992; Paterson et al. 1988, 1990; Weide et al. 1993; Liharska et al. submitted). To gain more insight in this phenomenon we have conducted additional crosses using a line with an introgression comparable to that in LA316 but originating from a different source (*L. pennellii*). From these crosses, we conclude that suppression of recombination occurs irrespective of the origin of the introgressed DNA and is influenced by the nature of flanking chromosomal segments.

Finally, by combining all the linkage data for both the short and long arm generated by various crosses we have been able to construct a composite marker-order map covering the entire chromosome 6.

Material and methods

Plant material

The genotypes used in the present study are listed in Table 1.

The introgression line C6-4 (kindly provided by Y. Eshed and D. Zamir) is an individual from the BC1S2C3 generation described by Eshed and Zamir (1994) and Eshed et al. (1992). As this plant still segregated for *B* and *sp*, it was selfed and from the offspring IL6-3* was selected. This individual had the desired phenotypic characteristics (*B*, *sp*+) and also proved homozygous for the *L. pennellii* introgression on chromosome 6, as determined by molecular analysis using the marker TG548 and TG221. IL6-3* is thus comparable to the line IL6-3 described by Eshed and Zamir (1994).

Molecular probes

Molecular genetic linkage analysis was carried out using tomato genomic (TG-) clones developed by Tanksley et al. (1992).

DNA methodology

Plant DNA was isolated from leaves as described previously (Van der Beek et al. 1991). Probes were labelled with $\alpha[^{32}P]$ dATP using the random hexamer method (Feinberg and Vogelstein 1983). Hybridisation of Southern blots was performed as described (Klein-Lankhorst et al. 1991). All other DNA methodologies were carried out according to Sambrook et al. (1989).

Linkage analysis and map construction

To obtain populations segregating for both classical and molecular markers, we crossed LA316 to the *L. esculentum* line W602 ($n_{F_2} = 789$), and IL6-3* was crossed to both W602 ($n_{F_2} = 889$) and W605 ($n_{F_2} = 575$). Analysis of F_2 populations thus provided accurate linkage data for morphological markers in a genetic background suitable for molecular linkage analysis. F_2 plants from these crosses with a recombinant phenotype for the respective morphological

Table 1 Plant material

Code	Chromosome 6	Origin	Source/reference
LA316	*B*	TGC[a]	Tigchelaar and Tomes (1974); Rick (1988)
IL6-3*	*B*	$BC_1S_2BC_3$(M82 × LA716)	Eshed and Zamir (1994)
W602	*m-2, gib-1*	F_2(W335 × W606)	WAU[b]
W605	*yv, m-2, og, sp, c*	F_2(W606 × *og, sp* breeding line)	WAU
W6Dc-1	*c*	F_2(W606 × LA716)	WAU, Van Wordragen et al. (1994)

[a] Tomato Genetics Cooperative Seed Stock Center, Davis, Calif.
[b] Wageningen Agriculture University, Department of Genetics. Genotypes developed at the Department of Genetics of the Wageningen Agriculture University are indicated by the letter W prefixed to a number

markers were selected for restriction fragment length polymorphism (RFLP) linkage analysis. Estimates of recombination frequencies were calculated from F_2 data using the RECF2 programme that produces maximum likelihood estimates and standard errors (Koornneef and Stam 1992). Genetic maps were constructed employing the mapping program JOINMAP (Stam 1993). Statistical procedures used to calculate the relative distances between the markers have been described by Weide et al. (1993).

Results

Characterisation of the introgression line LA316

To permit mapping of both classical and molecular markers in the telomere proximal region of the long arm of chromosome 6, we have employed the line LA316. This line, originally selected as a *B*-carrying line from the second backcross generation of a *L. esculentum* Indiana Baltimore × *L. hirsutum* PI126445 interspecific cross (Tigchelaar and Tomes 1974; C. Rick personal communication), carries a *L. hirsutum*-derived introgression of unknown size at the distal part of the long arm of chromosome 6. The extent of the introgressed region in LA316 was determined by conducting molecular analysis employing markers already assigned to chromosome 6 (Tanksley et al. 1992). *Hirsutum/esculentum* polymorphisms were assessed by Southern analysis of genomic DNA from LA316, *L. esculentum* cv 'Moneymaker' and the *L. hirsutum* donor, PI126445, following digestion with a panel of ten restriction enzymes (Table 2). As for 'Moneymaker' and LA316, 20 out of 22 markers tested that map below TG253 were polymorphic. From marker TG444 upwards no polymorphisms were found between LA316 and 'Moneymaker', though differences between 'Moneymaker' and PI126445 were still detected. Therefore, the introgression probably starts between TG253 and TG444 and extends until TG221, the most distal marker on Tanksley's 1,000-marker map (Fig. 1). However, since sequence polymorphism was also detected between PI126445 and the *L. hirsutum* introgression in LA316, it was not possible to precisely delimit the centromere proximal border of the introgression in LA316.

Construction of an integrated map for the distal part of the long arm

In order to generate recombinants around *B*, we crossed LA316 (*B*) to the *L. esculentum* marker line W602, which

Table 2 Restriction fragment length polymorphisms between LA316, containing a *L. hirsutum* introgression, and *L. esculentum* cv 'Moneymaker'

TG-clone[a]	*Bam*HI[b]	*Bgl*II	*Bst*NI	*Dra*I	*Eco*RI	*Eco*RV	*Hae*III	*Hin*dIII	*Taq*I	*Xba*I
TG436	–	–	–	–	–	–	–	–	–	–
TG118	–	–	–	–	–	–	–	–	–	–
TG240	–	–	–	–	–	–	–	–	–	–
TG406	–	–	–	–	–	–	–	–	–	–
TG73	–	–	–	–	–	–	–	–	–	–
TG446	–	–	–	–	–	–	–	–	–	–
TG357	–	–	–	–	–	–	–	–	–	–
TG444	–	–	–	–	–	–	–	–	–	–
TG253	–	–	–	–	+	+	–	–	–	–
TG552	+	+	+	+	H	+	+	+	+	+
TG435	–	–	+	+	+	+	–	–	+	H
TG162	–	–	+	+	–	+	+	+	+	+
TG383	–	+	+	+	+	–	–	–	+	–
TG579	–	–	+	+	+	+	+	+	–	+
TG275	–	+	H	+	+	–	–	–	+	+
TG279	nd	nd	–	+	+	–	–	–	+	–
TG578	–	+	+	+	nd	–	+	–	–	+
TG548	+	+	+	+	–	+	+	+	+	+
TG477	–	nd	+	+	–	+	+	+	+	+
TG99	–	–	H	–	–	E	–	+	+	–
TG539	+	–	–	–	–	+	+	+	+	+
TG581	–	+	+	+	+	–	–	+	+	–
TG642	–	–	–	–	–	–	–	–	–	–
TG215	–	–	+	+	–	–	nd	nd	+	–
TG314	nd	+	nd	+	+	+	+	+	+	–
TG193	nd	+	nd	–	–	–	–	–	–	+
TG115	–	+	+	+	+	+	+	–	–	+
TG482	+	+	–	+	–	–	nd	–	+	–
TG220	–	–	–	–	–	–	–	–	–	–
TG221	–	+	+	+	–	+	–	+	+	+

[a] TG-clones are ordered according to their map-position

[b] Total genomic DNA from *L. esculentum* LA316 and *L. esculentum* cv 'Moneymaker' was digested with the restriction enzymes indicated and subjected to Southern analysis using the TG-clones listed as probes. –, No polymorphism; +, co-dominant polymorphism; H, dominant polymorphism, only *hirsutum* allele detected; E, dominant polymorphism, only *esculentum* allele detected; nd. no data

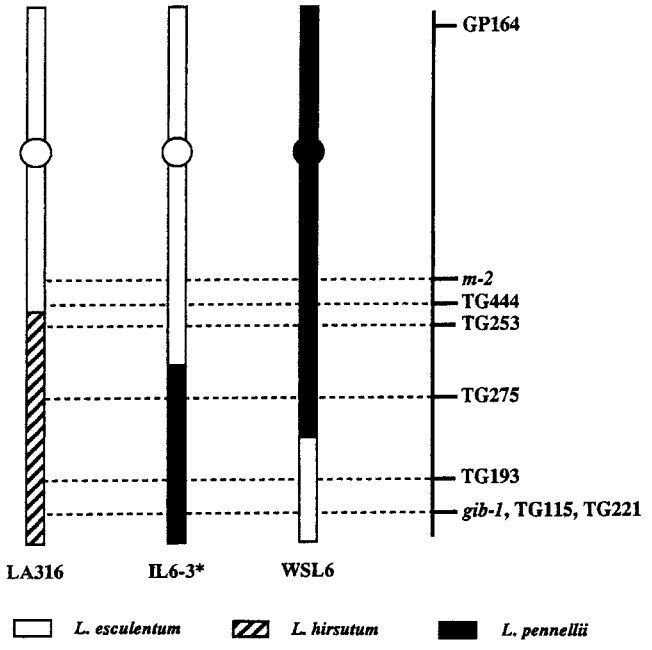


Fig 1 Genetic composition of chromosome 6 in introgression lines (described in the text). The introgressions are defined by the markers indicated on the *right*

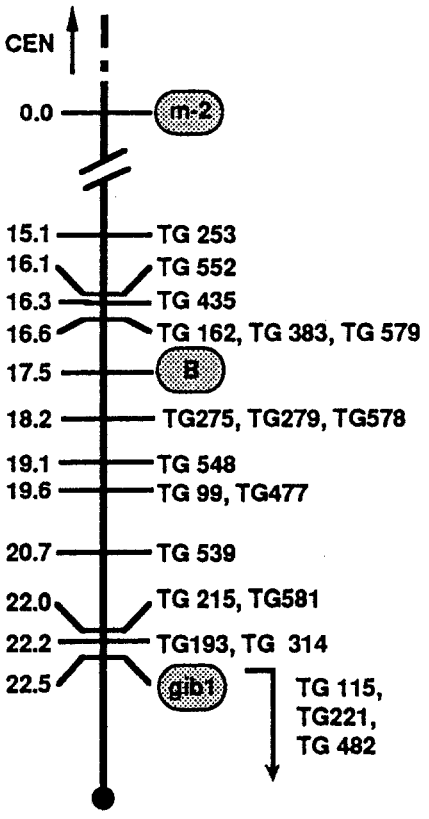


Fig 2 Integrated linkage map of the distal part of the long arm of tomato chromosome 6

carries the flanking markers *m-2* and *gib-1*. In a F_2 population of 789 individuals, 143 recombinants were identified that exhibited either the *m-2/gib-1*$^+$ or the *m-2*$^+$*/gib-1* phenotype (percentage recombination = 20.1 ± 1.6). In this subpopulation the fruit colour marker *B* was scored, resulting in a recombination percentage of 15.8 ± 1.4 for *m-2–B* and 3.5 ± 0.7 for *B* and *gib-1*.

Of the 129 recombinants subjected to molecular analysis, 93 had cross-overs between *m-2* and TG253, which is outside the *L. hirsutum* introgression, and were therefore not analysed further. The remaining 36 recombinants were used to construct the integrated linkage map as presented in Fig. 2. The map shows the relative positions of 3 morphological (*m-2*, *B* and *gib-1*) and 20 molecular markers. The fruit colour locus *B* is bordered by two clusters of markers: TG162, TG383 and TG579 proximal to the centromere and TG275, TG279 and TG578 on the opposite site. The gibberellin-deficiency locus *gib-1* is flanked on one site by TG193 and TG314. Three additional linked markers, TG115, TG221 and TG482, could not be resolved from this locus. Since recombinants were selected in the region above *gib-1*, these 3 markers can map at or below *gib-1*. On the other hand, several other markers previously found in three clusters (TG435/TG552, TG477/TG548 and TG215/TG314) (Tanksley et al. 1992) were clearly resolved in this cross, thus providing further map resolution. Since the *L. hirsutum* introgression did not encompass the region above TG253, the map in Fig. 2 displays a gap between this marker and *m-2*. This region has, however, been mapped in detail earlier (Weide et al. 1993).

In comparison to other maps published previously (Tanksley et al. 1992; Weide et al. 1993) the resolution of the present integrated map of the distal part of chromosome 6 is high. Within the introgressed region the average distance between the loci is 0.6 cM, with 20 molecular and 2 morphological markers mapping in a 7.4-cM interval.

Distribution of recombination along the long arm

The map deduced from the crosses involving the *L. hirsutum* introgression line LA316 showed that recombination in the *m-2–gib-1* interval (22.5 cM) was strongly reduced as compared to recombination in crosses employed in constructing both the classical map (34.4 cM; Weide et al. 1993) and the RFLP map (59.7 cM; Tanksley et al. 1992). Suppression of recombination in the region between *m-2* and *gib-1* was most pronounced in the interval TG275 to *gib-1* (threefold). To test whether this suppression depended on the origin of the introgressed wild germplasm, we also studied genetic distances in the *m-2–gib-1* interval using line IL6-3*, which carries an introgression from *L. pennellii* at a similar location as the introgression in LA316 (see Fig. 1). IL6-3* was crossed to chromosome 6 tester lines W602 and W605, and the F_2 progeny of these crosses was analysed for segregation of the morphological

markers *m-2*, *gib-1*, and *yv*, *m-2*, *c*, respectively. Between *m-2* and *gib-1* a recombination percentage of 27.7 ± 2.9 was found. Recombination between *yv* and *m-2* and between *m-2* and *c* was 32.4 ± 3.0% and 24.5 ± 2.6%, respectively. The linkage map calculated from the combined results from these crosses is shown in Fig. 3 together with additional linkage data gathered in this study and from the literature (see figure legend). If the classical map, which is based on intraspecific *L. esculentum* crosses, is taken as a reference it is obvious that in the IL6-3* crosses there is a strong suppression of recombination in the telomere proximal interval *c–gib-1*. Closer to the centromere (*yv–m-2* and *m-2–c*) the recombination frequencies are comparable to those derived from full intraspecific crosses. This is unlike the situation found in crosses that involved the chromosome 6 substitution line WSL6 (Weide et al. 1993), where suppression of recombination was restricted to the interval *yv–m-2*, but analogous to the LA316 cross. This indicates that the origin of the introgression did not influence the recombination rate. Remarkably, recombination between *m-2* and *c*/TG275 was similar in all of the crosses described in Fig. 3, irrespective of the presence of introgressed segments.

The complete marker-order map of tomato chromosome 6

In order to create a complete marker-order map of the entire tomato chromosome 6 we combined the data presented in this paper with the data published by Tanksley et al. (1992), Weide et al. (1993) and van Wordragen et al. (1994) (Fig. 4). Information on the relative position of the leaf morphology marker *c* was obtained from the analysis of the *c* deletion line W6Dc-1, which was hemizygous for this marker. This individual was identified in the F_1 offspring of *L. esculentum* W606 (*yv*, m-2, *c*) fertilised with irradiated *L. pennellii* (LA716) pollen (van Wordragen et al. 1994). Probing with molecular markers from the region of interest revealed that, in addition to *c*, the deletion encompassed 1 molecular marker, TG275.

The composite map in Fig. 4 displays the position of 15 classical genes, amongst which are morphological loci and isozyme and resistance genes, interspersed with a large number (59) of molecular markers. Also, the position of the centromere is indicated.

The only marker whose location does not follow unambiguosly from the four mentioned studies is *sp* (*self-pruning*). A map position of *sp* between *B* and TG275 was deduced from the following independent observations:

- the order *B*, *sp*, *c* has been determined very accurately by Ito and Currence (1974);
- *B* is between TG162 and TG275 (this report);
- *sp* is between TG162 and TG275 (Weide et al. 1993);
- *c* is below TG275 (Weide et al. 1993).

As the recombination frequencies of various marker pairs differ significantly among the component crosses used to construct the map, no genetic distances are indicated.

Discussion

In this report we present an integrated linkage map of the distal part of the long arm that carries the morphological loci *gib-1*, *B*, *c* and *sp*. In addition, we have

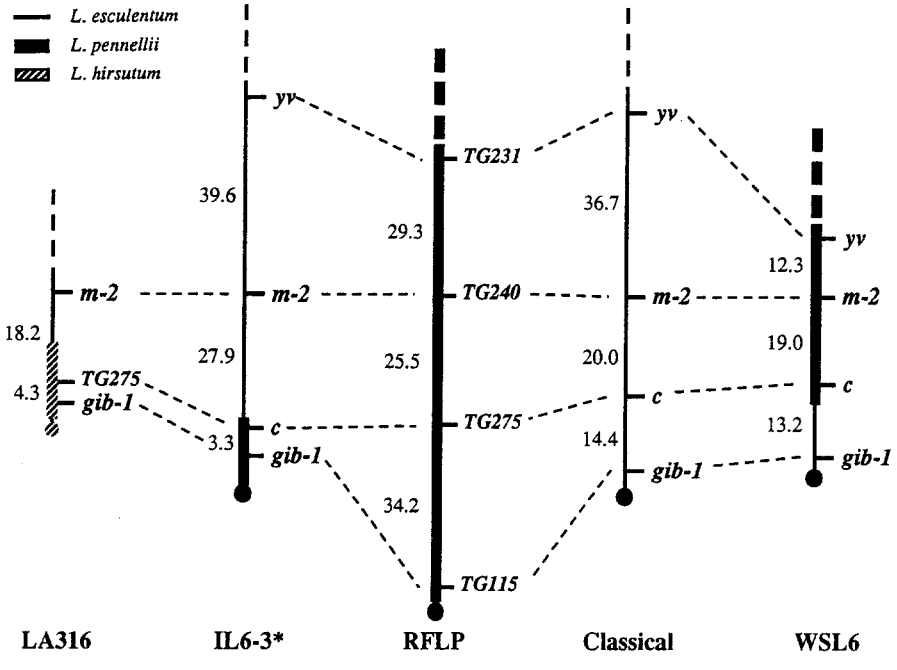
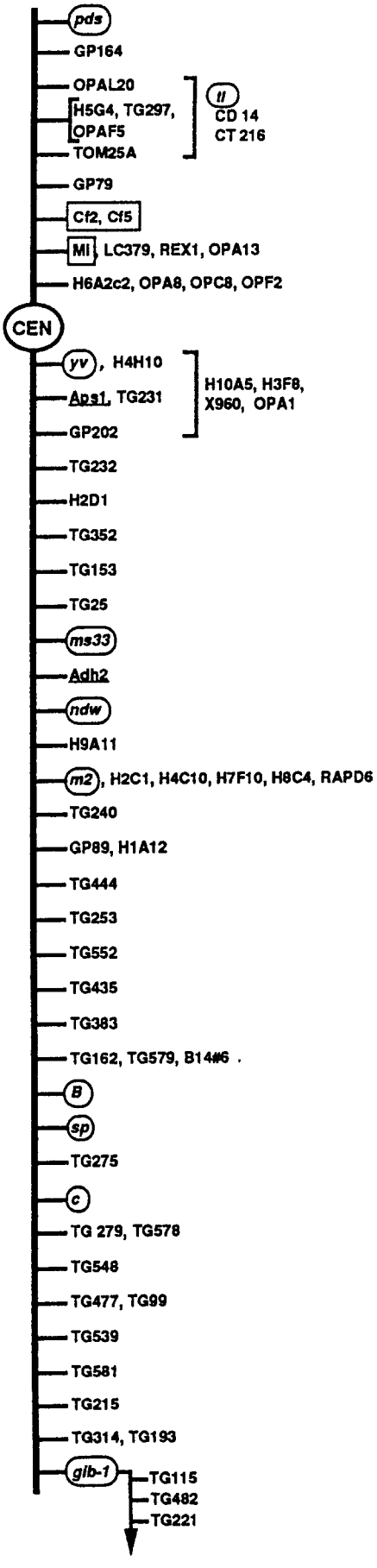


Fig 3 Schematic representation of the distribution on chromosome 6 in five different tomato crosses. *LA316*: map based on the cross LA316 × W602. *IL6-3**: combined map from the crosses IL6-3* × W602 and IL6-3* × W606. RFLP: molecular linkage map based on a full interspecific *L. esculentum* × *L. pennellii* cross (Tanksley et al. 1992). The indicated molecular markers cosegregate with, or are closely linked to, the corresponding morphological markers. *Classical*: map based on a variety of intraspecific crosses as presented in Weide et al. (1993). *WSL6*: map based on several crosses of *L. esculentum* marker lines to the chromosome 6 substitution line WSL6 (Weide et al. 1993). Figures are map units in centiMorgans



been able to construct a composite marker-order map of tomato chromosome 6, with many genes of economical importance now flanked by molecular markers. This map should serve in map-based cloning of chromosome 6 genes and marker-assisted breeding. The marker-order map encompasses 42 loci and shows a higher resolution than any linkage map previously published. In comparison, the RFLP map is comprised of 27 loci (Tanksley et al. 1992), whereas our previous version of the integrated map consists of 24 loci (Weide et al. 1993). For the first time linkage of molecular markers to the locus *gib-1* has been established. Furthermore, the map position of *B* and *c* is more precise than has been indicated in previous publications (Tanksley et al. 1992; Weide et al. 1993). The order of some markers deviates from the order published by Tanksley et al. (1992), with marker *B* now being positioned above TG275, TG115 below TG314 and TG193, and TG539 at a more telomere proximal position. Furthermore, several markers previously found to be clustered have been resolved.

When the linkage map for the distal part of the long arm based on the LA316 × W602 cross is compared to the map derived from the cross WSL6 × W606 (Weide et al. 1993), a remarkable discrepancy in map distances emerges. In the latter map, the distance between *c* and *gib-1* was 13.2 cM, which is 3 times the distance (4.3 cM) found for the comparable marker pair TG275–*gib-1* in the cross LA316 × W602. This difference may be attributed to the position of the respective introgressed regions, the *c*–*gib-1* interval is covered completely in LA316 and only partly in WSL6 (see Fig. 1). Thus, in the investigated region the overall homology to *L. esculentum* was less in LA316 than in WSL6, resulting in different recombination frequencies. However, it may be argued that LA316 and WSL6 are difficult to compare, since they contain introgressions from different origins. Therefore, more data concerning the phenomenon of recombination shrinkage were generated by analysing the crosses IL6-3* × W605. IL6-3* carries an *L. pennellii* introgression in the region that corresponds to the *L. hirsutum* introgression in LA316. Indeed, the distribution of recombination events along the chromosome was altered as expected; in the region of heterology, recombination was 3–4 times less than in the corresponding region in intraspecific crosses. However, in crosses involving IL6-3* or LA316 the respective recombination rates in this region were comparable, implying that the reduction of recombination does not depend on the origin of the introgressed region. On the other hand,

Fig. 4 Integrated marker-order map covering the complete tomato chromosome 6. *Encircled* morphological locus, *underlined* isozyme, *boxed* resistance gene. Information on map distances can be found in the individual linkage maps that were used to construct the map [this paper; Tanksley et al. (1992); Weide et al. (1993); van Wordragen et al. (1994)]

other data from our lab do indicate an effect of the source of the wild germplasm in such a way that suppression of recombination increases with increasing evolutionary distance of the donor of the introgressed segment to *L. esculentum* (Liharska et al. 1996). This is not necessarily contradictory to the results described here, since *L. pennellii* and *L. hirsutum* are at about equal evolutionary distances to *L. esculentum.* (Miller and Tanksley 1990).

Remarkably, recombination in the introgression line crosses was also reduced relative to that of the full interspecific *L. pennellii* × *L. esculentum* cross that served in constructing the RFLP map (Tanksley et al. 1992). Similar results were reported by Paterson et al. (1990). Analysis of a population of substitution lines revealed that recombination was markedly reduced in lines carrying heterozygous segments flanked by homozygous segments but not in a line in which a complete chromosome was substituted. Also, it is known that repeated backcrossing leads to a stronger suppression of recombination in the segments retained from the donor genome (Rick 1969), suggesting that recombination is not merely affected by the local level of homology but also by surrounding sequences, and to such an extent that recombination is strongly impeded at sites of regional low homology. Contradictory, in none of the crosses compared here did introgressed segments influence recombination in the central interval of the long arm flanked by *m-2* and *c*/TG275. This seems in accordance with the mechanism of chromosome pairing and synapsis, which start at the telomeres, whereas the last part of the tomato bivalents to synaps is the pericentromeric region (Stack and Anderson 1986). Non-efficient pairing could therefore have a larger effect on recombination in telomere and centromere proximal regions than in other, more neutral, parts of the chromosome.

A consequence of the divergent recombination patterns in crosses involving lines with various introgressions is that it will often be impossible to perform a statistically sound integration of linkage data derived from these crosses. On the other hand, mapping results from different crosses can be combined to constitute a marker-order map, as shown in this study. The absence of distances on such a map should not hinder its application, as genetic distances are always relative and therefore only pertinent to the cross they were derived from. The relative order of markers and, more specifically, the molecular markers flanking the gene or locus of interest is clearly of more practical importance. A marker-order map, as shown here for tomato chromosome 6, allows data from different origins to be combined to serve all researchers and breeders of *Lycopersicon* species, irrespective of the crosses involved.

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