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RESOURCE

Solanum pennellii (LA5240) backcross inbred lines (BILs) for high resolution mapping in tomato

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SUMMARY

Wild species are an invaluable source of new traits for crop improvement. Over the years, the tomato community bred cultivated lines that carry introgressions from different species of the tomato tribe to facilitate trait discovery and mapping. The next phase in such projects is to find the genes that drive the identified phenotypes. This can be achieved by genotyping a few thousand individuals resulting in fine mapping that can potentially identify the causative gene. To couple trait discovery and fine mapping, we are presenting large, recombination-rich, Backcross Inbred Line (BIL) populations involving an unexplored accession of the wild, green-fruited species *Solanum pennellii* (LA5240; the 'Lost' Accession) with two modern tomato inbreds: LEA, determinate, and TOP, indeterminate. The LEA and TOP BILs are in BC2F6–8 generation and include 1400 and 500 lines, respectively. The BILs were genotyped with 5000 SPET markers, showing that in the euchromatic regions there was one recombinant every 17–18 Kb while in the heterochromatin a recombinant every 600–700 Kb (TOP and LEA respectively). To gain perspective on the topography of recombination we compared five independent members of the *Self-pruning* gene family with their respective neighboring genes; based on PCR markers, in all cases we found recombinants. Further mapping analysis of two known morphological mutations that segregated in the BILs (*self-pruning* and *hairless*) showed that the maximal delimited intervals were 73 Kb and 210 Kb, respectively, and included the known causative genes. The 'Lost'_BILs provide a solid framework to study traits derived from a drought-tolerant wild tomato.

Keywords: Backcross Inbred Lines, *Solanum pennellii*, Introgression, fine-mapping, recombination rate, breeding.

INTRODUCTION

Tomato is choice crop for biodiversity breeding, due to the availability of seed of wild species accessions that were collected, studied, multiplied, and distributed to the community by the C.M. Rick Tomato Genetics Resource Center (TGRC; https://tgrc.ucdavis.edu/). The wild species accessions in the TGRC collection represent many natural populations that are now extinct due to agriculture and urban expansion (Chetelat et al., 2009). To harness this rich diversity, in the past few decades the tomato community has developed different introgression populations that carry marker-defined segments from the genomes of at least eight wild tomato accessions (Bai & Lindhout, 2007; Zamir, 2001). Such resources, which are commonly composed of 100–200 individuals, are large enough to map with confidence the effect of single genes/QTLs but too small to fine map the coding genes that are responsible for the phenotype. In 2007, with the aim to improve the resolution of the genotype to phenotype maps, we started to breed Backcross Inbred Line (BIL) populations that are of unparalleled size and mapping resolution. The interspecific BILs resulted from crosses with an unexplored accession of *Solanum pennellii* that was sequenced using nanopore technology (LA5240; 'Lost' Accession; Schmidt et al., 2017).

This green-fruited tomato accession is completely self-compatible and was selected as a donor parent for the new BIL resource, together with two modern lines: the determinate inbred LEA for open field culture and the indeterminate inbred TOP that is suitable for greenhouse cultivation.

The tomato wild species introgression populations facilitated the mapping of domestication and yield-related QTL (Bai & Lindhout, 2007). To pinpoint the specific open reading frames that drive such phenotypes, it is necessary to conduct high-resolution mapping by identifying recombinants in the vicinity of the QTL. This is a laborious task that requires patience and sound knowledge of genetics. One of the objectives in constructing the new BILs is to develop a public domain resource that is enriched with recombinants of the introgressed genome such that in most cases it will be possible to fine map a trait of interest without the need to breed and screen additional fine mapping populations.

RESULTS

BIL construction

Pollen from a single *S. pennellii* (LA5240) plant was crossed to the processing inbred LEA and a single F1 hybrid became the pollen donor and backcrossed to both LEA and TOP to generate a large number of backcross1 (BC1) seeds (Figure 1). Consequently, while the LEA-BILs segregate for a maximum of two alleles (one derived from *S. pennellii* and one from LEA), the TOP BILs segregate for three possible alleles (one derived from *S. pennellii*, one from LEA, and one from TOP). From each of the backgrounds, we planted ~2000 BC1 plants in the greenhouse and generated BC2 seed from the respective inbreds (Figure 2). Selfing of the BC2 was carried out for six generations until the plants reached BackCross-2-self 6 (BC2S6) at which stage DNA were extracted from the BILs and their parents and were subjected to SPET marker analysis (Barchi et al., 2019). We now have seed from approximately 1500 BILs in the LEA

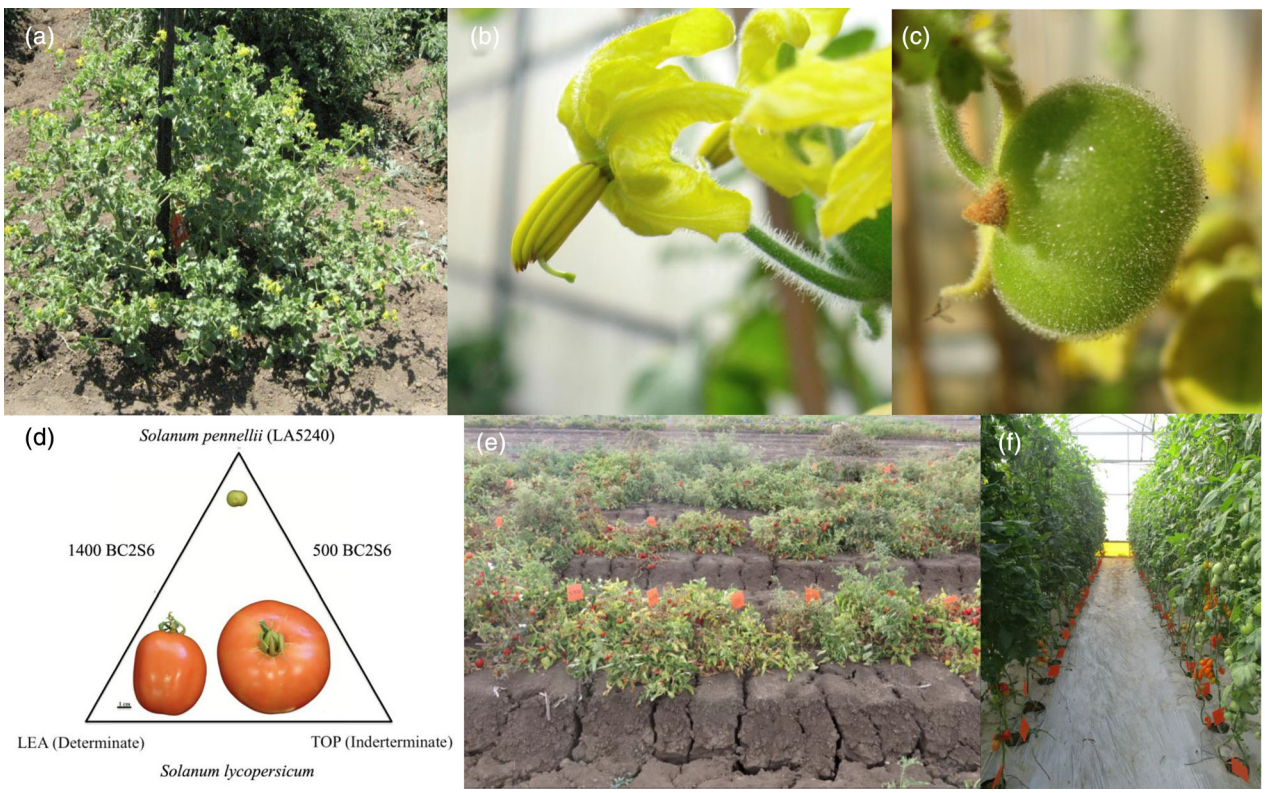

Figure 1. Phenotypic view of the *Solanum pennellii* BILs.
(a) LA5240 growing in the field in Akko, Israel. Whereas *S. pennellii* LA716 cannot grow in the field, possibly due to the *necrotic dwarf* mutation, LA5240 grows very well and produces many seed by self-pollination.
(b) Flower of LA5240 with the exerted stigma and the bent style that is a hallmark of this species in the tomato clade but is prevalent in other *Solanum* species.
(c) Ripe fruit of LA5240 with the characteristic green color and the sticky trichomes on the fruit epidermis.
(d) The simplified crossing scheme that generated the LEA and TOP BILs: BC2 derived from crossing LA5240 to the processing and fresh market parents was followed by six generations of selfing (BC2S6; for the detailed scheme see Figure 2).
(e) Screening of determinate processing LEA BILs and their hybrids (with LEA) for yield under deficit irrigation.
(f) Screening of the TOP BILs in the greenhouse showed a few lines that are fixed for LEA traits such as determinacy and ovate fruit shape.

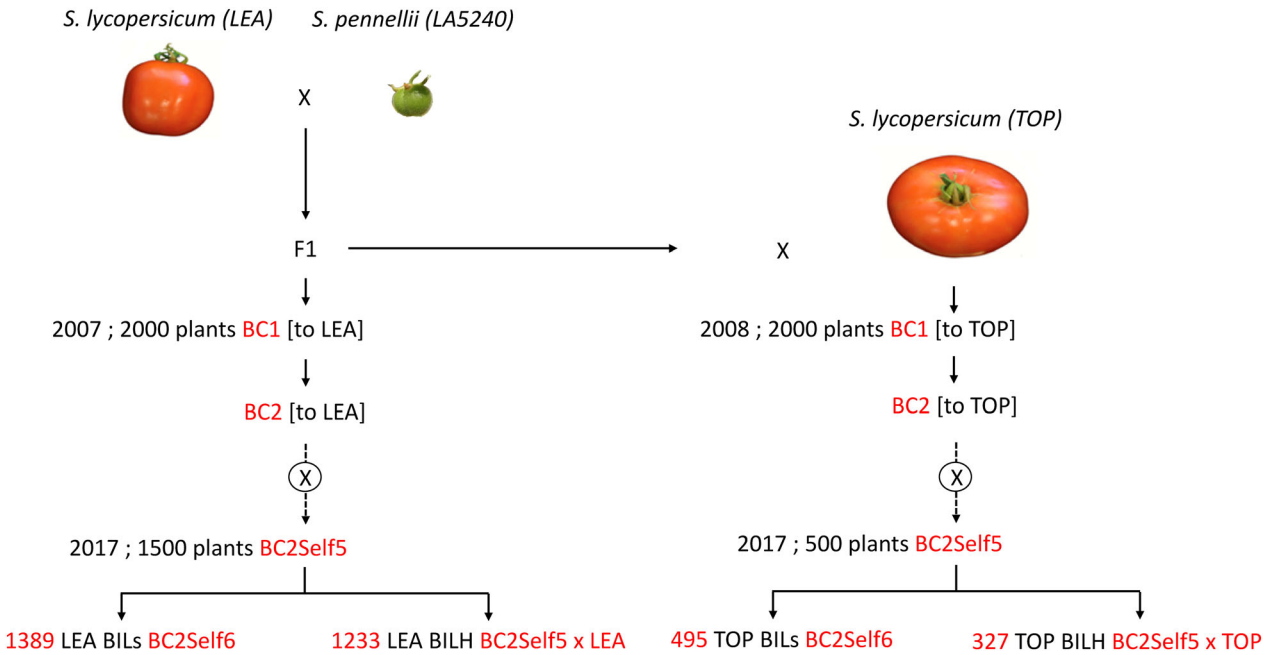

Figure 2. Crossing scheme of the BILs population development.

processing tomato inbred and 500 BILs in the TOP indeterminate background (sterility upon selfing was higher in the TOP background). In BC2S6 and earlier selfing generations, we observed a close phenotypic resemblance between the siblings of a particular BIL, indicating that the semi-industrial project of pollination, fruit harvest, seed extraction, and plantings was carried out accurately.

Genomic composition of the BILs

The F1 interspecific hybrid carried the entire *S. pennellii* genome and each backcross generation towards the cultivated background reduced the proportion of the wild alleles by half. In BC2 it is expected that an average plant will carry 25% of the *S. pennellii* genome, all in a heterozygous condition. In the following six selfing generations, the heterozygosity was reduced by half each generation and either the wild or the cultivated allele became fixed in a homozygous condition. Thus, in BC2S6 we expected that in both populations 12.5% of the markers would be homozygous for the *S. pennellii* allele. However, as is often the case in interspecific crosses, in both populations we observed an overall deficiency of the alleles of the wild species for most of the chromosomes (Zamir & Tadmor, 1986; Figure 3). In both the LEA and the TOP BILs, there was a higher-than-expected introgression of the short arm of chromosome 11, suggesting that this region harbors *S. pennellii* alleles that improve its transmission. The mean number of *S. pennellii* introgressions in the LEA BILs was 11, while in the TOP BILs the mean was 22 introgressions per line. It should be noted that we scored the TOP-BILs only for cultivated and wild alleles with no differentiation between the genome of the LEA and TOP. To discriminate between the *S. lycopersicum* inbreds it would be necessary to sequence the BILs and the inbreds. It should also be noted that both the LEA and TOP inbreds were derived from selfing of commercial F1 hybrids until generation F5. Thus, some residual polymorphism existed within the inbreds, particularly when comparing the early BIL backcross generations (BC1 and BC2) that were produced on multiple F5 and F6 plants of LEA and TOP. The seed of the parental accessions that we use today are in F12 and may not carry SNPs that segregated in F5 and F6.

Rates of recombination

The first phenotype that we analyzed for each of the BILs was the rate of recombination between markers that reside on the introgressed *S. pennellii* intervals. For each of the genotyped BILs, we counted the number of recombination events in euchromatic and heterochromatic regions on all chromosomes. Figure 4 shows the BIL-wide comparison of the genetic map (cM) and the physical map (Mbp) with high recombination in the euchromatin and much less in the heterochromatin: For the LEA BILs, we counted an average of one recombinant every ~18 Kb in the euchromatin and one recombinant every ~700 Kb in the heterochromatin. In the TOP BILs, the recombination estimates were very similar (euchromatin 17 Kb; heterochromatin 603 Kb). All the mapping analysis of this project was based on a SPET design that incorporated single nucleotide polymorphisms within the red-fruited species *S. lycopersicum* and

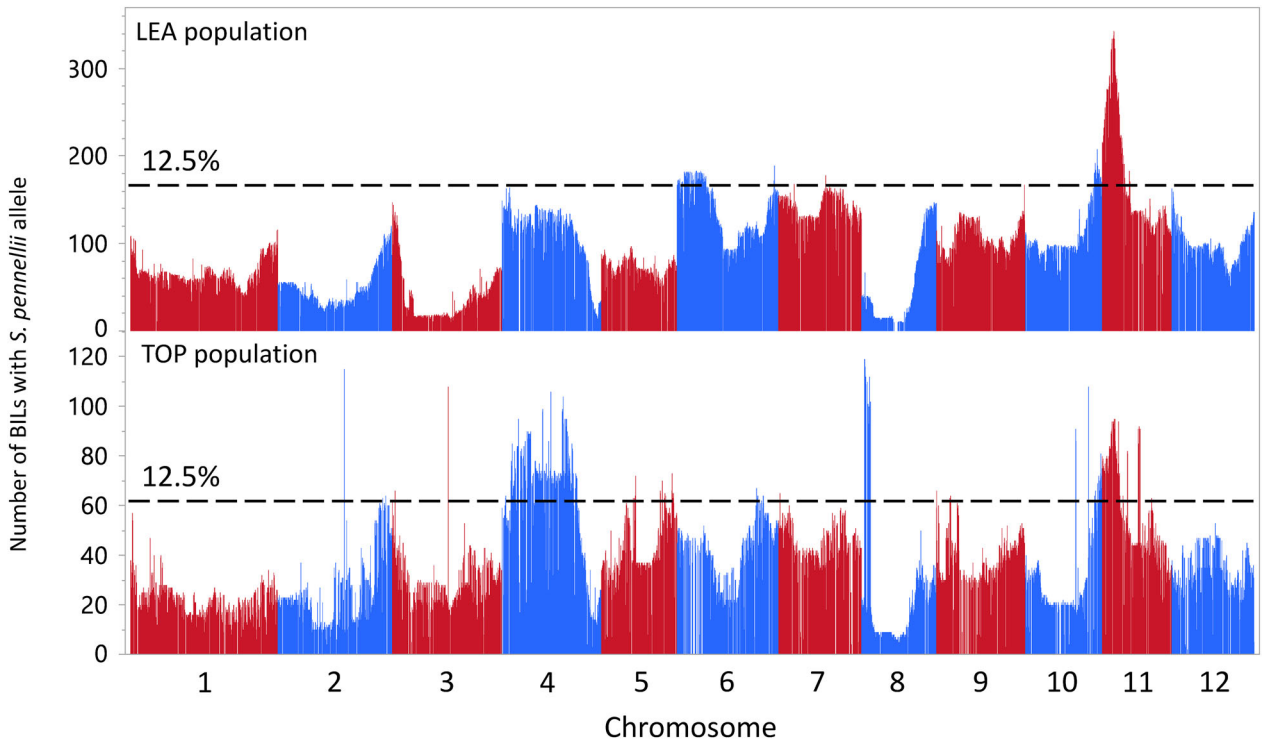

Figure 3. Genomic composition of the BILs.
A Manhattan plot of the prevalence of the *S. pennellii* alleles in 1389 BC2S6 LEA BILs and the 490 TOP BILs relative to the expected values of 12.5%.

with its wild progenitor, *S. pimpinellifolium* (Barchi et al., 2019). When the markers were analyzed on the BIL populations we noticed that in both LEA and TOP there were approximately 1000 regions that were devoid of *S. pennellii* markers. The largest such *S. lycopersicum*-specific region was on chromosome 3 and ranged from 11 Mbp in LEA to 8 Mbp in TOP (Table S1). The largest eight regions that were not detected in *S. pennellii* (i.e., *S. lycopersicum* specific) were found in both the LEA and TOP populations and are shown in Table S1. Considering that the *S. pennellii* and *S. lycopersicum* have an approximate genome size of 1.2 Gb and 0.8 Gb, respectively, we can safely assume that many sequences are present in the wild species and not in the cultivated tomato (Schmidt et al., 2017). The high frequency of structural variation detected in this study is consistent with recent pan-genome analyses of wild and cultivated tomato species (Alonge et al., 2020; Li et al., 2023).

To validate the BILs recombination rates described above we designed CAPs markers for five members of the *Self-pruning* gene family (Carmel-Goren et al., 2003; Pnueli et al., 1998), located on different chromosomes, and for their neighboring open reading frames (Table S2). In all cases, we found recombinants between the euchromatin-located *Self-pruning* genes and their closest neighbors. These results are in line with the average recombination estimates calculated from the SPET genotypes.

'Test driving' the BILs for mapping known phenotypes

The 'Lost' BILs in the TOP and LEA backgrounds inherited from the *S. pennellii* the mutant gene *h* (*hairless*), which results from a deletion of the entire coding region of the *H* (*Hairs*) gene (*C2H2 zinc-finger protein*) that encodes type-I trichomes, which are present in LEA and TOP (Figure 5a; Chang et al., 2018). The locus *H (Solyc10g078970*) is located on the long arm of chromosome 10 between 60 609 617 and 60 610 602 (assembly 2.5; The Tomato Genome Consortium, 2012) and our mapping analysis in both LEA and TOP placed the trichome phenotype in that region (Figure 5b,c). In the LEA BILs, we counted 110 lines that had an introgression in the *H* region, while in the TOP BILs, 26 lines carried the *S. pennellii* introgression. The LEA and TOP BILs with recombination events closest to *H* are shown in Figure 6 D where the recombinants p-17-1 and p-1925-1 delimited the maximal interval of H location to 210 176 Kb which contains 32 genes that contain the causal gene Solyc10g078970. A similar analysis was conducted in the LEA BILs for the *Self-pruning* gene that maps to chromosome 6 (Figure 6a; Pnueli et al., 1998). Six BILs with recombination events close to *Self-pruning* are also presented. The gene is found in an interval with a maximum span of 72 610 bp which includes a total of six genes among them the *Self-pruning* gene, Solyc06g074340. Taken together, the results show that the BILs represent a

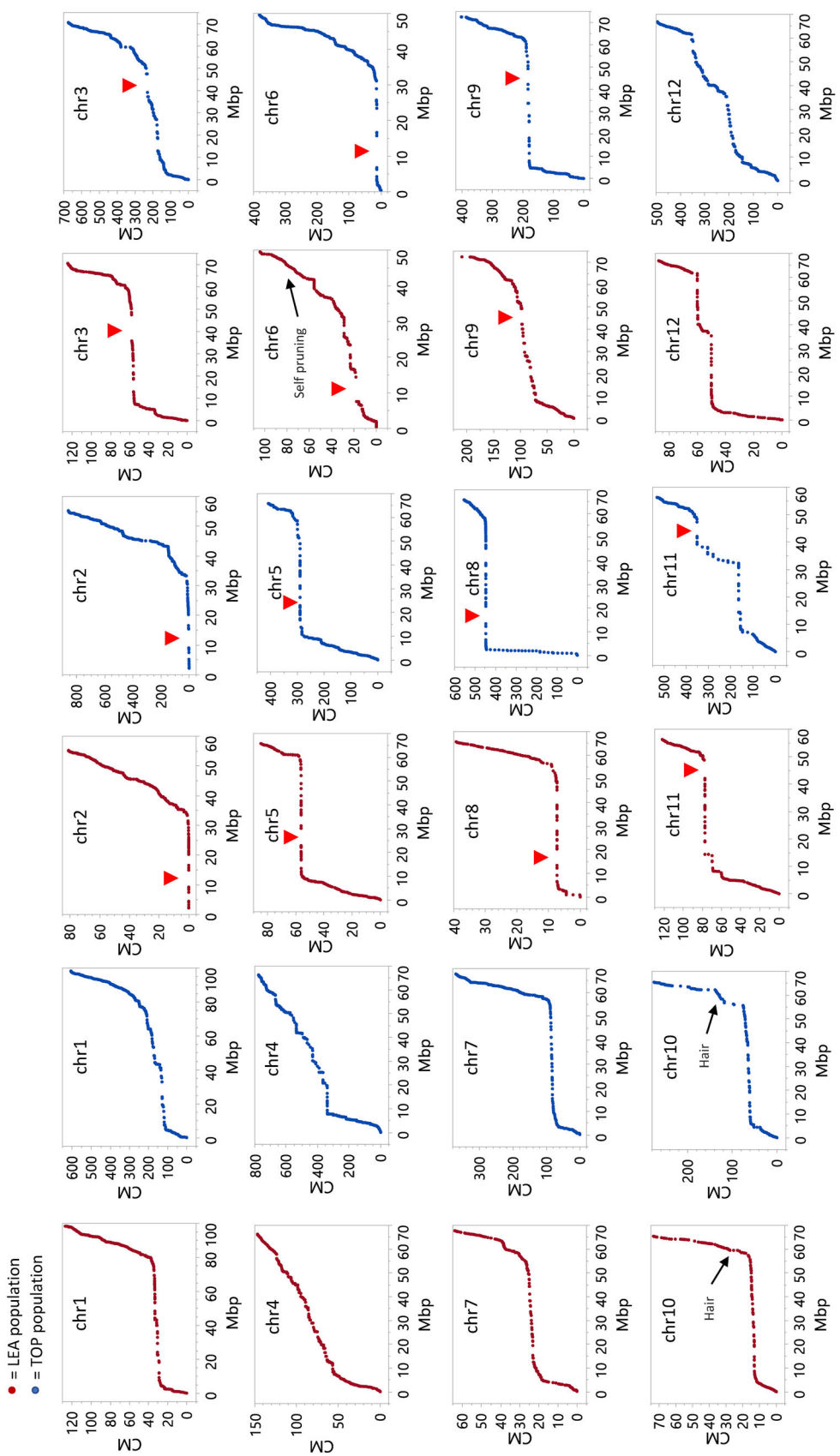

Figure 4. Plotting of the physical by genetic distances in the tomato genome.
Plots of the physical (Mbp) and genetic (cM) distances of 7699 markers in the LEA and 7108 markers in the TOP BILs. The graphs with red dots represent the LEA population and the graphs with the blue dots the TOP population. The red triangles point to the 10 largest gaps that were detected between the two species which are common to LEA and TOP. The location of the mapped mutants in the *Hairs* and *Self-pruning* loci is indicated.

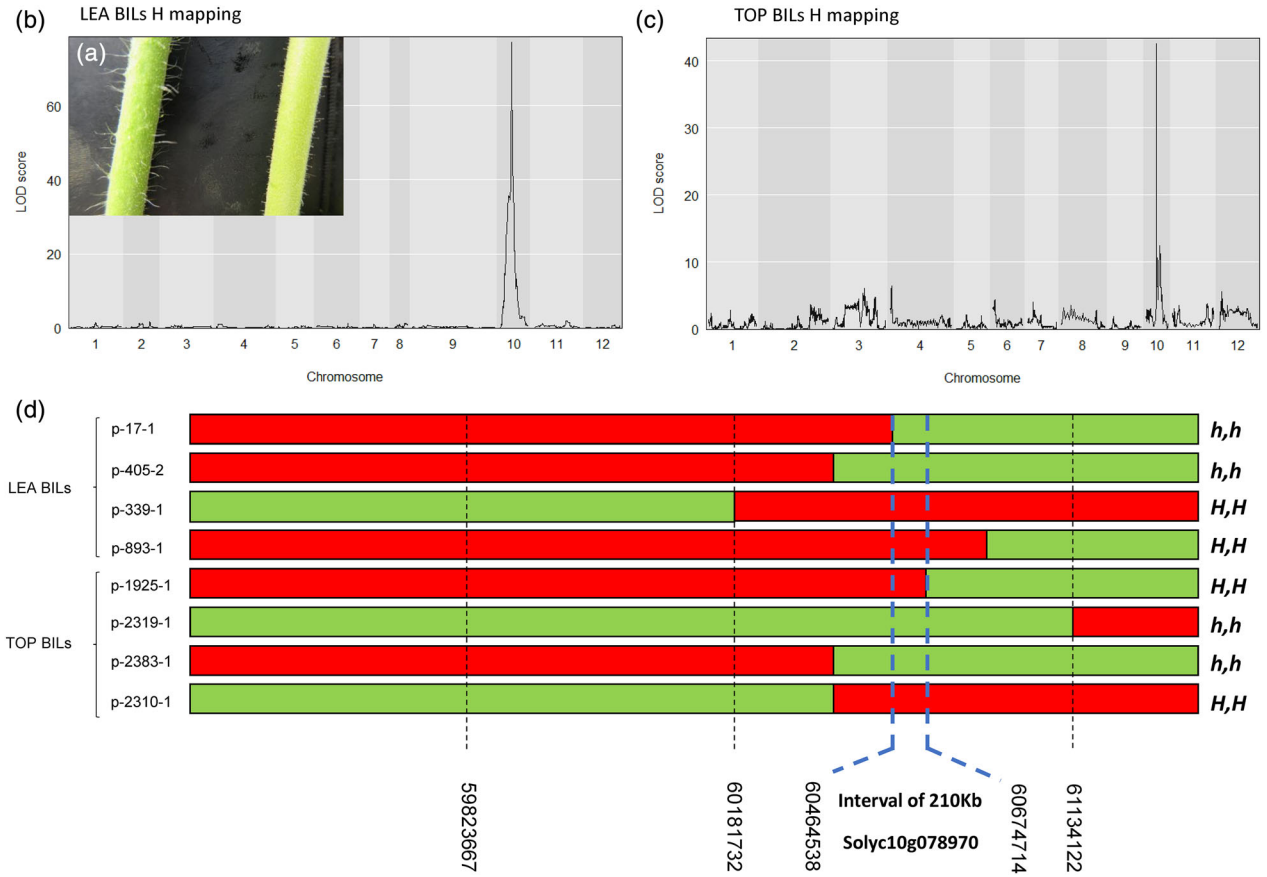

Figure 5. Genetic mapping of the *Hair* locus.
(a) Picture of the hairy stem (*Hairs*; left) of LEA and hairless stem (*hairs*, right) of *S. pennellii*.
(b) A Manhattan plot mapping of the *Hairs* locus in chromosome 10 in the LEA BILs.
(c) A Manhattan plot mapping the *Hairs* locus in the TOP BILs.
(d) Fine mapping of the *Hairs* gene using recombinants from the LEA and TOP BILs populations. Red segments indicate LEA/TOP alleles and green segments indicate the 'Lost' alleles. The blue lines delimit the maximal interval for the location of the *Hairs* gene.

permanent resource which can be used for the fine mapping of genes and QTL.

DISCUSSION

We are presenting a new population of backcross inbred lines for genetic mapping of traits derived from the wild tomato species *S. pennellii* (LA5240). The unique aspect of this BIL resource is that it includes lines with the genetic background of a determinate inbred LEA (1500 BILs) and the indeterminate line TOP (500 BILs). A total of 5000 SPET markers provided data on the segregations of 7699 segregating loci in the LEA background and 7060 loci in the TOP background. It is important to note that the TOP BILs include two cultivated tomato backgrounds since the interspecific hybrid that was used in the initial cross involved LEA and the *S. pennellii* accession (Figure 2). The markers used did not detect enough polymorphisms between LEA and TOP and thus we cannot map the LEA introgression in the TOP BILs and this task must await an analysis with a different marker system.

Comparison of the genotyping data of the two BILs highlighted a number of curious phenomena that are of biological interest, yet at this stage without validated explanations. (1) Recombination rates (percent recombinants in cM) over all the 12 chromosomes were 5.8 times higher in the TOP BILs compared with the LEA BILs (Table S3). The greatest difference was for chromosome 8 where TOP had a 14 times higher recombination percentage than LEA whereas for chromosome 9, TOP had only a 1.9-fold higher recombination than LEA. This difference in the rate of recombination could be associated with a slower rate of decay of heterozygosity in the TOP BILs compared to the LEA BILs as evident from the level of heterozygosity which was 5.4% for the TOP BILs and 2.9% for the LEA BILs. (2). The average number of introgressions in the TOP BILs was 22, which is twice as high compared to the LEA BILs (11). (3) Sterility upon selfing was three times higher for the TOP BILs compared to the LEA BILs, so that in both populations we started with 2000 plants in BC1 and at the end of the breeding process (summarized in Figure 2)

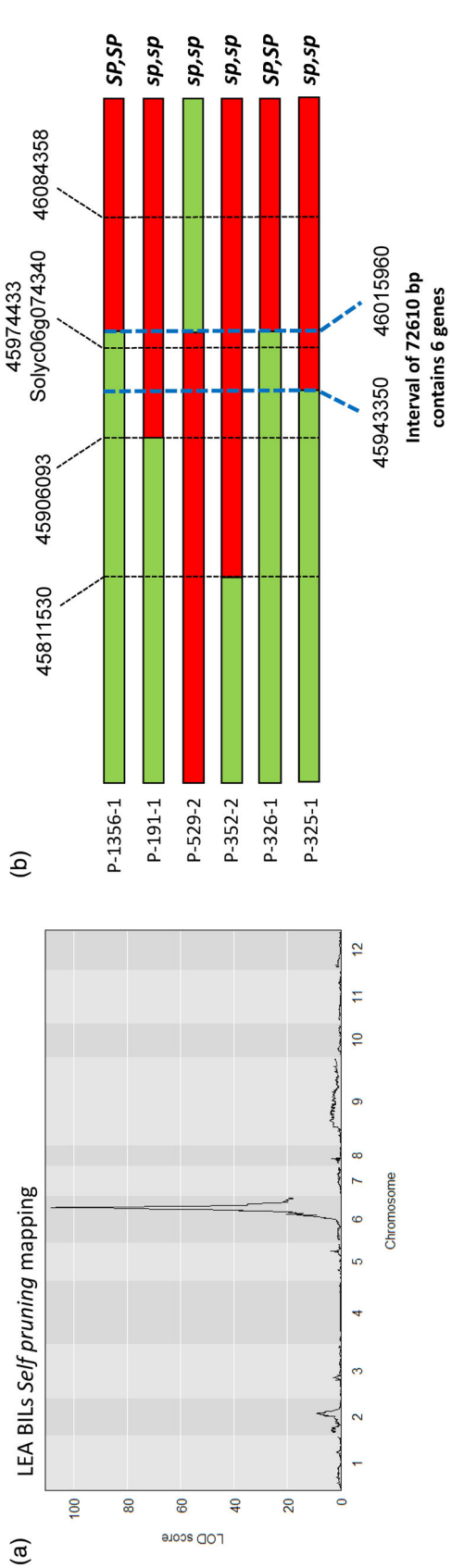

Figure 6. Genetic mapping of the *Self-pruning* locus.
(a) A Manhattan plot mapping the *SP* locus in chromosome 6 in the LEA BILs.
(b) Fine mapping of the *Self-pruning* gene using recombinants from the LEA BILs. Red segments indicate LEA alleles and green segments indicate the 'Lost' alleles. The blue lines delimit the maximal interval for the location of *Self-pruning*.

we obtained 1389 LEA BILs and only 495 TOP BILs. It is possible that some of the phenomena described above are causally related, however, to answer this point further experiments are needed.

One of the incentives for breeding a very large BIL population was to allow the analysis of epistasis between tomato QTLs in a genome-wide manner. The limiting factor for detecting such non-additive interactions of pairs of QTLs is the number of BILs that contain the two genomic regions. For example, to analyze epistasis between two independent genomic regions A and B we need to collect the phenotype of ~10 independent BILs that carry both segments A and B and compare it to the values obtained for the single introgressions. The LEA BILs were already used in such an epistasis study, which enabled the identification of 80 cases of epistasis for yield-associated traits (Torgeman & Zamir, 2023). A unique case of yield epistasis was found for *S. pennellii* introgressions on chromosome 1 and chromosome 7, which by themselves had no effect on yield, but when both introgressions were present in a heterozygous condition yield was increased by 20–50 percent. This result was validated in 3 years of field trials both in wide and dense spacing, showing that rare epistatic interactions can improve crop productivity via heterosis.

The results presented here on the high mapping resolution of the BILs and the ability to analyze genome-wide epistasis indicate that this new resource has potential value to the tomato research community. To enhance the usability of the BILs, we selected a set of 60 BILs from the LEA and a similar number from the TOP population that provide a complete coverage of the LOST genome. This initial set is being distributed to scientists who have a specific interest in particular phenotypes, for screening the parents, the F1 and the complete genome coverage set. Once a trait is mapped using the initial set, scientists can select the BILs that cover the interval and phenotype them to fine map the genes responsible for the trait of interest. As indicated by the mapping of *Hairs* and *Self-pruning,* it is possible that further mapping populations would be needed in order to associate a particular open reading frame with a phenotype of interest. The cultivated tomato and many other crop plants are composed of an array of recessive mutations that make them suitable for human cultivation. By the same token, the majority of the genes that are derived from wild species are dominant and therefore can be screened as BIL hybrids (BILHs) that are obtained from crossing of each of the BILs to their respective cultivated parents LEA or TOP. The advantage of the BILH is that their fertility is high compared to the BILs that carry a load of multiple homozygous *S. pennellii* introgressions and thus are less fertile. When we distribute the initial set, we also include the corresponding BILHs, that can be used both for genotyping and phenotyping. We are

increasing the seed of all the BILs and the BILHs under phytosanitary conditions that will allow us to send the seed to scientists in different countries. We believe that this unique resource has the potential to create a solid foundation for a collaborative project of the Solanaceae community with interest in the genetic basis of simple and complex epistatic traits in tomato.

MATERIALS AND METHODS

Plant material

S. pennellii LA5240 (the 'Lost' accession) was discovered as a misidentified line from the IPK Gatersleben collection (Schmidt et al., 2017). LA5240 is completely self-compatible and fertile which is a rare trait combination in this species (Figure 1). The 'Lost' accession was selected as the wild donor for a new BIL resource together with two modern inbreds, one for processing tomatoes in the open field (determinate, LEA) and the second for fresh market cultivation in greenhouses (indeterminate, TOP); Supplementary Figure S1. A single *S. pennellii* plant was crossed to the processing inbred LEA and an F1 hybrid was used as the pollen donor and backcrossed to both LEA and TOP to generate large amounts of backcross1 (BC1) seed; consequently, the TOP BILs segregate for three possible alleles (Figure 2). From each of the backgrounds ~2000 BC1 were planted in the greenhouse and generated BC2 seed from the respective inbreds. Selfing of the BC2 was carried out until the plants reached BackCross-2-self 6 (BC2S6). Throughout the BIL selfing 2–4 plants were planted from each BIL and seed was extracted from a random fertile plant (no direct selection). In cases where all plants of a particular BIL were sterile we went back two generations and planted eight plants with an attempt to recover fertility in the particular BIL. In BC2S5 we observed close phenotypic resemblance between the siblings of a particular BIL, indicating that the semi-industrial project of pollination, fruit harvest, seed extraction, and plantings was carried out accurately. We now have seed of 1500 Lost-BILs in the LEA background and in 500 BILs in TOP background that are stored in conditions of low temperature and humidity.

Genotyping and phenotyping

Leaflets of each of the BILs were collected from the open field-grown plants for the LEA BILs in Akko; Israel and from the greenhouse for the TOP BILs in Chatzav; Israel. DNA was extracted using the CTAB protocol and was diluted to a final concentration of 40–60 ng in a volume of 40 ul. DNA quantity and quality were determined using a Nanodrop ND-1000 spectrophotometer followed by electrophoresis on a 1% agarose gel. DNA quantity was validated using Qubit dsDNA BR Assay Kit (Life Technologies, Eugene, OR USA). The BILs DNA and that of the controls LA5240, LEA, TOP and M82 was genotyped by the Single Primer Enriched Technology (SPET) using the HiSeq2000 platform (Illumina, San Diego, CA, USA) in single-end mode (150 bp), by IGA Technology Services, Udine, Italy. A total of 173 000 SNPs were called and subjected to filtering using TASSEL v5.2.43: Sites with a depth of less than three reads or >50% missing data were filtered out as well as heterozygous markers, non-polymorphic markers, and markers with a minor allele frequency of <1%. In the TOP BILs we further filtered out 100 markers that were polymorphic between LEA and TOP. The final SNP set, following filtering, includes 7699 markers in 1389 lines in the LEA population and 7108 markers in 490 lines in the TOP population. Introgression bins and genetic distances were calculated using Asmap package in R software.

Throughout the autumn 2017, the LEA BILs (1389) and the TOP BILs (490) were grown in a greenhouse in Chatzav, Israel and scored for plant habit (determinate and indeterminate) and hairiness on stem (Hairy and hair absent). Genome scan for trait mapping analysis in the bi-parental populations was performed in R/qtl and R/qtl2 packages (Broman et al., 2003) by Haley–Knott regression and validated using single marker analysis (ANOVA) in JMP pro 16 software (SAS Institute, Cary, NC, USA).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Figure S1. The horticultural attributes of the inbreds LEA and TOP.

Table S1. The eight largest *S. lycopersicum* -specific regions that were not detected in the *S. pennellii* genome.

Table S2. CAPs markers for five members of the *self-pruning* gene family and their neighboring gene.

Table S3. The total length of the TOP and the LEA chromosomes (also shown in Figure 4) as determined from the recombination frequencies of the SPET markers of the two BIL populations. The ratio of the TOP length for each chromosome to the LEA chromosome and for the entire genome is shown.

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