Theor Appl Genet (2009) 118:927–935
DOI 10.1007/s00122-008-0950-9

ORIGINAL PAPER

A detailed synteny map of the eggplant genome based on conserved ortholog set II (COSII) markers

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Received: 9 October 2008 / Accepted: 8 December 2008 / Published online: 9 January 2009

Abstract We report herein the mapping of 115 PCR-based orthologous markers, including 110 conserved ortholog set or COSII markers, on the reference RFLP map of eggplant. The result permitted inference of a detailed syntenic relationship between the eggplant and tomato genomes. Further, the position of additional 522 COSII markers was inferred in the eggplant map via eggplant-tomato synteny, bringing the total number of markers in the eggplant genome to 869. Since divergence from their last common ancestor approximately 12 million years ago, the eggplant and tomato genomes have become differentiated by a minimum number of 24 inversions and 5 chromosomal translocations, as well as a number of single gene transpositions possibly triggered by transposable elements. Nevertheless, the two genomes share 37 conserved syntenic segments (CSSs) within which gene/marker order is well preserved. The high-resolution COSII synteny map described herein provides a platform for cross-reference of genetic and genomic information (including the tomato genome sequence) between eggplant and tomato and therefore will facilitate both applied and basic research in eggplant.

Communicated by M. Xu.

Electronic supplementary material The online version of this article (doi:10.1007/s00122-008-0950-9) contains supplementary material, which is available to authorized users.

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Introduction

Eggplant (mainly *Solanum melongena* L.) is a common fruit vegetable in Asia and Europe with world production of 21 million tons for year 2007 (http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567#ancor). It was domesticated in the Indo-Burma region, and was mentioned in some Sanskrit documents 300 BCE (Daunay and Janick 2007). In the past decades, efforts have been undertaken to collect and conserve eggplant germplasm in Asia, Europe and USA (Daunay et al. 1999, 2001). Eggplant breeding has focused on the yield, fruit quality, and adaptation to different climates and pests/diseases resistance (Daunay et al. 2001). Many of the morphological and agronomical traits important in eggplant are also shared by tomato, potato and pepper. In most cases, the genetics of these traits has been more thoroughly studied in these latter species (Daunay et al. 2001). Therefore, a genetic map of eggplant and comparative mapping relative to other solanaceous species should further facilitate genetic analyses and breeding studies in eggplant (Daunay et al. 2001; Doganlar et al. 2002a, b).

Eggplant is the third solanaceous species after pepper (Tanksley et al. 1988) and potato (Tanksley et al. 1992) that's been subject to comparative mapping relative to tomato. Doganlar et al. (2002a) developed an eggplant genetic map based on tomato-derived restriction fragment length polymorphism (RFLP) markers, which consisted of 12 linkage groups and spanned 1,480 cM. Comparison of the maps of eggplant and tomato revealed 23 paracentric inversions and 5 translocations. However, the map was based on RFLP markers, which are expensive and labor intensive—making it inaccessible to many researchers. To remedy this situation, we aimed to map a subset of PCR-based COSII markers onto the previously published eggplant map (Doganlar et al. 2002a). COSII markers represent

conserved, single copy genes in the families Solanaceae and Rubiaceae, and are anchored directly to the Arabidopsis genome (Wu et al. 2006). They are currently being mapped in a wide sample of species throughout these two families. Since they are PCR-based, they can be readily assayed on standard agarose gels—making them accessible to most breeders/geneticists in a broad range of research environments.

Materials and methods

Genetic mapping in eggplant

The mapping population was comprised of 58 F2 individuals from an interspecific cross between *S. linnaeanum* Hepper & Jaeger MM195 and *S. melongena* L. MM738, which was originally produced by Dr. M. C. Daunay at the Institut National de la Recherche Agronomique, France. Genomic DNA of the eggplant mapping population as well as the two mapping parents was provided by Drs. Anne Frary and Sami Doganlar at the Izmir Institute of Technology, Urla, Izmir Turkey. A set of 232 tomato-derived RFLP markers had been genotyped in the above population, and resulted in an eggplant genetic map of 12 linkage groups and a depiction of the syntenic relationship between the eggplant and tomato genomes (Doganlar et al. 2002a).

A total of 110 COSII markers, previously mapped in the tomato genome, and five tomato-derived markers—T0463, T1065, T1480, T1933 and U217183, where COSII markers were not available, were selected primarily in the regions with identified chromosome rearrangements between the genomes of eggplant and tomato (Doganlar et al. 2002a). Universal Primers of COSII markers (Wu et al. 2006), based on sequence alignments of orthologs from multiple solanaceous species, were used to amplify orthologous segments from the above two parents of the mapping population. If the previous COSII primers did not provide suitable polymorphic fragments for mapping in eggplant, a second primer pair was designed in a different region of the same sequence alignment using the method described in Wu et al. (2006). Amplicon size differences between the two parents were used to genotype the mapping population directly; otherwise single band amplicons were purified and sequenced. The amplicon sequences were then aligned and examined for polymorphisms using the program CAPSdesigner (http://www.sgn.cornell.edu/tools/caps_designer/caps_input.pl). Thereafter, the mapping population was genotyped via CAPS (Cleaved Amplified Polymorphic Sequence) assays (Konieczny and Ausubel 1993). In the cases where CAPS assays were not feasible, other SNPs (Single Nucleotide Polymorphisms) were exploited for mapping using dCAPS (derived Cleaved Amplified Polymorphic Sequence) assays designed by the program dCAPS (Neff et al. 1998, 2002).

For the five tomato-derived markers, primers were designed in the tomato EST/unigene sequences and used to amplify orthologous fragments from the two eggplant parents. Then the same method as that described above for COSII markers were used to genotype these markers in the eggplant mapping population. Information regarding all mapped COSII and tomato-derived markers in this work can be found in supplementary Table S1.

Subsequently the above 115 markers were combined with the original 232 markers for map construction using Mapmaker computer program (Lander et al. 1987). For the purpose of comparison with tomato, a modified framework (markers order at LOD > 3 by command "ripple") relative to that in Doganlar et al. (2002a) was prepared to include COSII markers. Only framework markers were used to calculate map distances by the Kosambi mapping function (Kosambi 1944). Additional markers were then positioned on the framework as interval markers by commands "try" and "ripple".

Genetic mapping in tomato

The tomato mapping population was an F2 population of 80 individuals derived from an interspecific cross *S. lycopersicum* LA925 × *S. pennellii* LA716 (Frary et al. 2005; Fulton et al. 2002). Currently, more than 2,500 markers have been mapped in this population of which 877 are COSII markers (Wu et al. 2006). For the purpose of comparison with eggplant, a modified tomato genetic map was prepared of which the framework is predominantly based on the COSII markers (supplementary Figure S1). The complete tomato map is available at Solanaceae Genomics Network (http://www.sgn.cornell.edu/cview/map.pl?map_id=9&show_offsets=1&show_ruler=1) and bulk download of all COSII marker information is available at SGN FTP site (ftp://ftp.sgn.cornell.edu/COSII).

Results

COSII marker polymorphism

Approximately 200 COSII markers were tested in both mapping parents—*S. linnaeanum* Hepper & Jaeger MM195 and *S. melongena* L. MM738. In six cases, the two parents had different amplicon sizes detectable on agarose gels (>30 bp) (supplementary Table S1); for another 104 cases, it was possible to design CAPS or dCAPS assays based on SNPs detected in the amplicon sequences of the two parents. The amplicon sequences were then aligned with the COSII consensus sequence used for primer design and thus confirmed the amplification of orthologous fragments.

A subset of 87 COSII markers in the latter category, which have a minimum of 200 bp sequenced exon and/or intron, was subject to further analysis (supplementary Table S2; sequences and sequence alignments are available at ftp://ftp.sgn.cornell.edu/COSII/eggplant_mapping). The intron positions of the COSII markers have been predicted previously based on comparison with the Arabidopsis orthologs (Wu et al. 2006). Analysis of these amplicon sequences further confirmed the conserved intron positions between the family Solanaceae and Arabidopsis. Not surprisingly, the average SNP frequency is significantly higher in intron (103 bp/SNP) than exon (180 bp/SNP). INDELs (Insertion-Deletions) were identified in 32 out of the 74 introns but only 1 out of 21 exons (supplementary Table S2). In addition, the most highly polymorphic markers distribute across the entire map (supplementary Table S2), therefore they can potentially be useful for breeders to assess germplasm collections.

Genetic map construction

We surveyed primarily COSII markers in the regions with identified chromosomal rearrangements (Doganlar et al. 2002a). About 110 of them gave usable polymorphisms for genetic mapping—including amplicon size differences, CAPS and dCAPS. These COSII markers, as well as five tomato-derived markers—T0463, T1065, T1480, T1933 and U217183, were then scored in the eggplant mapping population. The current eggplant genetic map contains 347 markers, of which 253 markers (73%) are ordered at LOD > 3 (Table 1). The remaining 94 markers were assigned into framework marker intervals at LOD < 3. The 12 linkage groups correspond to the 12 chromosomes in the haploid chromosome set of eggplant, ranging from 105 cM (E2) to 159 cM (E3). The entire map spans 1,535 cM, with an average density of one framework marker every 6.1 cM (Table 1; Fig. 1).

Syntenic relationships of the eggplant and tomato genomes

Although 232 tomato-derived RFLP markers were mapped and used for eggplant-tomato synteny map by Doganlar et al. (2002a), only a subset of 174 markers were mapped on the current tomato mapping population (Frary et al. 2005; Fulton et al. 2002) and thus were usable for eggplant-tomato comparisons in this current work. As a result, deductions concerning the syntenic relationships of the eggplant and tomato genomes were based on 110 COSII markers and 179 tomato-derived markers. Hereafter these 289 orthologous markers are referred to as "synteny markers".

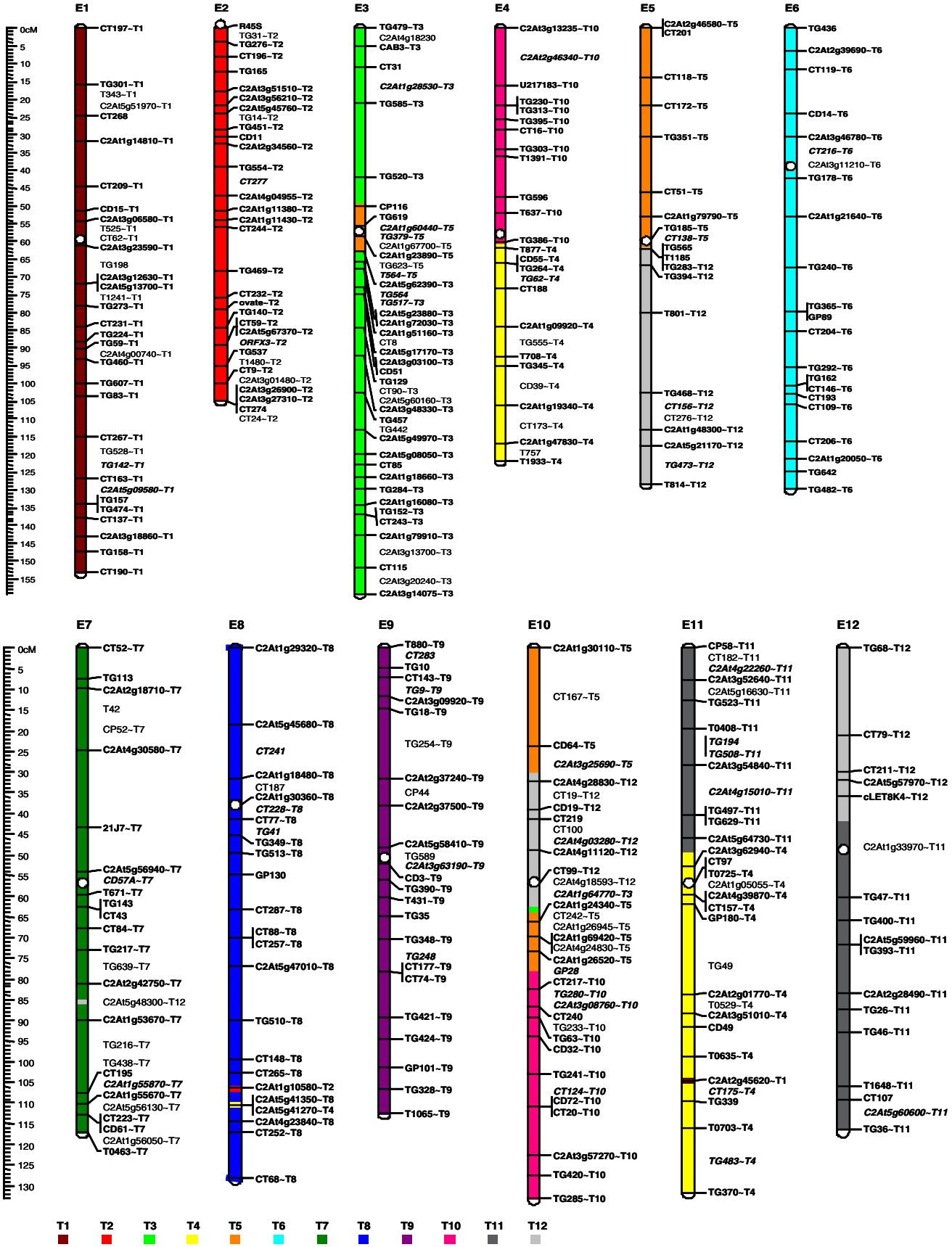
In this work, synteny marker pair (SMP) and CSS were used to assess the degree of synteny between eggplant and tomato. A SMP is defined as a pair of orthologous markers that are adjacent to each other in both genomes. To minimize erroneous results, we searched for SMPs only within the subset of synteny markers that had been mapped and ordered in both genomes with high confidence (LOD > 2). The resultant 123 SMPs were then coalesced into CSSs defined as shared blocks of genes/markers with preserved order between genomes (Nadeau and Taylor 1984). Markers ordered at LOD < 2 on either map were included in the analysis only in reference to interchromosomal translocations or a single gene transposition. The result was the identification of 37 CSSs shared between eggplant and tomato genomes (supplementary Figure S2). The CSSs ranged in size from 3 to 105 cM with an average size of 34 cM (cM value based on the eggplant map, Table 1). They covered from 57% (E11) to 98% (E9) of different eggplant linkage groups and totaled 1,241 cM corresponding to 81% of the eggplant map.

Table 1 Statistics of the eggplant genetic map and the eggplant-tomato comparative map

Eggplant linkage group	E1	E2	E3	E4	E5	E6	E7	E8	E9	E10	E11	E12	Sum
Map distance (cM)	153	105	159	122	128	130	117	128	112	133	132	116	1,535
Number of markers	35	33	44	27	21	22	28	25	27	35	33	17	347
Number of framework markers	25	26	28	21	17	20	18	21	20	20	22	15	253
Number of synteny markers	32	27	33	24	18	17	21	21	21	31	28	16	289
Number of COSII markers	9	11	21	5	4	5	10	9	5	14	12	5	110
Number of SMP[a]	17	10	10	11	10	8	5	13	13	10	10	6	123
Number of CSS[b]	3	5	2	3	2	3	2	2	2	6	3	4	37
Min./Max. length of CSS (cM)	38/57	7/33	15/89	15/61	59/62	11/71	4/70	10/105	35/75	3/30	12/38	15/42	–
Mean length of CSS (cM)	49	17	52	38	60	35	37	58	55	16	25	25	–
Number of translocations	0	0	1	1	1	0	0	0	0	2	1	1	–
Number of inversions	1	3	3+	3	0	2	1	0	1	5+	3	2	24+

[a] SMP synteny marker pair

[b] CSS conserved syntenic segment


E1
E2
E3
E4
E5
E6
E7
E8
E9
E10
E11
E12
T1 T2 T3 T4 T5 T6 T7 T8 T9 T10 T11 T12

◀ **Fig. 1** The genetic map of eggplant. Eggplant linkage groups are designated as E1–E12. Markers in *bold* and by *tick marks* are framework markers (LOD > 3); marker in *bold*, *italic* are interval markers with 2 ≤ LOD < 3; others are interval markers with LOD < 2; cosegregating markers are denoted by a *vertical bar*. "∼Tx" following the name of a marker indicates its chromosome location on the tomato map. Each tomato chromosome is assigned a different color (see color codes at the end of the figure) and the corresponding eggplant chromosome segment(s) are painted with the same color. Putative centromere position of each eggplant linkage group is based on eggplant-tomato synteny and indicated by a *white dot*

The syntenic relationships between eggplant and tomato are depicted with eggplant linkage groups and their homologous tomato chromosomes/segments side by side (Fig. 2 and supplementary Figure S2). The following discussion will focus on deciphering the chromosomal rearrangements that differentiate the genomes of eggplant and tomato, especially those in addition to, or different from, those reported in Doganlar et al. (2002a), which hereafter is referred to as 2002 map. To declare a disruption in synteny between the two genomes, two criteria had to be met. First, a structural difference was inferred only if two or more linked markers (in at least one genome) confirmed the rearrangement (an inversion involving one end synteny marker and one internal synteny marker was also accepted); Second, for inversions, the involved markers should be positioned at LOD ≥ 2 on both maps. This method is less likely to declare false-positive rearrangements, but may result in some rearrangements not being deciphered. For the purpose of comparison, we describe how the eggplant genome differs with respect to the tomato genome which is used as the standard of reference. However, we do not wish to imply that any of the discussed structural difference in eggplant are derived or ancestral, unless additional information can be brought to bear from a third genome (e.g. potato or pepper). For convenience, hereafter tomato chromosomes will be referred to as T1–T12 (Frary et al. 2005; Fulton et al. 2002), eggplant linkage groups as E1–E12 (Doganlar et al. 2002a). The syntenic relationship of each eggplant linkage group relative to that of tomato is discussed below.

E1 versus T1

An inversion (not in the 2002 map) was identified near the top of E1 and T1, and C2At2g45620 in T1 was mapped to E11, otherwise marker order and gene content are well preserved between E1 and T1. (Fig. 2 and S2)

E2 versus T2

Three inversions, instead of two in the 2002 map, differentiate E2 and T2. The upper inversion is derived in eggplant since pepper and tomato/potato share the same gene order; the larger, lower one must have occurred in tomato/potato lineage since eggplant agrees with pepper, while the smaller one (between TG140 and CT59) is derived in eggplant (Tanksley et al. 1992; Wu et al. submitted). The inversion in the 2002 map involving CT232 and the tomato fruit shape gene *ovate* was not observed in the current map, which may be due to mapping of CT232 at low confidence in the current tomato map. (Fig. 2 and S2)

E3 versus T3 and T5

E3 consists of the entire T3 (except for C2At1g64770 mapped to E10) and two small segments from T5. Two or more inversions differentiate E3 and T3. The two T5 segments, located near T5 top and T5 centromere respectively, were mapped close to each other on E3 and the marker order was further shuffled by at least one inversion. Interestingly in the pepper map, the two T5 segments were also mapped to one region (Wu et al., submitted), which suggested pepper and eggplant represented the ancestral condition, however, the non-reciprocal translocation is specific to eggplant. (Fig. 2 and S2)

E4 versus T4 and T10

E4 combines upper T10 and lower T4. Two T10 markers mapped in this work, C2At2g46340 and U217183, suggest three inversions between E4 and upper T10, which was missing in the 2002 map. On the other hand, both gene order and gene content are well conserved between lower E4 and lower T4. (Fig. 2 and S2)

E5 versus T5 and T12

E5 is comprised of lower T5 and lower T12. In both segments eggplant and tomato share conserved gene order and gene content. (Fig. 2 and S2)

E6 versus T6

In addition to the inversion near the top of E6 and T6, which was also identified in the 2002 map, a second inversion was revealed by two markers at the bottom of the two chromosomes. Otherwise the gene order and the gene content are well preserved. (Fig. 2 and S2)

E7 versus T7

The two inversions reported in the 2002 map could not be confirmed by the current map; instead, a new inversion was identified near the end of E7 and T7. Moreover, C2At5g48300 in T12 was mapped to E7. (Fig. 2 and S2)

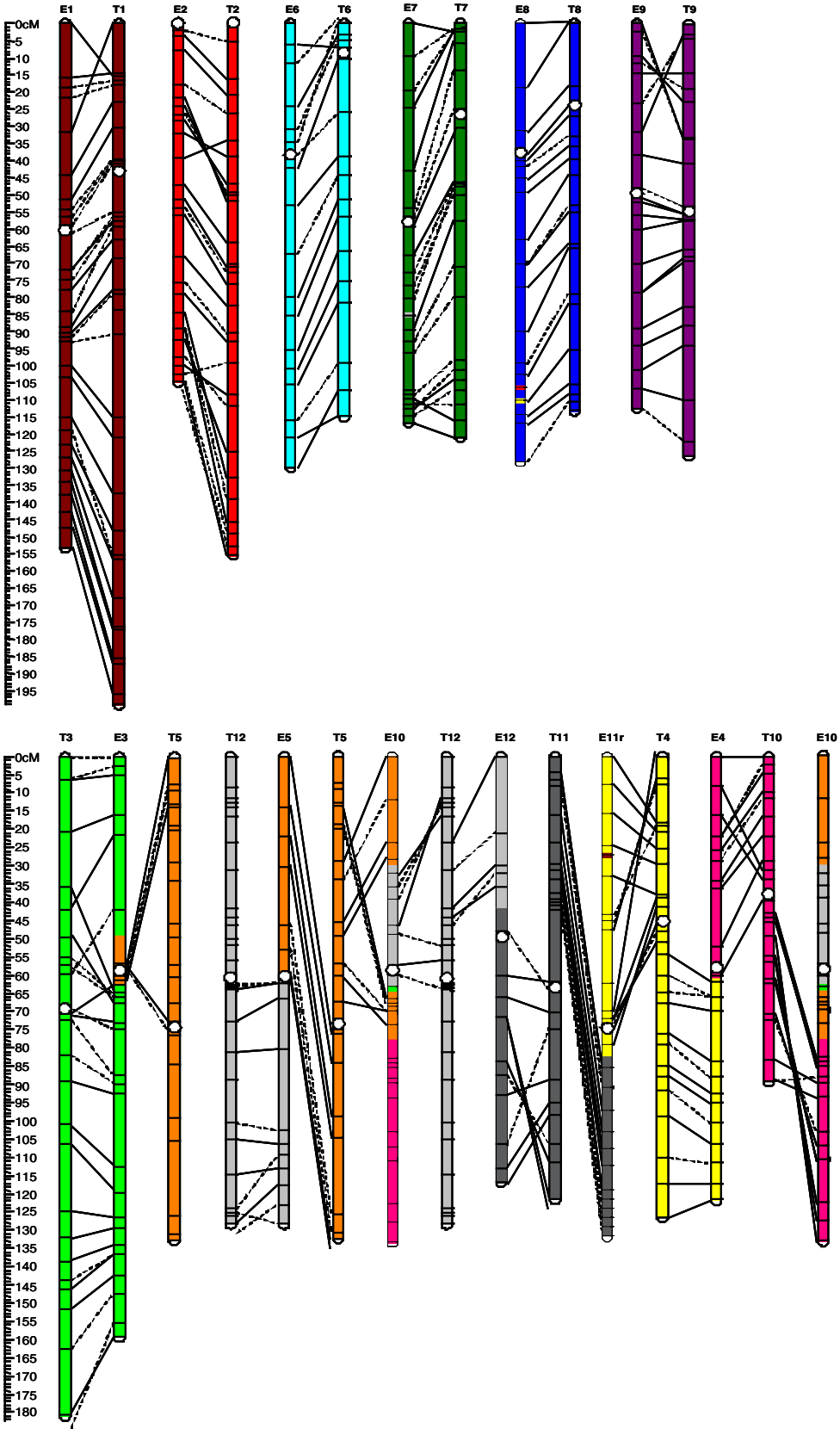


Fig. 2 Comparative maps of the eggplant and tomato genomes (see close-up in supplementary Figure S2). Color coding and chromosome designation follow Fig. 1. E11 is in reversed order (E11r) relative to that in Doganlar et al. (2002a) for a better depiction of synteny. Tomato centromere positions (Frary et al. 2005) and the syntenic positions in the eggplant map are indicated by *white dots*. *Solid lines* connect markers mapped at LOD ≥ 2 on both maps while *dash lines* connect those mapped at LOD < 2 on either map, only the former of which were used to infer inversions between the two genomes

E8 versus T8

Both gene order and gene content are in good agreement between E8 and T8 except that E8 gained two additional markers—C2At1g10580 from T2 and C2At5g41270 from T4. (Fig. 2 and S2)

E9 versus T9

E9 and T9 differ in an inversion near the top. Eggplant may represent the ancestral arrangement in that its gene order is consistent with that of potato and pepper (Tanksley et al. 1992; Wu et al., submitted). (Fig. 2 and S2)

E10 versus T5, T10 and T12

E10 combines most of the upper T5, lower T10 and two segments of T12, which suggests a minimum number of two translocations since divergence of eggplant and tomato/potato. Since pepper linkage group 10 has retained all the T10 markers (Wu et al., submitted), the translocations are likely to have occurred in the lineage leading to eggplant. Several inversions exist in these segments, one in the upper T12 segment, three in the T10 segment and multiple in the T5 segment. Furthermore, C2At1g64770 from T3 was mapped to E10. (Fig. 2 and S2)

E11 versus T11 and T4

E11 has two segments homologous to upper T11 and upper T4 respectively. E11 agrees with upper T11 in both gene order and gene content. On the other hand, E11 and upper T4 differ in three inversions (one missing in the 2002 map) and that E11 gained C2At2g45620 from T1 while lost C2At5g41270 from T4. (Fig. 2 and S2)

E12 versus T11 and T12

E12 combines a T12 segment and lower T11. E12 shares the same gene order with the T12 segment while differs from lower T11 in two inversions, which likely have occurred in tomato since eggplant shares the same gene order with pepper (Wu et al., submitted). (Fig. 2 and S2)

Discussion

Structural differences between the eggplant and tomato genomes

Comparative mapping between eggplant and tomato has revealed that paracentric inversions and translocations (especially with break points at or near the centromeres) are the major rearrangements that have differentiated these two genomes. A minimum number of 24 inversions, two per chromosome on average, differentiates the eggplant and tomato genomes, most likely all of which are paracentric. Further comparison with the potato and pepper maps (Tanksley et al. 1992; Wu et al. submitted) suggested that, the majority of the inversions are specific to eggplant; however, in the following areas—lower E2, top E6, upper E9, lower E10 and lower E12, eggplant shares the same gene order with pepper (*Capsicum*) while differs from its relatives in the same genus *Solanum*—tomato and potato. For these latter cases, based on the principle of parsimony, it's likely that the ancestral genome of these two genera has the same arrangement as that of pepper and eggplant while the inversions are derived in the lineage leading to tomato and potato or more recently in the tomato lineage (E9).

Six eggplant chromosomes (E3, E4, E5, E10, E11 and E12) were involved in one or more translocation events. The majority of those events are reciprocal except for one that moved a T5 segment to E3. Parsimony analysis of the transition from the tomato karyotype (T4, T5, T10, T11 and T12) to the eggplant karyotype (E4, E5, E10, E11 and E12) suggested a minimum number of four reciprocal translocations (Fig. 3), however, the order and timing of these events remains uncertain.

The phenomenon of single gene movement between eggplant and tomato is not as common as that between pepper and tomato (Wu et al., submitted). Only five single markers have been mapped to non-homologous chromosomal regions, C2At5g48300 from T12 to E7, C2At1g10580 from T2 to E8, C2At5g41270 from T4 to E8, C2At1g64770 from T3 to E10 and C2At2g45620 from T1 to E11. As discussed in pepper-tomato comparison (Wu et al. submitted), these single gene movements are possibly due to transposon-mediated gene transpositions.

The use of synteny to predict the position of additional COSII markers in the eggplant map

The detailed synteny between eggplant and tomato genomes can generally be used to infer the relatively precise map positions of additional COSII markers on the eggplant maps—thereby facilitating mapping studies in eggplant and permitting comparisons between eggplant and tomato QTL studies. As described earlier, 123 SMPs were identified between the two genomes. Gene content and gene order between a Syntenic Marker Pair in both eggplant and tomato are likely to have been preserved since eggplant-tomato divergence. Thus, we searched for COSII markers from tomato that are located within SMPs, but not yet mapped on eggplant. To be more conservative, this analysis was only applied on the mapped tomato COSII markers, which have been confirmed to be single copy and have

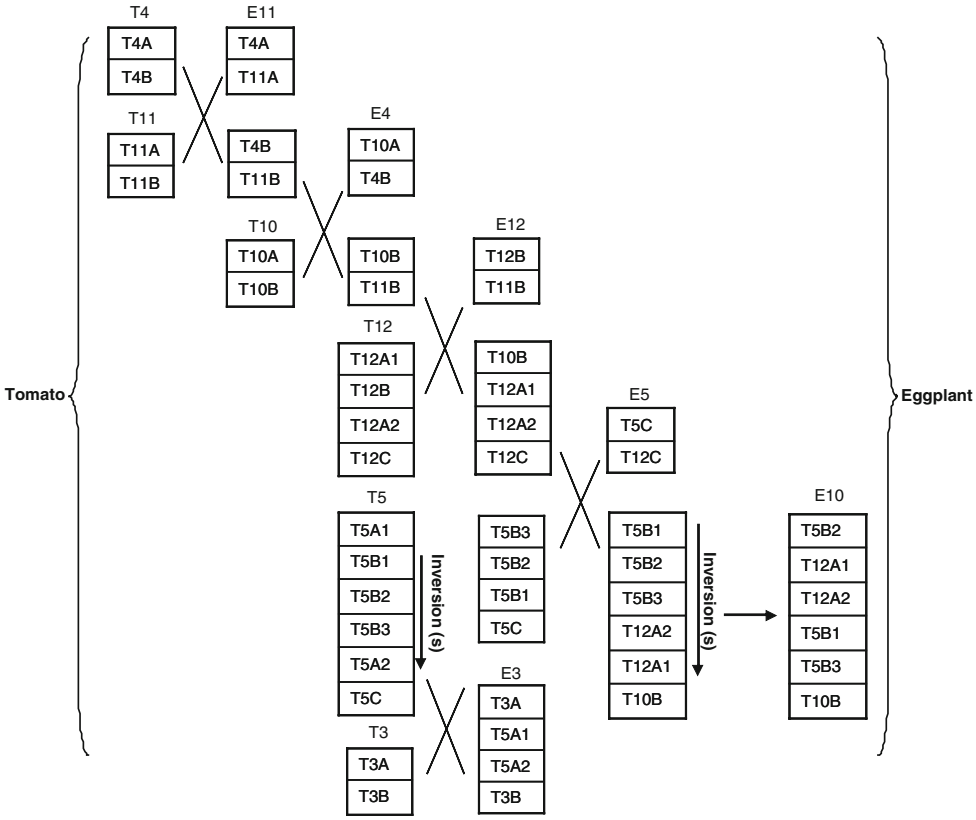


Fig. 3 One possible evolutionary pathway based on parsimony showing a minimum number of one non-reciprocal and four reciprocal translocations between the genomes of eggplant and tomato. A–C and 1–3 represent chromosome segments. A cross indicates a translocation with unknown direction

eggplant orthologs (Wu et al. 2006). We referred to these as "inferred eggplant COSII markers". As a result, an additional set of 522 COSII markers could be integrated into the eggplant map—bringing the total COSII markers in the eggplant map to 632 (Figure S3). Subsequently a random set of eight inferred eggplant COSII markers were selected and subject to actual mapping in the eggplant genome. Six of them each were mapped to the same SMP interval as predicted and the other two each to an interval nearby but still within the same CSS, which thus confirmed the validity of this approach.

Conclusions

A set of 115 PCR-based orthologous markers, including 110 COSII makers, was mapped in the eggplant genome based on a published eggplant map of 12 linkage groups and 232 markers (Doganlar et al. 2002a). Mapping of COSII markers in both eggplant and tomato genomes permitted us to infer a detailed syntenic relationship between the two genomes and thus will advance the study of genome evolution in the family Solanaceae. Parsimony analysis revealed a minimum number of 24 inversions and 5 translocations that have differentiated the eggplant and tomato genomes. Nonetheless, we were able to identify 37 Conserved Syntenic Segments (CSSs)—defining majority of the eggplant and tomato genomes within which gene/marker order have been well preserved, and thus to infer the map position of an additional set of 522 COSII markers in the eggplant genome. Therefore, the high-resolution synteny map will provide a platform for cross-reference of genetic and genomic information between eggplant and tomato (including the tomato genome sequence), and facilitate both applied and basic research in eggplant.

Acknowledgments We thank Dr. Anne Frary and Dr. Sami Doganlar (Izmir Institute of Technology, Urla, Izmir Turkey) for providing genomic DNA and genotype data of the mapping population. We also thank Dr. Lukas Muller (Boyce Thompson Institute for Plant Research, Ithaca, NY, USA) and his bioinformatics group for hosting the maps and the marker data in Solanaceae Genomics Network (http://www.sgn.cornell.edu). This work was supported by NSF Plant Genome Award DBI-0421634 (ST).

References

Daunay MC, Janick J (2007) History and iconography of eggplant. Chron Horticult 47:16–22

Daunay MC, Dalmon A, Lester RN (1999) Management of a collection of Solanum species for eggplant (Solanum melongena) breeding purposes. In: Nee M, Symon DE, Lester RN, Jessop JP (eds) Solanaceae IV. Royal Botanic Gardens/Kew, London, pp 369–383

Daunay MC, Lester RN, Gebhardt G, Hennart JW, Jahn M, Frary A, Doganlar S (2001) Genetic resources of eggplant (Solanum melongena L.) and allied species: a new challenge for molecular geneticists and eggplant breeders. In: Van den berg RG, Barendse

GW, Mariani C (eds) Solanaceae V. Nijmegen University Press, Nijmegen, pp 251–274

Doganlar S, Frary A, Daunay MC, Lester RN, Tanksley SD (2002a) A comparative genetic linkage map of eggplant (Solanum melongena) and its implications for genome evolution in the Solanaceae. Genetics 161:1697–1711

Doganlar S, Frary A, Daunay MC, Lester RN, Tanksley SD (2002b) Conservation of gene function in the solanaceae as revealed by comparative mapping of domestication traits in eggplant. Genetics 161:1713–1726

Frary A, Xu YM, Liu JP, Mitchell S, Tedeschi E, Tanksley S (2005) Development of a set of PCR-based anchor markers encompassing the tomato genome and evaluation of their usefulness for genetics and breeding experiments. Theor Appl Genet 111:291–312

Fulton TM, Van der Hoeven R, Eannetta NT, Tanksley SD (2002) Identification, analysis, and utilization of conserved ortholog set markers for comparative genomics in higher plants. Plant Cell 14:1457–1467

Konieczny A, Ausubel FM (1993) A procedure for mapping Arabidopsis mutations using codominant ecotype-specific pcr-based markers. Plant J 4:403–410

Kosambi DD (1944) The estimation of map distances from recombination values. Ann Eugen 12:172–175

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Nadeau JH, Taylor BA (1984) Lengths of chromosomal segments conserved since divergence of man and mouse. Proc Natl Acad Sci U S A 81:814–818

Neff MM, Neff JD, Chory J, Pepper AE (1998) dCAPS, a simple technique for the genetic analysis of single nucleotide polymorphisms: experimental applications in Arabidopsis thaliana genetics. Plant J 14:387–392

Neff MM, Turk E, Kalishman M (2002) Web-based primer design for single nucleotide polymorphism analysis. Trends Genet 18:613–615

Tanksley SD, Bernatzky R, Lapitan NL, Prince JP (1988) Conservation of gene repertoire but not gene order in pepper and tomato. Proc Natl Acad Sci USA 85:6419–6423

Tanksley SD, Ganal MW, Prince JP, Devicente MC, Bonierbale MW, Broun P, Fulton TM, Giovannoni JJ, Grandillo S, Martin GB, Messeguer R, Miller JC, Miller L, Paterson AH, Pineda O, Roder MS, Wing RA, Wu W, Young ND (1992) High-density molecular linkage maps of the tomato and potato genomes. Genetics 132:1141–1160

Wu FN, Mueller LA, Crouzillat D, Petiard V, Tanksley SD (2006) Combining bioinformatics and phylogenetics to identify large sets of single-copy orthologous genes (COSII) for comparative, evolutionary and systematic studies: a test case in the euasterid plant clade. Genetics 174:1407–1420

Wu FN, Eannetta NT, Xu YM, Durrett R, Mazourek M, Jahn M, Tanksley S. A high density COSII map of the pepper genome provides a detailed picture of Synteny with tomato and new insights into recent chromosome evolution in the genus Capsicum. (submitted)