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**The *ORGAN SIZE (ORG)* locus modulates both vegetative and reproductive gigantism
in domesticated tomato**

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Running title: Genetic control of organ gigantism in tomato

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1 **Background and aims:** Gigantism is a key component of the domestication syndrome, a
2 suite of traits that differentiates crops from their wild relatives. Allometric gigantism is
3 strongly marked in horticultural crops, causing disproportionate increases in the size of edible
4 parts such as stems, leaves or fruits. Tomato (*Solanum lycopersicum*) has attracted attention
5 as a model for fruit gigantism, and many genes have been described controlling this trait.
6 However, the genetic basis of a corresponding increase in size of vegetative organs
7 contributing to isometric gigantism, has remained relatively unexplored.

8 **Methods:** Here, we identified a 0.4 Mbp region on chromosome 7 in introgression lines (ILs)
9 from the wild species *Solanum pennellii* in two different tomato genetic backgrounds (cv.
10 M82 and cv. Micro-Tom) that controls vegetative and reproductive organ size in tomato. The
11 locus, named *ORGAN SIZE*(*ORG*), was fine-mapped using genotype-by-sequencing. A
12 survey of literature revealed that *ORG* overlaps with previously mapped QTLs controlling
13 tomato fruit weight during domestication.

14 **Key results:** Alleles from the wild species led to reduced cell number in different organs,
15 which was partially compensated by greater cell expansion in leaves but not in fruits. The
16 result was a proportional reduction in leaf, flower and fruit size in the ILs harbouring the
17 alleles from the wild species.

18 **Conclusions:** Our findings suggest that selection for large fruit during domestication also
19 tends to select for increases in leaf size by influencing cell division. Since leaf size is relevant
20 for both source-sink balance and crop adaptation to different environments, the discovery of
21 *ORG* could allow fine-tuning of these parameters.

22 **Key words:** cell division; cell expansion; domestication; fruit size; gigantism; organ size;
23 *Solanum*; tomato; wild relatives
24
25

Introduction

The domestication syndrome is the suite of phenotypic changes that occurred through artificial selection to transform wild species into crops (Evans 1996). Some of the most commonly found traits in crops are increased apical dominance, determinate growth and loss of natural seed dispersal (Meyer *et al.* 2012; Denham *et al.* 2020). An increase in the size of certain organs, or gigantism, is also widespread, particularly in horticultural crops (Schwanitz 1957). Gigantism can be isometric, *i.e.* a proportional increase in all body parts, but most generally occurs through allometric alterations in the relative size of certain plant structures (Niklas 2004). A prime example is the species *Brassica oleracea*, where multiple cultivated strains were produced through artificial selection on the differential growth of edible organs such as stems (kohlrabi), buds (cabbage, Brussels sprouts), leaves (kale) and flowers (broccoli, cauliflower) (Prakash *et al.* 2011). Although increased organ size can be explained by alterations in cell division and expansion (Krizek 2009), it also requires physiological alterations to transform larger organs into stronger photosynthetic sources or sinks (Garcia *et al.* 2023). Given that photosynthesis as a biochemical process has not been improved by crop domestication or breeding (Sinclair *et al.* 2019), most of the genetic gains in productivity have occurred indirectly through changes in plant development (Greenland *et al.* 1997; Zsögön and Peres 2018).

In tomato (*Solanum lycopersicum* L.), gigantism is evidenced in the phenomenal increase in fruit size when compared to its wild progenitor *S. pimpinellifolium* (Tanksley 2004). The genetic basis of tomato fruit size control has attracted considerable attention (Chevalier *et al.* 2011; Beauchet *et al.* 2021; Pereira *et al.* 2021; Zhao *et al.* 2022). Increased fruit size in tomato involves mutations in multiple loci, some of which have been characterized at the molecular level, for instance *fruit weight 2.2* (*fw2.2*), *fw3.2*, *fw11.3*, *fasciated* (*fas*), *locule number* (*lc*) and *EXCESSIVE NUMBER OF FLORAL ORGANS*

1 (*ENO*). All of them are involved in fundamental processes of plant developmental such as
2 cell division, expansion and differentiation. The *FW2.2* gene is a negative regulator of cell
3 division responsible for up to 30% of the increase in fruit size when comparing lines
4 harbouring small- and big-fruit alleles (Frary *et al.* 2000). *FW3.2* and *FW11.3* were identified
5 as a P450 enzyme of the CYP78A subfamily (*SIKLUH*) and a *Cell Size Regulator* (*CSR*),
6 controlling cell division and expansion, respectively (Chakrabarti *et al.* 2013; Mu *et al.*
7 2017). Unlike *fw2.2*, *fw3.2* and *fw11.3*, which mostly affect fruit size, *fas* and *lc* also control
8 fruit shape. The big-fruit *fas* and *lc* alleles increase the number of carpels, altering cell
9 differentiation through the CLAVATA3-WUSCHEL module (Schoof *et al.* 2000). The
10 increase in the number of carpels often results in larger and wider fruits with many locules
11 and pronounced ribbing (Lippman and Tanksley 2001; van der Knaap and Tanksley 2003).
12 The *lc* mutant phenotype is caused by two single-nucleotide polymorphisms (SNPs)
13 downstream of the coding region of the *WUSCHEL* (*WUS*) gene (Muños *et al.* 2011). The *fas*
14 mutation is a partial loss of expression caused by a chromosome inversion with a break point
15 in the vicinity of the *CLAVATA3* (*CLV3*) gene (Xu *et al.* 2015), a negative regulator of *WUS*
16 (Schoof *et al.* 2000). Lastly, *ENO* is an AP2/ERF transcription factor that interacts
17 synergistically with *lc* and *fas*, causing a substantial increase of the *WUS* expression domain,
18 which results in enlarged floral meristems (Fernández-Lozano *et al.* 2015; Yuste-Lisbona *et*
19 *al.* 2020). The *ENO* domestication allele (a promoter deletion that reduces its expression) also
20 affects stem cell fate, giving rise to multilocular fruits that derive from the larger floral
21 meristem.

22 Compared with the genetic regulation of fruit growth, relatively little is known about
23 the control of vegetative organ size. In many crops, domestication entailed the selection of
24 plants with bigger shoots and leaves. This is well documented in peppers (*Capsicum spp*;
25 Jarret *et al.* 2019), sunflower (*Helianthus annuus*; Warburton *et al.* 2017), soybeans (*Glycine*

1 *max*; Kofsky *et al.* 2018) and common beans (*Phaseolus vulgaris*; Herron *et al.* 2020). It is
2 also evident when comparing the leaves of wild species and the cultivated tomato
3 [Supplementary data Fig. S1]. The proportional increase in the size of vegetative parts of
4 cultivated tomato is likely to be a component of isometric gigantism during domestication.
5 Here, we hypothesized that if vegetative gigantism is under genetic control, the wild species'
6 alleles leading to reduced organ size could be found through wide crosses between cultivated
7 tomato and its wild relative species. We selected *S. pennellii* LA0716 as a wild parent, due to
8 its well annotated genome sequence (Bolger *et al.* 2014) and its rich repertoire of genomic
9 tools, such as fully sequenced introgression lines (ILs) (Alseikh *et al.* 2013; Chitwood *et al.*
10 2014). We crossed *S. pennellii* to the cultivated tomato cv. Micro-Tom (MT) and after
11 successive backcrosses and phenotypic selection, we isolated an IL with reduced vegetative
12 and reproductive organs compared to the recurrent parent MT. We mapped this introgression
13 to chromosome 7 and named the locus *ORGAN SIZE* (*ORG*). We show that *ORG* leads to
14 reduced organ size through changes in cell division, and that it segregates as a monogenic,
15 semi-dominant Mendelian locus. Our fine mapping results show that the *ORG* candidate
16 genes overlap a previously described domestication sweep (Lin *et al.* 2014). We speculate on
17 the impact of this locus in the tomato domestication syndrome and discuss its potential
18 exploitation for crop breeding.

19

20 **Materials and methods**

21

22 *Plant material*

23 The wild relatives of tomato used in this work were *S. pennellii*(LA0716), *S. chilense*
24 (LA1969), *S. peruvianum*(LA1537), *S. neorickii*(LA1322), *S. chmieslewskii*(LA1028), *S.*
25 *habrochaitesf. glabratum*(PI134417), *S. habrochaitesf. hirsutum*(LA1777), *S. galapagense*

1 (LA1401), *S. pimpinellifolium* (CNP384), and *S. lycopersicum* var. *cerasiforme* (LA1320).
2 Domesticated tomatoes of the cultivars Micro-Tom (MT) (LA3911), M82 (LA3475),
3 Moneymaker (LA2706) and Santa Clara (Brazilian local cultivar) were also used. The *S.*
4 *pennellii* chromosome 7 introgression lines (ILs) harboring alleles of *ORGAN SIZE* (*ORG*),
5 *BRILLIANT COROLLA* (*Bco*) (Chetelat 1998) and *Rg7H* (Pinto *et al.* 2017) were obtained
6 through repeated backcrossing between cultivated MT as a pollen receptor and *S. pennellii*, as
7 described in Carvalho *et al.* (2011). Seeds of the tomato wild relatives were obtained from the
8 UC Davis/C.M. Rick Tomato Genetics Resource Center, maintained by the Department of
9 Plant Sciences, University of California, Davis, CA 95616. Seeds of MT were kindly donated
10 by Prof. Avram Levy (Weizmann Institute of Science, Israel) in 1998 and kept as a true-to-
11 type cultivar through self-pollination.

12 *Growth conditions*

13 Plants were grown in a greenhouse at the Laboratory of Plant Developmental
14 Genetics, ESALQ-USP, (543 m a.s.l., 22° 42' 36" S; 47° 37' 50" W), Piracicaba, SP, Brazil.
15 Automatic irrigation took place four times a day. Growth conditions were: mean temperature
16 of 28°C, 11.5 h/13 h (winter/summer) photoperiod, 250–350 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ PAR
17 irradiance, attained by a reflecting mesh (Aluminet, Polysack Indústrias Ltda, Leme, Brazil).
18 Seeds were germinated in 350 mL pots with a 1:1 mixture of commercial potting mix
19 Basaplant® (Base Agro, Artur Nogueira, SP, Brazil) and expanded vermiculite supplemented
20 with 1 g L⁻¹ 10:10:10 NPK and 4 g L⁻¹ dolomite limestone (MgCO₃ + CaCO₃). Upon the
21 appearance of the first true leaf, seedlings were transplanted to pots containing the soil mix
22 described above, except for NPK supplementation, which was increased to 8 g L⁻¹. In
23 addition, MT and *ORG* plants received a supplementary fertilization of 0.5g of NPK

1 formulation 10:10:10 after flowering. Cultivated and wild tomato plants were supplemented
2 with 2g of NPK formulation 10:10:10 per plant.

3 4 *Phenotypic characterization*

5 We scanned all leaves of the MT and *ORG* plants 40 days after germination (dag) and
6 determined the leaf area using ImageJ software (<http://rsbweb.nih.gov/ij/>). For the
7 characterization of floral whorls, we evaluated: length of petals and sepals; corolla area; and
8 ovary weight, height and diameter. To measure ovary length and height we used a
9 magnifying glass (Leica S8AP0, Wetzlar, Germany), coupled to a camera (Leica DFC295
10 Wetzlar, Germany). To determine ovary weight we determined the weight of 1.5 mL
11 Eppendorf microtubes with 1 mL of distilled water, before and after collection of 10 ovaries.
12 Ovary weight was then determined as the difference between initial and final tube weight.
13 We also evaluated the leaf area and ovary weight of M82 plants and introgression lines (ILs)
14 from chromosome 7, using the same methodology as for MT and *ORG*.

15 16 *MT and ORG productivity traits*

17 We hand-pollinated MT and *ORG* plants with pollen from MT and *ORG* plants,
18 because the *ORG* genotype displayed low fruit set. Various ovaries were pollinated, but after
19 fruit set confirmation (five days after pollination), we performed selective fruit removal to
20 allow only five fruits to set on each plant.

21 Productive performance of plants was assessed 90 days after germination. The
22 following parameters were determined: mean weight per fruit; total soluble solids content in
23 fruits (Brix); locule number and number of seeds per fruit; and weight of 10 seeds. Total
24 soluble solids content of fruits was assessed using a digital refractometer (PR-101, Atago,
25 Tokyo, Japan).

1

2 *Source-sink ratio in MT and ORG plants*

3 To determine whether leaf area of *ORG* plants is a limiting factor for fruit
4 development (since leaves and fruits are the major sources and sinks of photoassimilates,
5 respectively), we manipulated plants creating three categories based on different source-to-
6 sink ratios. Thus, we kept the same amount of source tissue (leaves) in all plants of each
7 genotype and altered the sink strength by changing fruit number (either three, six or nine per
8 plant, to produce high, medium or low source-to-sink ratios, respectively). We removed side
9 branches to prevent them from acting as alternative sinks. The following parameters were
10 then determined: total fruit weight per plant (yield); average fruit weight and whole-plant leaf
11 area.

12

13 *Mapping and PCR amplification of DNA markers*

14 We designed molecular markers to discover polymorphisms between tomato and *S.*
15 *pennellii* in the region comprising the IL-7-2 and part of the IL 7-4 (Chitwood *et al.*, 2014).
16 The sequences and types of molecular makers are shown on **Supplementary Table S1**. Two
17 further genotypes harbouring genome segments of *S. pennellii* for chromosome 7, *Brilliant*
18 *corolla*(*Bco*) and *Regeneration 7h*(*Rg7H*), both in cv. MT, were characterized molecularly
19 and phenotypically. Cross-referencing information from these genotypes and the ILs in the
20 M82 background we constructed a map with the putative location of the *ORG*locus.

21 Genomic DNA extraction from young leaves was performed as described by Fulton *et*
22 *al.* (1995). PCR was performed using the following program: a denaturation step at 95°C for
23 2 min, 35 cycles of 30 s at 95°C, 60s at 56°C, 90 s at 72°C, and a final cycle at 72°C for 7
24 min. When required, restriction enzyme analysis [**Supplementary Table S1**] was performed
25 following the manufacturer's recommendations (NEB, Bethesda, USA). The final PCR

1 products were analyzed via 1.5% (m/v) agarose gel electrophoresis, stained with SYBR Gold
2 (Invitrogen).

3 4 *Histological and microscopic analyses*

5 Samples of MT and *ORG* ovaries/fruits at -8, -4, 0, 4 and 8 days, and fruit pericarps at
6 12 and 16 days (anthesis = 0), were collected and fixed in Karnovsky solution (Karnovsky
7 1965), and vacuum-infiltrated for 15 min. The times referred to as -8 and -4 days correspond
8 to 8 and 4 days before anthesis (dba), respectively. We based the dba on the length of closed
9 flower buds, previously calibrated (4 mm = 8 dba and 6 mm = 4 dba). To calculate the days
10 after anthesis (daa), the flowers were marked with sewing thread at anthesis.

11 Samples were next dehydrated in an increasing ethanol series (10–100%), and
12 infiltrated into synthetic resin, using a HistoResin embedding kit (Leica, [www.leica-](http://www.leica-microsystems.com)
13 [microsystems.com](http://www.leica-microsystems.com)), according to the manufacturer's instructions. The tissues were sliced
14 using a rotary microtome (Leica RM 2045, Wetzlar, Germany), stained with toluidine blue
15 0.05% (Sakai 1973), and photographed in a microscope (Leica DMLB, Heidelberg,
16 Germany), coupled to a Leica DFC310 camera (Wetzlar, Germany). Histological analysis of
17 ovaries was performed in the central region of the outer pericarp of the fruits, and the area
18 and number of cells were determined using ImageJ software (<http://rsbweb.nih.gov/ij/>). This
19 histological analysis also was performed in the mature leaves of these genotypes adopting the
20 procedures described above. The area and number of cells in the adaxial leaf epidermis of the
21 MT and *ORG* genotypes was also evaluated using the leaf dental resin imprinting technique
22 (Weyers and Johansen 1985).

23 24 *Quantitative real-time reverse transcription PCR*

1 Total RNA was extracted from ovaries/fruits at -8, -4, 0, 4 and 8 days, and fruit
2 pericarps at 12 and 16 days (anthesis = 0), using Trizol reagent (Invitrogen), as indicated by
3 the manufacturer, and treated with RQ1 RNase-Free DNase (Promega). Fruit pericarps were
4 carefully collected from the central region of the outer pericarp of the fruits, at 12 and 16
5 days. After DNase treatment, a single-strand cDNA was synthesized from total RNA (1µg)
6 by reverse-transcription, using RevertAid RT Reverse Transcription Kit (Thermo Fisher
7 Scientific).

8 Gene expression analyses were performed on a Rotor-Gene Q real-time PCR cycler
9 (Qiagen), using Kapa Sybr Fast qPCR Master Mix (Kapa Biosystems) and specific primers
10 for *CYCB2;1*(Solyc02g082820), *FW2.2*(Solyc02g090730), *FW3.2* (Solyc03g114940) and
11 *EXP5* (Solyc02g088100) genes. The reactions were amplified for 2 min at 95 °C, followed by
12 40 cycles of 95 °C for 15 s and 60 °C for 30 s. The threshold cycle (C_T) was determined.
13 Melting curve analysis was performed with each primer set to confirm the presence of only a
14 single peak before the gene expression analyses. Two technical replicates were analyzed for
15 each of three or four biological samples. The relative transcript accumulation was normalized
16 to an *ACTIN* (Solyc04g011500) gene. The fold changes for each gene were calculated using
17 the equation $2^{-\Delta\Delta CT}$ (Livak and Schmittgen 2001). Primer sequences used to qRT-PCR are
18 shown in **Supplementary Table S1**.

19

20 *In silico analysis of probable ORG region*

21 The genomes of *S. lycopersicum* SL2.50 (<https://solgenomics.net/>) and *S. pennellii*
22 LA0716 (Bolger *et al.*, 2014) were aligned and plotted with Mummer v4.0.0 (Marcais *et al.*,
23 2018). Variants of *S. pennellii* LA0716 versus SL2.50 within the *ORG* region were obtained
24 through the Wageningen resequencing project (Aflitos *et al.*, 2014). The coding sequences of
25 the genes within the region were obtained from Solanaceae Genomics Network

(<https://solgenomics.net/>) and similarities between tomato and its wild relative were tested with BLAST v2.10.0 (Camacho *et al.*, 2009). The Circos plot was created with Circos v0.69.9 (Krzywinski *et al.*, 2009) on Windows 10. The synteny plot was created with the genoPlotR package (Guy *et al.*, 2011) within R (Team, 2017).

Genotyping by sequencing (GBS)

DNA was extracted from young leaf samples (~10 mm length) that were freeze-dried (CoolSafe™ 55-9; Scanvac, Lynge, Denmark) overnight. Leaf samples were powdered in a Star-Beater (VWR, Lutterworth, UK) at 30 Hz for 30s in 2 mL microcentrifuge tubes containing two 5 mm acid-rinsed soda-glass balls. DNA was extracted from ~50 mg samples with an E.Z.N.A® Plant DNA Kit (VWR, Lutterworth, UK). DNA fragment size was assessed on a 1% agarose gel in Tris/Borate/EDTA to confirm that all samples had the majority of DNA fragments >10 kilobases.

The GBS library was prepared using the restriction enzyme *MseI* and sequenced on an Illumina NextSeq 500 V2 by LGC Genomics (Berlin, Germany). The 150 base-pair paired-end reads were aligned to the *Solanum lycopersicum* reference genome (SL2.50) with BWA v0.7.15 (Li and Durbin, 2009). The SAM files were processed with Samtools Fixmate v1.3.1 (Li *et al.*, 2009). InDels were realigned with GATK's IndelRealigner v3.8-0 (McKenna *et al.*, 2010; DePristo *et al.*, 2011) before variant calling with Samtools Mpileup v1.3.1 and Bcftools Call v1.3 (Li, 2011).

The raw VCF files of the GBS sample, a 40× resequenced Micro-Tom (Cranfield University, unpublished data) and the resequencing of *S. pennellii* LA0716 (Aflitos *et al.*, 2014), were combined into an index using Tersect (Kurowski and Mohareb, 2020). Tersect was used to determine which variants were shared between the *ORG* IL and *S. pennellii* LA0716, excluding the variants shared with Micro-Tom. The variants output from Tersect were then filtered as follows: all variants with a quality score less than 20, a mapping quality

1 score below 40 and a raw read depth either below 10 and above 200 were removed. In
2 addition, heterozygous variants were removed. The variant density of the filtered variants
3 over a 10 kb window (5 kb sliding) were plotted across all 12 chromosomes with ggplot2
4 (Wickham, 2016) within R.

5 *Statistical analysis*

6 Statistical analysis was performed using SAS software (SAS Institute Inc., Cary, NC,
7 USA). The variables data were submitted to analysis of variance (ANOVA) and the means
8 compared by the Student's t- or Tukey's test. When the data did not meet the assumptions of
9 ANOVA, we performed to non-parametric analysis, using Wilcoxon rank sum or Dunn's test
10 to compare the means.

11

12 **Results**

13 *Natural genetic variation for leaf size in tomato*

14 Compared to domesticated tomato cultivars, most wild relatives of the tomato have
15 small leaves [**Supplementary data Fig. S1**]. Thus, we decided to look for a genetic
16 determinant of leaf size in the wild species. We crossed *S. pennellii* LA0716 to the cultivated
17 tomato cv. Micro-Tom (MT). Upon self-fertilization of the F₁ population, we selected F₂
18 plants with small leaves, from which we collected pollen to backcross (BC) to MT. After six
19 rounds of backcrossing (BC₆) to the recurrent parental (MT), self-fertilization (BC₆F₂),
20 phenotypic screening, and further self-fertilization (BC₆F_n), we produced an introgression
21 line (IL) with reduced leaf size in the MT background, which we called *ORGAN SIZE (ORG)*
22 (Fig. 1). *ORG* plants show a very conspicuous phenotype for leaf size: the difference in leaf
23 size between MT and *ORG* was consistent across all leaves and developmental stages (Fig.
24 1). Monogenic segregation of *ORG* was verified on a segregating population of MT and
25 *ORG*. We determined leaf size in F₁ hybrids between MT and *ORG* [**Supplementary data**

1 **Fig. S2A]**, and the intermediate phenotype suggested that *ORG* behaves as a semi-dominant
2 gene [**Supplementary data Fig. S2B**].

3
4 *The smaller leaf in ORG is caused by reduced cell division*

5 Change in organ size is due to either altered cell proliferation or expansion, or a
6 combination of both (Krizek 2009). We analysed *ORG* leaves and found enlarged epidermal
7 [**Supplementary data Fig. S3A-C**] and mesophyll [**Supplementary data Fig. S3D-F**] cells
8 compared to MT. This suggests that the smaller leaves of *ORG* are caused by reduced cell
9 proliferation as evidenced by cell number and density of *ORG* compared to MT. On the other
10 hand, the increased cell size in *ORG* can be better explained by the compensatory system that
11 operates in leaves as part of the Neo-Cell Theory (Tsukaya, 2002). The greater palisade
12 parenchyma cell size promoted an increase in leaf thickness in *ORG* [**Supplementary data**
13 **Fig. S3G-I**]. We next performed a time course analysis of reproductive growth starting eight
14 days before anthesis and until 16 days after anthesis and verified a decrease in the size of
15 styles, ovaries and fruits in *ORG* (Fig. 2). As in the case of leaves, the reduction was caused
16 by lower cell numbers, which we verified as a reduced number of cell layers in the pericarp
17 (Fig. 2C). The ovary cells of *ORG* were also smaller than MT cells at anthesis and post-
18 anthesis (Fig. 2D). Other floral organs, namely, petals and sepals, were also reduced in *ORG*
19 flowers compared to MT [**Supplementary data Fig. S4A-D**]. The reduced size of floral
20 organs may have strong consequences on fruit development, given their impact on ovary size
21 [**Supplementary data Fig. S4E-H**].

22
23 *Fruit weight and yield are reduced in ORG*

24 The size and shape of the ovary before anthesis is strongly correlated with the final
25 size and shape of the fruit (Grandillo *et al.*, 1999; Azzi *et al.*, 2015). Thus, we next analysed

1 the potential impact of *ORG* on fruit development. Fruit set was reduced in heterostylis *ORG*
2 flowers, so we hand-pollinated emasculated MT and *ORG* flowers in a reciprocal cross.
3 Several ovaries per plant were pollinated, but after fruit set confirmation (five days after
4 pollination), we performed selective fruit removal to allow only five fruits to set on each
5 plant. The presence of *ORG* ovaries had a substantial impact on the final fruit size regardless
6 of pollen origin (Fig. 3). Fruit weight was 31-37% lower in *ORG* than in MT ($P < 0.0001$)
7 [Supplementary table S2]. *ORG* fruits have higher total soluble solids content (°Brix)
8 compared to MT [Supplementary data Fig. S5A]. We further observed that *ORG* had a
9 similar frequency of locule number per fruit [Supplementary data Fig. S5B] and reduced
10 seed number (Fig. 3A). Reciprocal crosses indicated that the reduction in seed number is
11 determined by *ORG* ovaries rather than pollen [Supplementary data Fig. S5C].

12 We next addressed the possibility that reduced fruit size could be the consequence of
13 altered photosynthetic source-sink relationships due to reduced leaf area. We thus
14 manipulated the plants to maintain the availability of sources (leaves) constant and altered the
15 source:sink ratio by changing the number of sinks (fruits). Three treatments were performed:
16 either three, six or nine fruits were allowed to set on each plant. To ensure that additional
17 sinks did not interfere in the results, we also pruned all the plants to remove side shoots. The
18 results are summarized on Fig. 3C-E. *ORG* plants produced consistently smaller fruits than
19 MT in all treatments (Fig. 3C). The increase in fruit number, from three to six, promoted a
20 reduction in fruit weight only in MT plants, suggesting that leaf area was a limiting factor to
21 the final fruit weight in MT, since the leaf area was similar in both experimental conditions
22 (Fig. 3D). On the other hand, when the number of fruits was increased from six to nine, there
23 was a reduction in the final fruit weight for both genotypes. These results suggest that the
24 smaller leaf of *ORG* could also account for its reduced fruit size, but only under full fruit
25 load. Therefore, the primary cause of the reduced fruit size in *ORG* is likely a direct effect of

1 this organ development from pre-anthesis (Fig. 2C). In addition, the presence of the *ORG*
2 introgression reduced yield in all treatments (Fig. 3E).

3 4 5 *Expression patterns of genes related to cell division and expansion are altered in ORG*

6 The results described so far suggest that the transcriptional activity of genes involved
7 in the control of cell division and expansion could be altered in *ORG*. To assess this, we
8 extracted mRNA from ovaries/fruits at -8, -4, 0, 4 and 8 days, where -8 and -4 mean pre-
9 anthesis, 0 is the day of anthesis and 4 and 8 mean post-anthesis stages. Additionally, we
10 isolated mRNA from fruit pericarps at 12 and 16 days to analyse the transcriptional profile of
11 a set of genes related to the control of cell division/expansion: *CYCLIN B2;1*
12 (Solyc02g082820), *FW2.2*(Solyc02g090730), *FW3.2/SIKLUH* (Solyc03g114940) and
13 *EXPANSIN PRECURSOR 5*(Solyc02g088100).

14 In ovary/fruit tissues, we verified that the mRNA levels of the cell-division genes
15 *CYCB2;1*and *FW3.2* showed greatest expression in both genotypes at 4 days pre-anthesis
16 (Fig. 4). *CYCB2;1* was higher in MT than *ORG* especially in pre-anthesis and anthesis stages
17 (at -4, -8, and 0 days), while *FW3.2* was higher in anthesis and post-anthesis stages (at 0, 4
18 and 12 days). On the other hand, *FW2.2*, another cell-division gene, but a negative regulator,
19 was highly expressed at 4 and 8 days post-anthesis in both genotypes. Quantitative variation
20 in *FW2.2* expression was observed pre- and post-anthesis between genotypes (at -4 and 8
21 days, respectively), whereas *ORG* ovaries showed significant increased levels of this
22 transcript compared than MT (Fig. 4C). After 4 days post-anthesis, the expression of the cell-
23 expansion gene *EXP5*, a member of the α -expansin gene family, increased in in both
24 genotypes (Fig. 4D). However, ovaries of *ORG* plants displayed a significant decrease in the
25 expression of this gene at anthesis compared to MT. Similar behavior was observed 16 DPA.

1 The inconsistency between *EXP5* expression and the smaller fruit size of *ORG* at days 4, 8
2 and 12 post-anthesis is likely to be explained by the fact that at these stages the main process
3 governing fruit size is not cell expansion, but cell division (Tanksley, 2004).

4

5 *The ORG locus is located on chromosome 7*

6 We next conducted a genotyping by sequencing (GBS) analysis to determine the size
7 and location of the *S. pennellii* introgression in *ORG*. The results show a discrete region in
8 the terminal end of the long arm of chromosome 7 encompassing ~11 Mb (Fig. 5A). No
9 further segments of *S. pennellii* genome were found on other chromosomes. Based on the
10 SL2.50 tomato genome annotation, the introgression region contains 1169 genes. A closer
11 look at the introgressed region evidenced of a small double recombination, from position
12 64,826,717 to 65,444,176, encompassing 78 tomato genes which score as *S. lycopersicum*
13 (Fig. 5B).

14

15 *Fine-mapping of ORG using introgression lines*

16 To reduce the list of candidate genes for *ORG*, we next analysed two other
17 introgression lines (ILs) of *S. pennellii* LA0716 in the MT background previously generated
18 in our laboratory: *Brilliant corolla*(*Bco*)and *Regeneration 7H*(*Rg7H*), both of which
19 partially overlap either end of the *ORG* introgression (Fig. 6). We used the span of the
20 introgressions in *Bco* [Supplementary data Fig. S6] and *Rg7H*(Pinto *et al.* 2017) and the
21 extent of their overlap with *ORG* to narrow down the candidate region for *ORG*. Given that
22 neither of these ILs show the reduced organ phenotype of *ORG* (Fig. 6B-C), the resulting
23 candidate region is located between positions 65,444,176 and 66,373,175 (Fig. 6A).

24 We took advantage of the existing collection of ILs from *S. pennellii* in tomato cv.
25 M82 as a tool to further refine the above chromosome location (Zamir and Eshed 1994;

1 1995). The introgressions were precisely delimited by sequencing by Chitwood *et al.*(2014),
2 who also characterized terminal and lateral leaflet size in the ILs. Their results revealed the
3 existence of a QTL for reduced leaflet size on both IL7-2 and IL7-3 (Fig. 7A-B). We also
4 cultivated ILs harbouring *S. pennellii* genomic segments on chromosome 7 (IL7-1; IL7-2,
5 IL7-3; IL7-4 and IL7-5) and determined their leaf and ovary size. We found a reduction in
6 the ovaries of both IL7-2 and IL7-3, compared to M82, but under our growth conditions only
7 IL7-2 showed consistently smaller leaves than the parental line **[Supplementary data Fig.**
8 **S7]**. We found a discrepancy between the Chitwood *et al.* dataset and ours for leaf size on
9 IL7-1, but the consistently smaller pistils in IL7-2 and IL7-3 helped us delimit the right
10 border of the candidate region to 65,865,655, narrowing the interval to 421,479 bp (Fig. 7C).

11

12 *Genomic analysis of ORG and identification of candidate genes*

13 The resequenced dataset of tomato and wild relative accessions (Aflitos *et al.*2014)
14 was used to identify the polymorphisms of *S. pennellii* when aligned with *S. lycopersicum*
15 (SL2.50) in the *ORG* region. We found 58 CDS within the *ORG* region in the *S. pennellii*
16 genome and 65 CDS within *S. lycopersicum*, with considerable synteny (Fig. 7D). Within the
17 *ORG* region, an alignment of the *S. pennellii* genome sequence (Spenn-ch07:76,477,056-
18 76,940,423) with *S. lycopersicum* (SL2.50ch07:65,444,176-65,865,655) showed that the two
19 genomes were structurally similar **[Supplementary data Fig. S8]**. We therefore investigated
20 the similarities and differences in the coding sequences (CDS) between the two genomes with
21 BLAST **[Supplementary table S3]**. We found a total of 6,009 polymorphisms, 5,093 of
22 which were single-nucleotide polymorphisms (SNPs) and 916 were insertions-deletions
23 (InDels). Additionally, there were 304 moderate effect missense variants affecting 58 genes
24 **[Supplementary Table S4]** and 18 high effect polymorphisms (e.g. frameshift variants, stop
25 gained) **[Supplementary Table S5]**. There was one *S. pennellii* CDS without a

1 corresponding match in *S. lycopersicum*, *i.e.* a new gene within the *ORG* region, namely
2 Sopen07g031050 (hypothetical protein). Additionally, there were six presence-absence
3 variants (PAVs) in *S. lycopersicum* without a corresponding match in *S. pennellii*
4 **[Supplementary Table S6]**, *i.e.* six genes lost in the *ORG* region, namely, a Yippee family
5 protein (Soly07g062900), a nucleolar GTP-binding protein 2 (Soly07g063280), a Tir 2C
6 resistance protein (Soly07g063360) and three CDS annotated as ‘unknown protein’. The
7 genes Sopen07g031090 and Sopen07g031100, both being putative Yippee family zinc-
8 binding proteins, produced multiple significant matches with Soly07g062880,
9 Soly07g062890 and Soly07g062910. Additionally, Sopen07g031530 (beta glucosidase 46)
10 and Sopen07g031540 (hypothetical protein) produced only partial matches with
11 Soly07g063370 (beta glucosidase) and Soly07g063380 (unknown protein), respectively;
12 indicating that the gene pairs share conserved regions but are otherwise dissimilar (Fig. 7D).

13 In summary, *ORG* is a natural genetic variation located on chromosome 7, which
14 controls both vegetative and reproductive organ size in tomato. Its primarily effect seems to
15 be in cell division, as evidenced by its impact on ovary size. However, additional effects on
16 cell expansion and source-sink dynamics, possibly due to the smaller leaf size, cannot be
17 ruled out.

18

19 Discussion

20 The genetic basis of fruit gigantism has been extensively explored in tomato and a
21 number of major genes controlling that trait have been identified (Nesbitt and Tanksley 2001;
22 Causse *et al.* 2004; Muños *et al.* 2011; Chakrabarti *et al.* 2013; Mu *et al.* 2017). However, the
23 genetic mechanisms behind isometric gigantism between vegetative and reproductive organs
24 are unknown. Are they driven pleiotropically by genes for fruit gigantism that operate on the
25 meristem simultaneously controlling vegetative and reproductive development, or are they

1 the product of indirect selection on independent loci necessitated by the altered source-sink
2 relationships between vegetative or reproductive organs? As a starting point to address this
3 question, we set out to discover genetic determinants for changes in the size of vegetative
4 organs in the tomato. We thus identified *ORGAN SIZE (ORG)*, an introgression with reduced
5 leaf size but which also showed smaller reproductive organs, namely flowers and fruits.

6 Instead of the conventional approach of QTL mapping, which sometimes is followed
7 by fine-mapping and gene cloning, we revisited the alternative, forward genetics strategy, of
8 wide cross followed by controlled introgression (Rick, 1969). We crossed *S. pennellii* to the
9 tomato cv. Micro-Tom (MT) and conducted multiple rounds of crosses and backcrosses to the
10 recurrent domesticated parental, selecting plants with smaller leaves in each generation. Our
11 results, which identified the *ORG* locus, tie up previous, independent studies of the genetic
12 control of leaf (Holtan and Hake, 2003; Chitwood *et al.*, 2014) and fruit (Grandillo *et al.*
13 1999; van der Knaap and Tanksley 2003; Causse *et al.* 2004; Barrantes *et al.* 2016) size in
14 tomato using QTL analysis. Hence, a survey of previous studies that identified putative QTLs
15 for increased fruit weight during tomato domestication and breeding reveal a chromosomal
16 region overlapping *ORG* (Fig. 8). However, none of these studies reported alterations in
17 vegetative development associated to fruit weight QTLs. This indicates that controlled
18 introgression guided by phenotypic selection is a powerful tool that, unlike QTL mapping,
19 allows the detection of genes (or closely linked genes) that control more than one trait
20 simultaneously. Either QTL mapping, or its more up-to-date variant, genome-wide
21 sequencing analysis (GWAS), are useful to detect multiple genes spread out in the genome
22 controlling one trait, but on the other hand, are prone to miss pleiotropic or tightly linked
23 genes controlling multiple traits, because generally only one phenotype is analysed at a time
24 (Zhu *et al.* 2022). As will be discussed below, the findings presented herein strongly indicate
25 that *ORG* exerts pleiotropic control over both leaf and fruit size due to its primarily impact on

1 cell division. Nonetheless, we cannot entirely dismiss the possibility that the fruit size in
2 *ORG* is also an indirect outcome of its reduced leaf area, possibly arising from source-sink
3 constraints.

4 Genotyping-by-sequencing showed *ORG* to harbour 1169 genes in approximately 11
5 Mb of *S. pennellii* genome. This represents 1.15% of the tomato genome, which is a good fit
6 with the theoretically expected proportion of donor genome after six rounds of back-crossing
7 (Stam and Zeven 1981). Although the segregation data indicate that *ORG* behaves as a
8 Mendelian, semi-dominant gene, we cannot at this stage exclude the possibility that the IL
9 harbours two or more genes controlling similar traits on chromosome 7. However, we
10 showed that the common denominator for the reduced size of vegetative and reproductive
11 organs in *ORG* is a reduction in the number of cells, possibly through alteration of cell
12 division rate, as suggested by histological characterizations and gene expression analyses for
13 *CYCB2;1*, *FW2.2* and *FW3.2*. This trait could be under pleiotropic control of a single gene. In
14 fact, our analysis of the genes contained in the candidate region shows variation between *S.*
15 *pennellii* and *S. lycopersicum* for genes predicted to be involved in the control of cell
16 division, as well as regulatory genes that could control the size of organs [Supplementary
17 tables S4, S5]. Lin *et al.* (2014), analyzing the genome sequence of 360 tomato accessions,
18 identified an interval containing 19 putative domestication genes on chromosome 7. All 19
19 genes are contained within the list of 58 candidates for the *ORG* region. This paves the way
20 for the future identification and validation of, potentially, a single genetic variant (*e.g.* SNP,
21 InDel, PAV) that controls organ size and underpins tomato domestication.

22 Increased organ size, or gigantism, is a recurrent domestication trait observed in many
23 crops. Selection for increased size of edible parts led to allometric increases in reproductive
24 organs. However, domesticated plants also tend to present gigantism in vegetative parts, *e.g.*
25 larger leaves and thicker stems in *Phaseolus vulgaris* (Donald and Hamblin, 1983), larger

1 leaves in eggplant (Page *et al.*, 2019) and soybean (Kofsky *et al.*, 2018). The tomato shows
2 striking increases in fruit size (Tanksley 2004), but also leaf area, and stem thickness
3 compared to its wild relatives (Milla and Matesanz, 2017).

4 This isometric size change could lead to a better balance between photosynthetic
5 sources and fruit sinks. On the other hand, when we altered the relative strength of the sinks
6 by allowing only three, six or nine fruits to develop in either MT or *ORG* plants, we found an
7 inverse correlation between fruit number and size in MT but not in *ORG*. In addition, the
8 reduction in fruit size of MT has no penalty in its final yield. These results suggest two
9 things. First, that the reduced size of *ORG* fruits is an intrinsic trait, possibly a developmental
10 result of smaller ovaries, and not an indirect consequence of reduced leaf area (photosynthetic
11 source). The second is that leaf area does not always directly limit fruit (sink) size and/or
12 yield. In agreement with this, both experimental and modelling work have shown that
13 moderate defoliation does not have a negative effect on crop yield, implying that source
14 strength is not always limiting (*i.e.*, provided water and nutrient availability are sufficient and
15 that photosynthesis is not light limited) (Heuvelink *et al.* 2005). An extreme situation is found
16 in garden peas (*Pisum sativum*), where leaf area reduction has been a breeding goal to reduce
17 interplant competition and increase yield (Cousin, 1997). Mutants of the ‘leafless’ and ‘semi-
18 leafless’ type show 40% lower leaf area with up to 20% higher yield and better standing
19 ability, which in turn facilitates mechanical harvesting (Checa *et al.* 2020). The increased
20 popularity and growing market niche for ‘gourmet’ cherry tomatoes opens up the perspective
21 of using *ORG* for breeding varieties with smaller fruits and leaves to improve agronomic
22 management (*e.g.* reduced fertilizer and water use) (Sarlikioti *et al.* 2011).

24 Conclusions

Based on the analysis of natural genetic variation, we have described a potential genetic determinant for increased leaf and fruit size in cultivated tomato. Our results could unveil a novel link in the genetic control of isometric fruit and leaf gigantism in tomato. Further research to determine the molecular identity of the genetic variant underlying the *ORG* phenotype is underway. Molecular characterization of *ORG* will allow its analysis in other *Solanum* species closer to the cultivated tomato, such as *S. pimpinellifolium*, providing more direct evidence for selection in this region during tomato domestication (Lin et al., 2014). This knowledge would also be a valuable addition in the repertoire of gene targets that can be manipulated with ideotype breeding (Donald, 1968; Zsögön *et al.* 2017) or *de novo* domestication platforms (Gasparini *et al.* 2021; Curtin *et al.* 2022).

Supplementary Data

Supplementary data consist of the following. **Table S1:** Oligonucleotide sequences used for genotyping and quantitative PCR analyses in this work. **Table S2:** Fruit weight of MT and *ORG* plants. **Table S3:** Similarities and discrepancies between coding sequences of *S. pennelliiv.* *S. lycopersicum* candidate genes. **Table S4:** Polymorphisms with a moderate effect on gene function for *S. pennelliiv* *S. lycopersicum* within the *ORG* region. **Table S5:** Polymorphisms with a high effect on gene function for *S. pennelliiv* *S. lycopersicum* within the *ORG* region. **Table S6:** Coding sequences of *S. lycopersicum* with no match on the *S. pennellii* genome assembly. **Figure S1:** Leaf size increases during tomato domestication and improvement. **Figure S2:** Heterozygous *ORG* plants (*ORG/+*) show an intermediate leaf area compared to MT and homozygous *ORG* plants. **Figure S3:** Smaller leaf size in *ORG* is caused by reduced cell division. **Figure S4:** *ORG* reduces organ size in all floral whorls. **Figure S5:** Fruit traits are altered in *ORG* plants. **Figure S6:** GBS defines the span of the introgression in the *Brilliant corolla* (*Bco*) introgression line. **Figure S7:** Characterization of

1 *S. pennellii* introgression lines (IL) in chromosome 7. **Figure S8:** Alignment plot of the *S.*
2 *pennellii* and *S. lycopersicum* genomes within the *OR* region.

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19 **Data availability statement**

20 All data supporting the findings of the present study are available within the paper and
21 its supplementary material files.

23 **Conflict of interest declaration**

24 No conflict of interest declared.

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10

11 **Figure legends**

12

13 **Figure 1. A tomato introgression line (IL) from *S. pennellii* with reduced organs (*ORG*) size. A.**
 14 Crossing scheme to create an introgression line with smaller leaves in the tomato cv Micro-Tom (MT)
 15 background. **B.** Representative population of MT (left) and *ORG* (right) plants, 25 days after
 16 germination (dag). **C.** Side and top view of MT (top) and *ORG* (bottom) plants. **D.** Leaf series of MT
 17 (top) and *ORG* (bottom) genotypes. C1 and C2 mean cotyledons and L1 to L5 represent leaf series
 18 from the first to the fifth one.). Scale bar=5 cm. **E.** Area of the cotyledons and the leaf series of MT
 19 (gray bar) and *ORG* (white bar) plants, 40 dag. Data are mean $\pm$ s.e.m. (n=14 leaves). Statistical
 20 significance was tested by Student's *t*-test ($***p<0.001$).

21

22 **Figure 2. *ORG* affects cell number and size during fruit development. A.** Developing ovary/fruit
 23 at -8, -4, 0, 4, 8, 12 and 16 days (anthesis = 0). MT (top) and *ORG* (bottom). Scale bar=5mm. **B.**
 24 Longitudinal sections of MT (top) and *ORG* (bottom) pericarp at -8, -4, 0, 4, 8, 12 and 16 days
 25 (anthesis = 0). Scale bar = 150 μ m. **C.** Time course of the number of cell layers in the longitudinal

1 sections of MT (gray bar) and *ORG* (white bar) ovary/fruit pericarp. Insert in top of this figure
 2 represents how the counting of the cells was performed and red lines delimited cell perimeter (n=30).
 3 **D.** Time course of cell size in the cell layers of MT (gray bar) and *ORG* (white bar) (n=30). Data are
 4 mean $\pm$ s.e.m. Statistical significance was tested by Student's *t*-test ($*p<0.05$, $***p<0.001$, *ns*
 5 indicates non-significant differences).

6
 7 **Figure 3. Fruit growth and source-sink relationships are altered in *ORG*.** **A.** Representative ripe
 8 fruits from ovaries of MT (♀) and *ORG* (♀) pollinated with MT (♂) and *ORG*(♂) pollen. Scale bar=1
 9 cm. **B.** Mean (red) and median (black) values of fruit weight of MT (gray box) and *ORG* (white box)
 10 ripe fruits pollinated with MT (n=10) and *ORG*(n=14) pollen. Data are mean $\pm$ s.e.m. Statistical
 11 significance was tested by Student's *t*-test ($***p<0.001$). **C-E.** Average values of fruits weight (C),
 12 leaf area (D) and yield (E) from MT (gray bar) and *ORG* (white bar) plants pruned to three, six and
 13 nine fruits (n=6 plants per treatment). Data are mean $\pm$ s.e.m. Different capital and lowercase letters on
 14 the symbols indicate significant differences by Tukey's test ($p<0.001$) between the treatments in MT
 15 and *ORG* genotypes, respectively.

16
 17 **Figure 4. Altered patterns of gene expression in *ORG*.** Time course of transcript levels of cell
 18 division- and expansion-related genes in ovaries/fruits of MT (gray bar) and *ORG* (white bar)
 19 genotypes. Relative (to actin control) transcript levels of *CYCB2;1* (**A**), *FW3.2* (**B**), *FW2.2* (**C**), and
 20 *EXP5* (**D**) in ovaries/fruit at -8, -4, 0, 4, 8 days and fruit pericarp at 12 and 16 days (anthesis = 0).
 21 Data are mean $\pm$ s.e.m (n=3 biological replicates indicated with black dots). Statistical significance was
 22 tested by Student's *t*-test ($*p<0.05$, $**p<0.01$, $***p<0.001$).

23
 24 **Figure 5. GBS defines the span of the introgression in the *ORG* introgression line (IL).** **A.**
 25 Genome-wide density of unique variants shared between *ORG* and *S. pennellii* LA0716 in the genetic
 26 background of tomato cv Micro-Tom. **B.** Close up view of the introgression on chromosome 7.

27

1 **Figure 6. Mapping refines the candidate region for *ORG*.** A. Two introgression lines (ILs) in the
2 tomato cv Micro-Tom (MT) background that contain different segments from *S. pennellii*
3 chromosome 7 (*Bco* and *Rg7H*) were mapped to refine the candidate region harboring the *ORG* locus
4 (red segment). B. Representative leaf of MT, *ORG*, *Rg7H* and *Bco* genotypes. Scale bar = 5 cm. (C-
5 D) Leaf area (C) and ovary weight (D) of MT, *ORG*, *Rg7H* and *Bco* (n=10). Data are mean±s.e.m.
6 Statistical significance was tested by Student's *t*-test (** $p < 0.01$, *** $p < 0.001$).

9 **Figure 7. Analysis of the genomic region containing *ORG*.** Terminal (A) and lateral (B) leaflet area
10 of M82 and chromosome 7 introgression lines (ILs) from *S. pennellii*. Data are mean ± s.e.m.
11 Statistical significance was tested by Student's *t*-test (* $p < 0.05$, *** $p < 0.001$, *ns* indicates non-
12 significant differences). Redrawn from Chitwood *et al.* (2014). (C) Chromosomal position of *S.*
13 *pennellii* genome segments in tomato cv. M82 background in chromosome 7. The location of the
14 *ORG* candidate region is shown in red. (D) Synteny plot of the coding sequences (CDS) within the
15 *ORG* region between *S. lycopersicum* and *S. pennellii* genomes. The similarity between the CDS of *S.*
16 *lycopersicum* (SL2.50) and *S. pennellii* (Spenn) were tested with BLAST+ and variant effect
17 prediction was obtained from the resequenced dataset (Aflitos *et al.* 2014). Key: Dark green, CDS that
18 match with a high level of similarity, but *S. pennellii* alleles contain single nucleotide polymorphisms
19 (SNPs). Light green, *S. pennellii* alleles contain insertions and deletions (InDels). Red, *S. pennellii*
20 alleles contain variants predicted to cause loss of function. Blue, complex relationship between *S.*
21 *lycopersicum* and *S. pennellii* alleles, *i.e.* multiple matches between different genes. Grey, partial
22 matches between *S. lycopersicum* and *S. pennellii* alleles, *i.e.* CDS with conserved regions but
23 otherwise dissimilar. Black, genes present in *S. lycopersicum* or *S. pennellii* only.

25 **Figure 8. Colocalization of *ORG* and previously mapped fruit size QTLs.** The *ORG* region
26 coincided with previously mapped QTLs (Quantitative Trait Loci) affecting fruit weight on
27 chromosome 7. See text for details. Bars indicate the approximate QTL location.

1

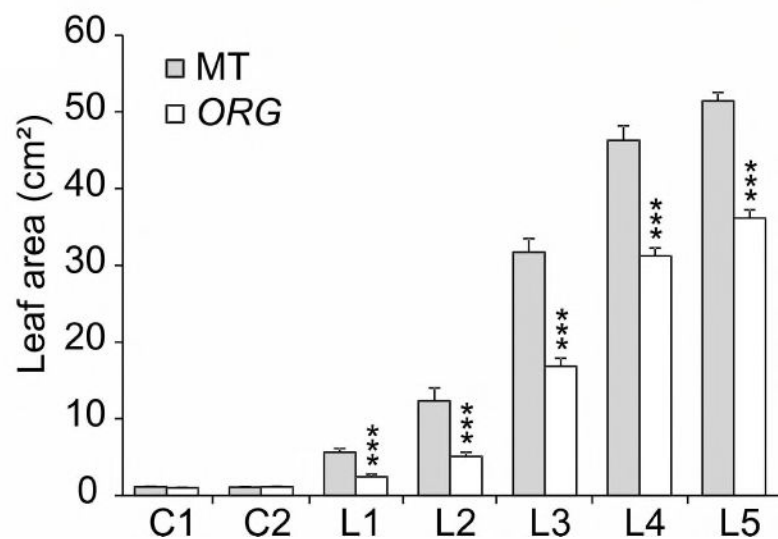
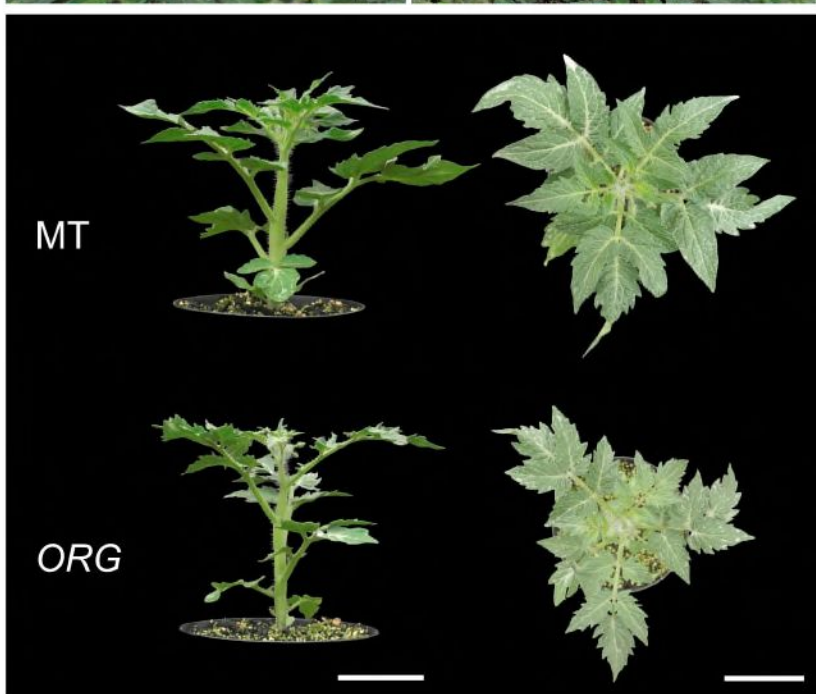
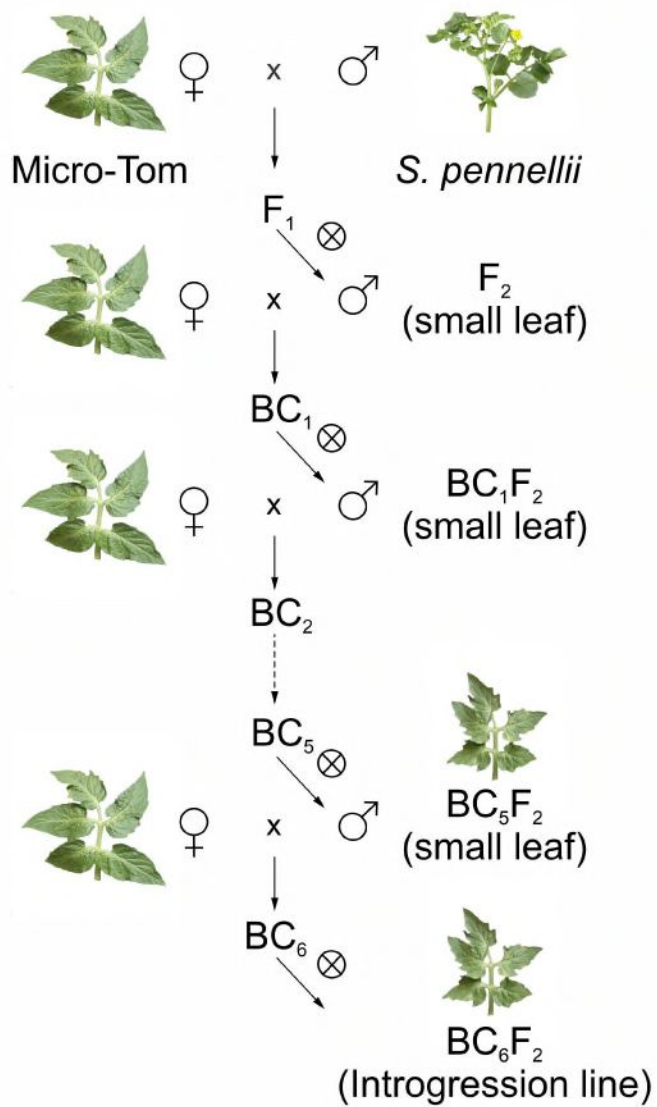
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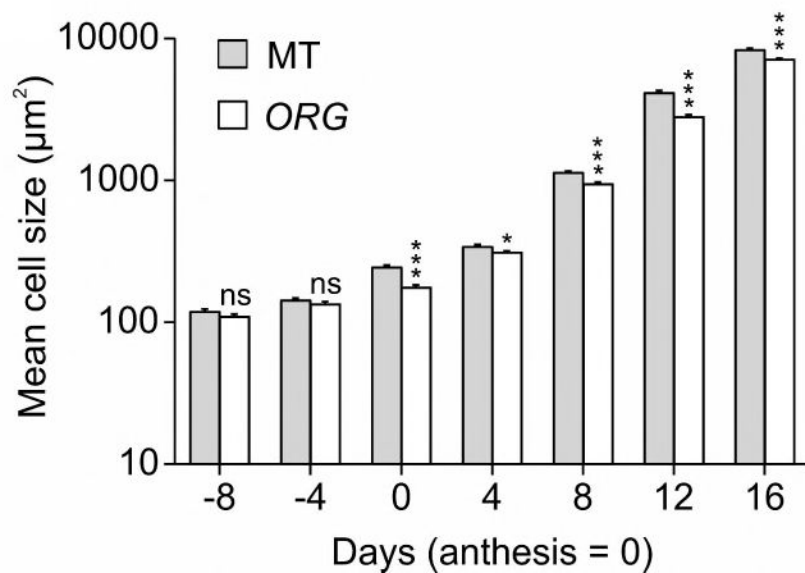
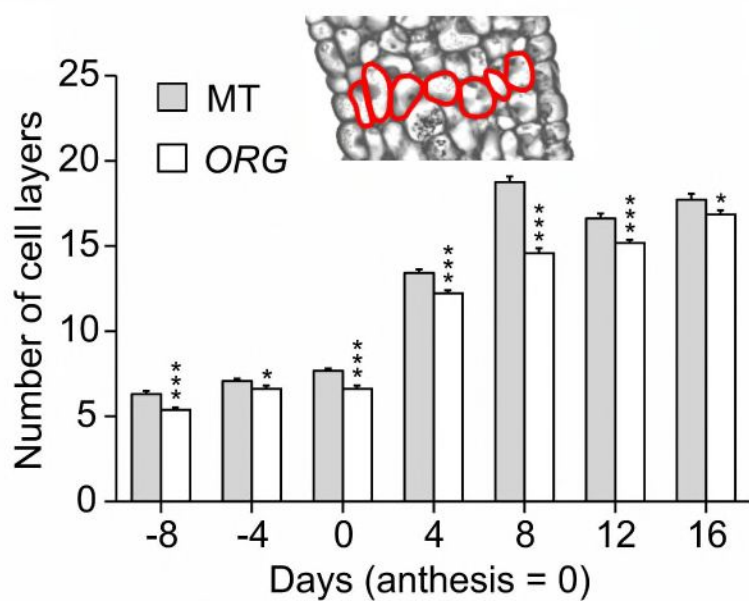
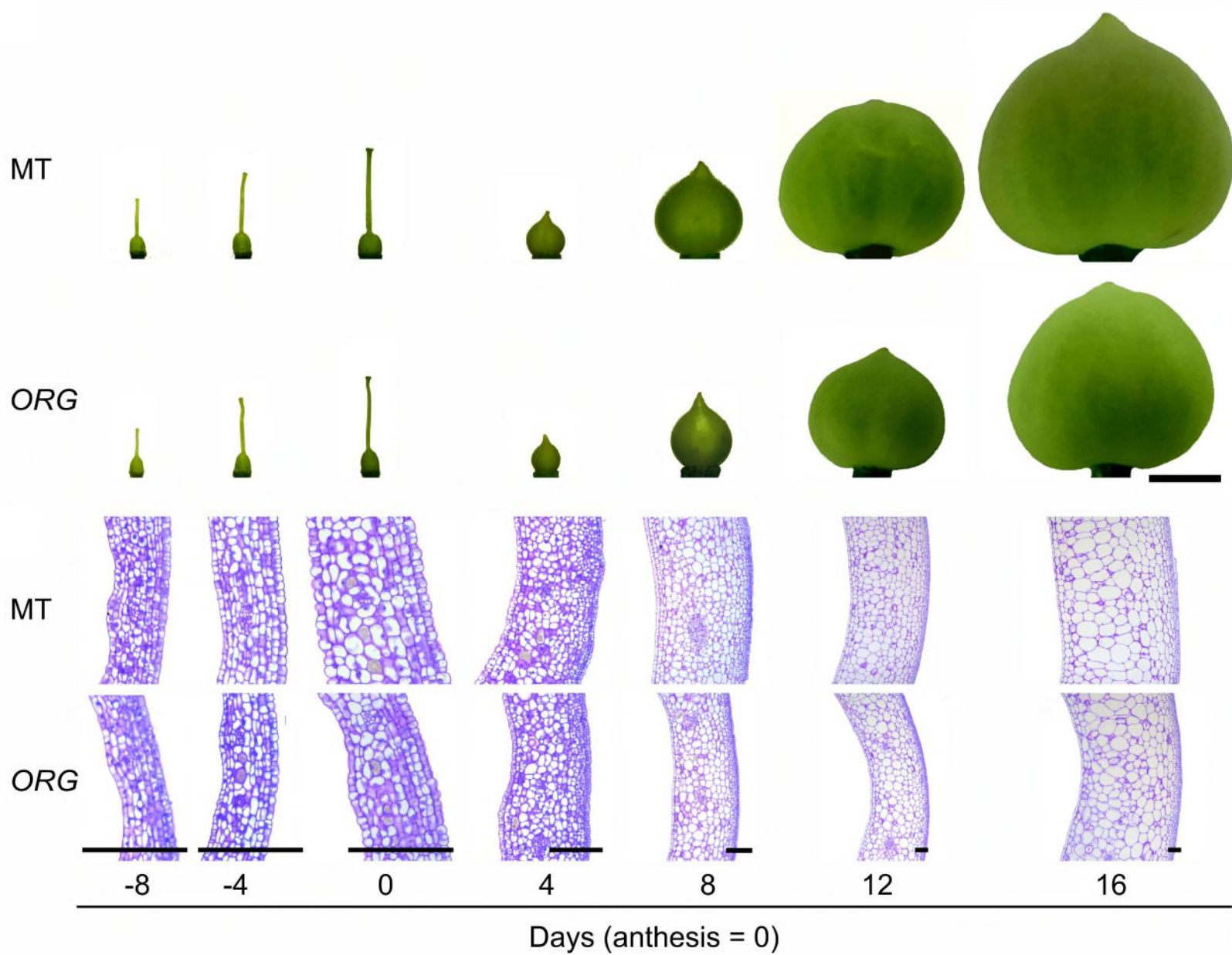
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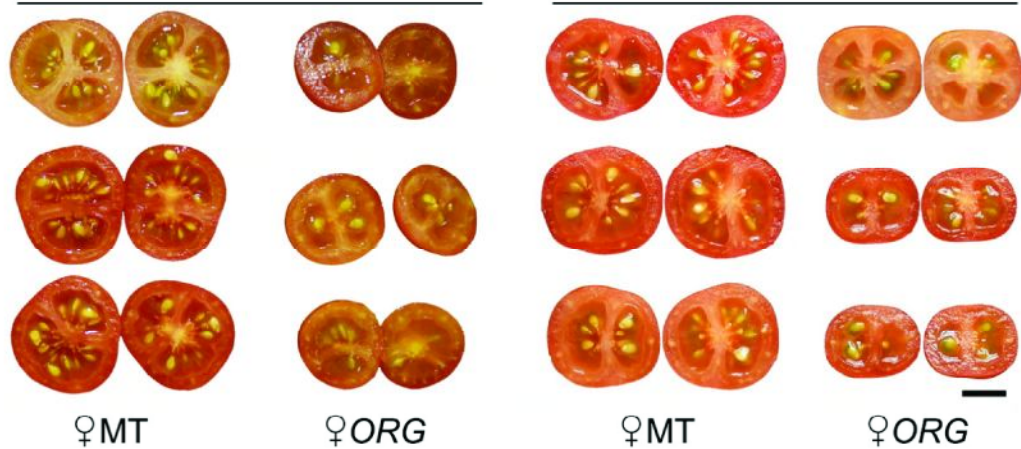
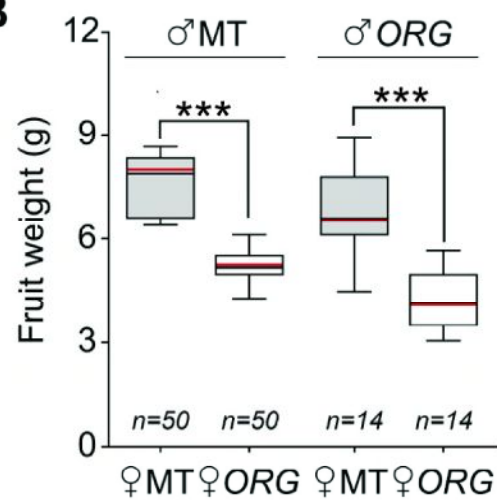
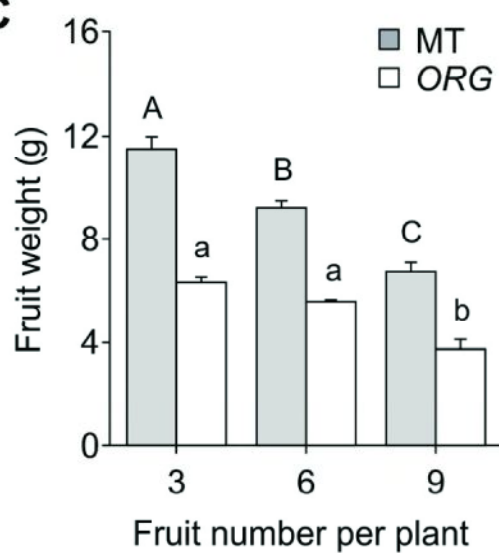
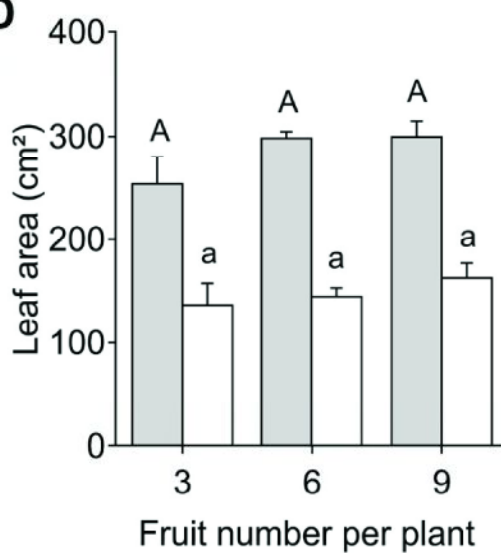
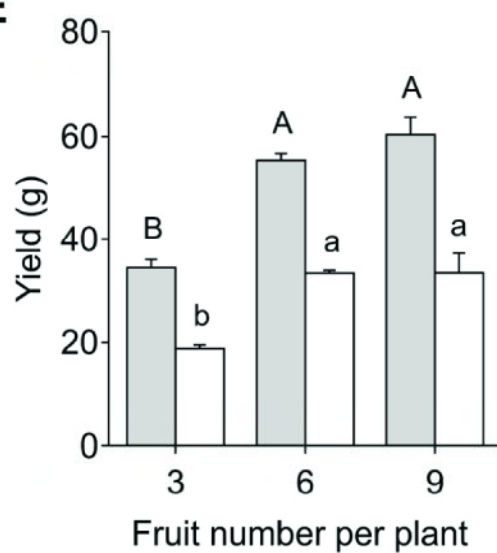
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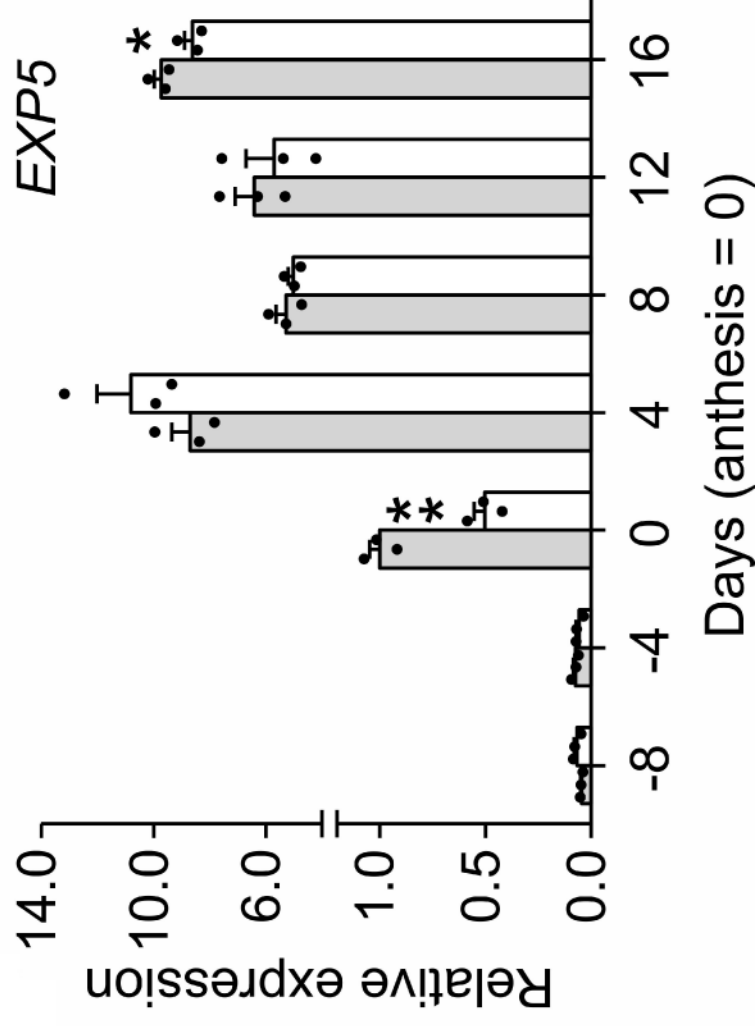
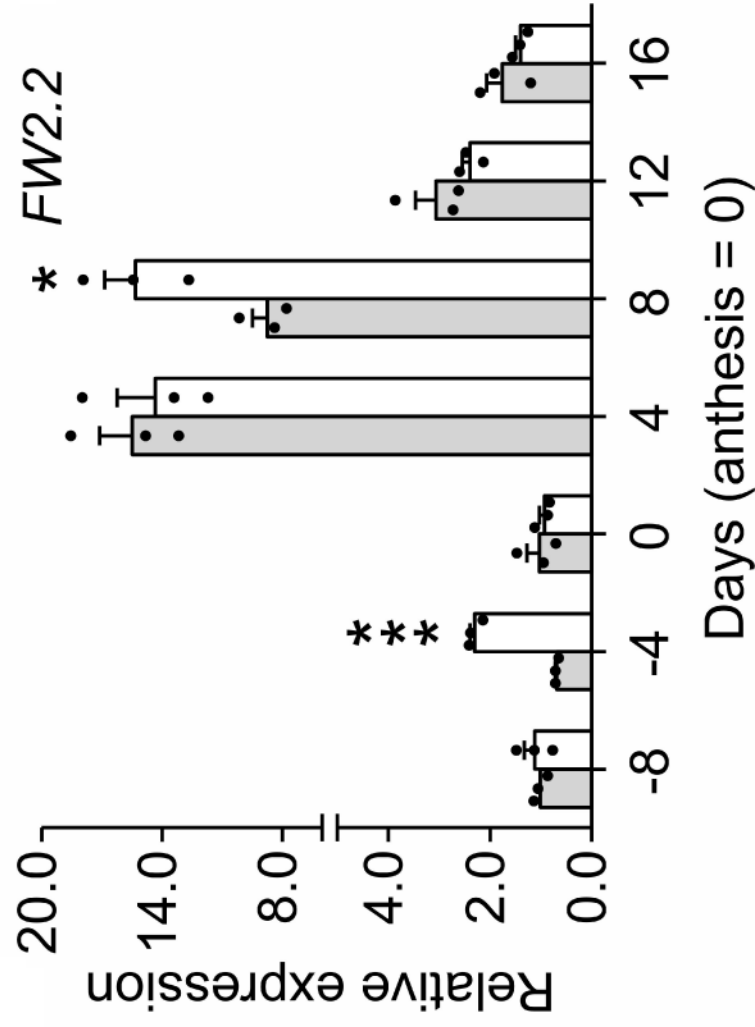
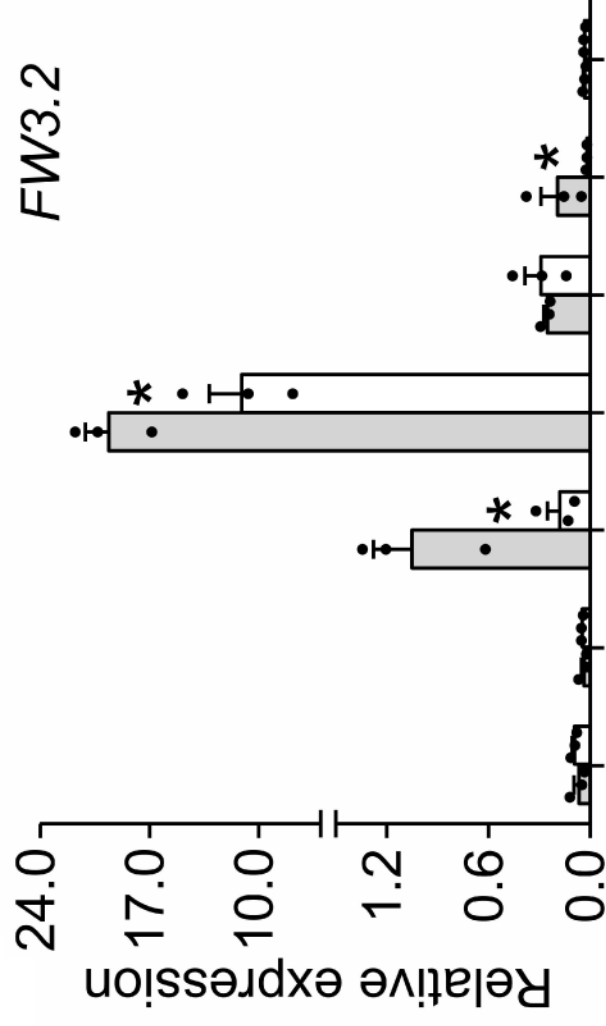
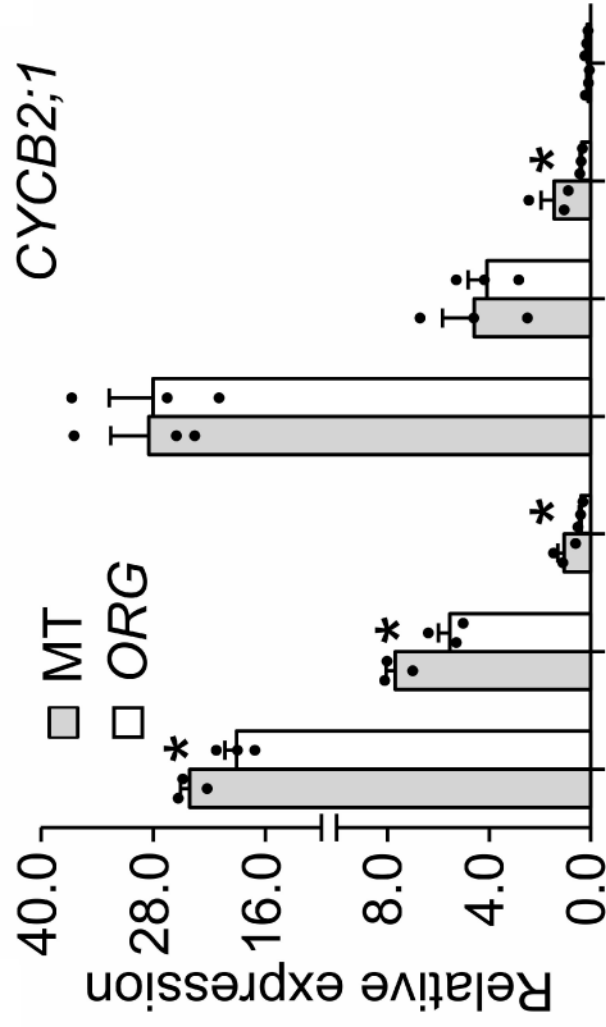
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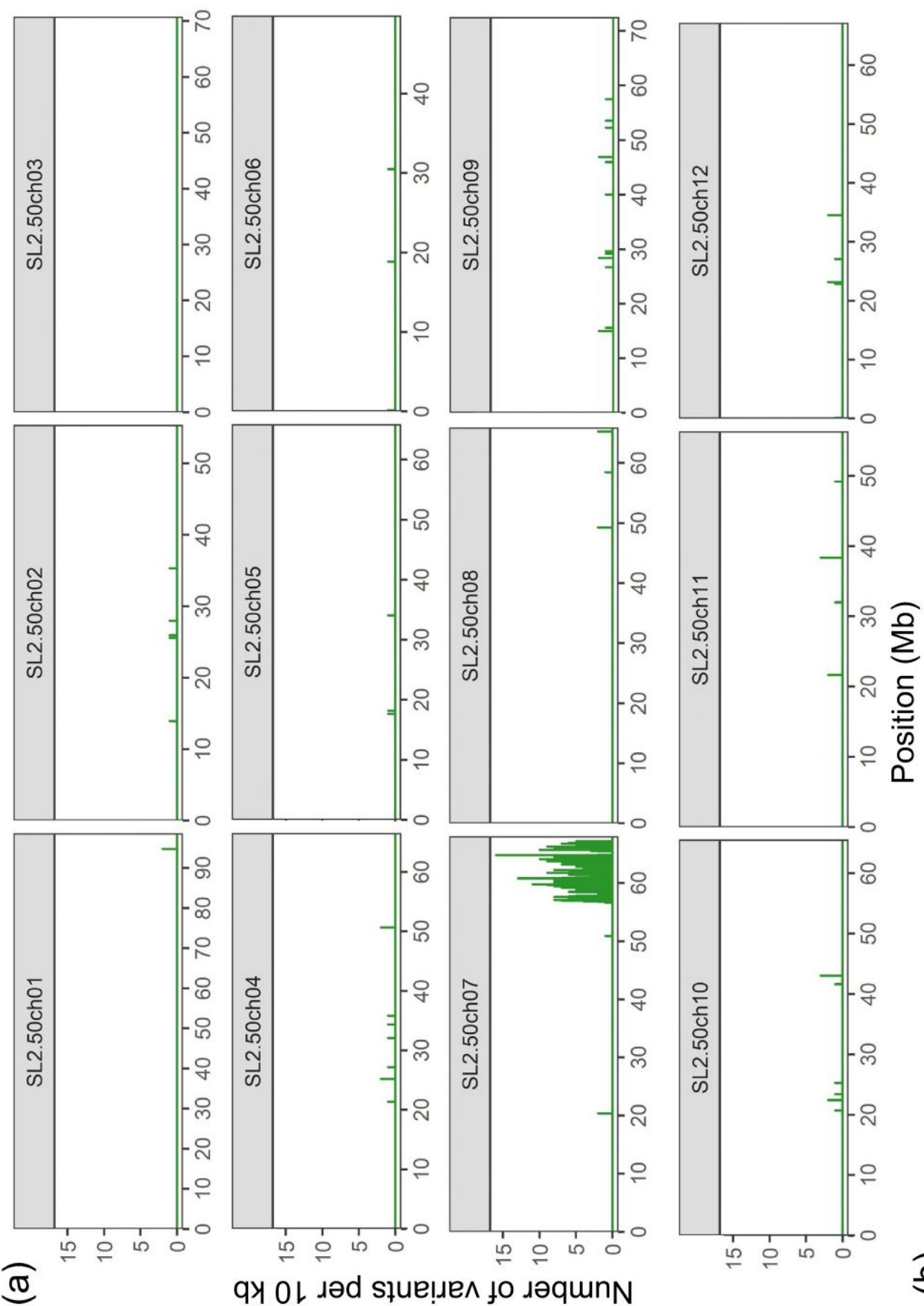




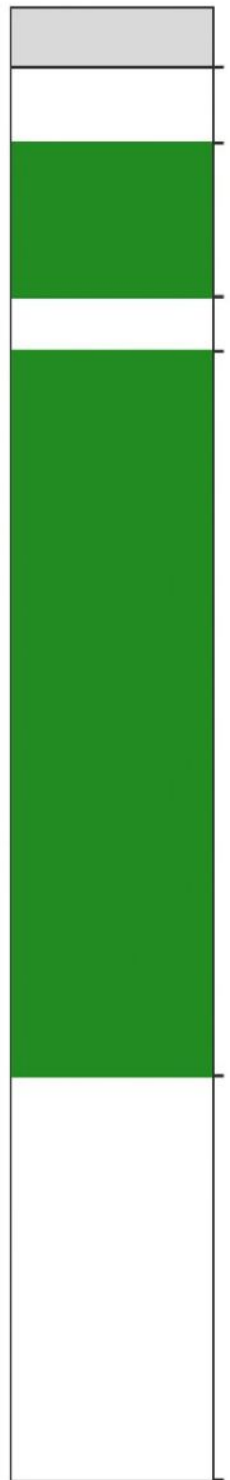
A σ MT σ ORG**B****C****D****E**

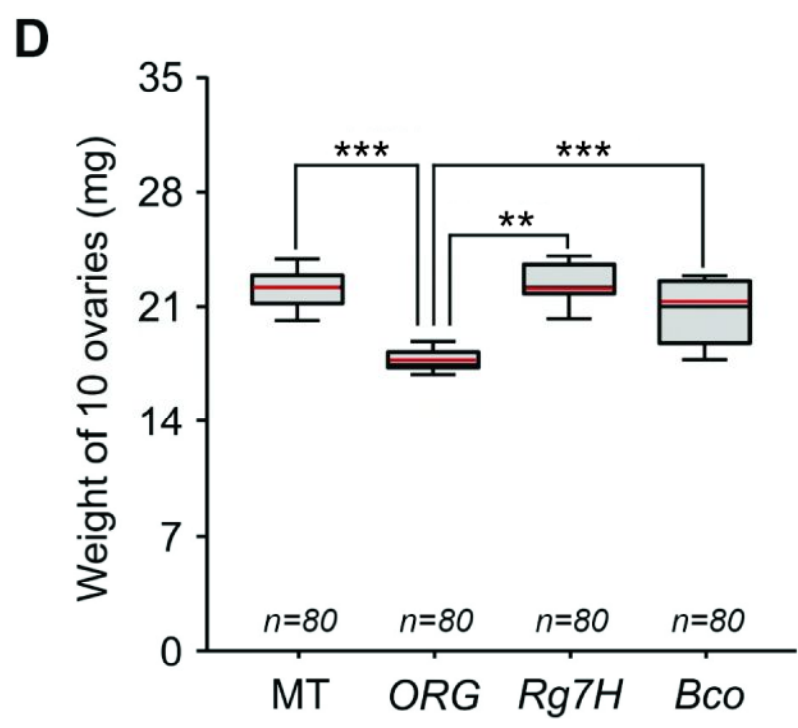
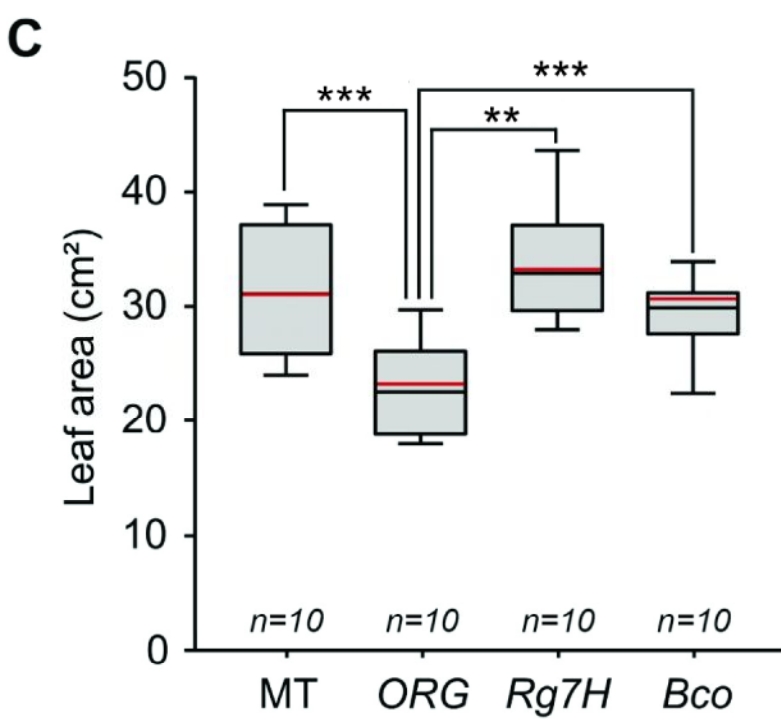
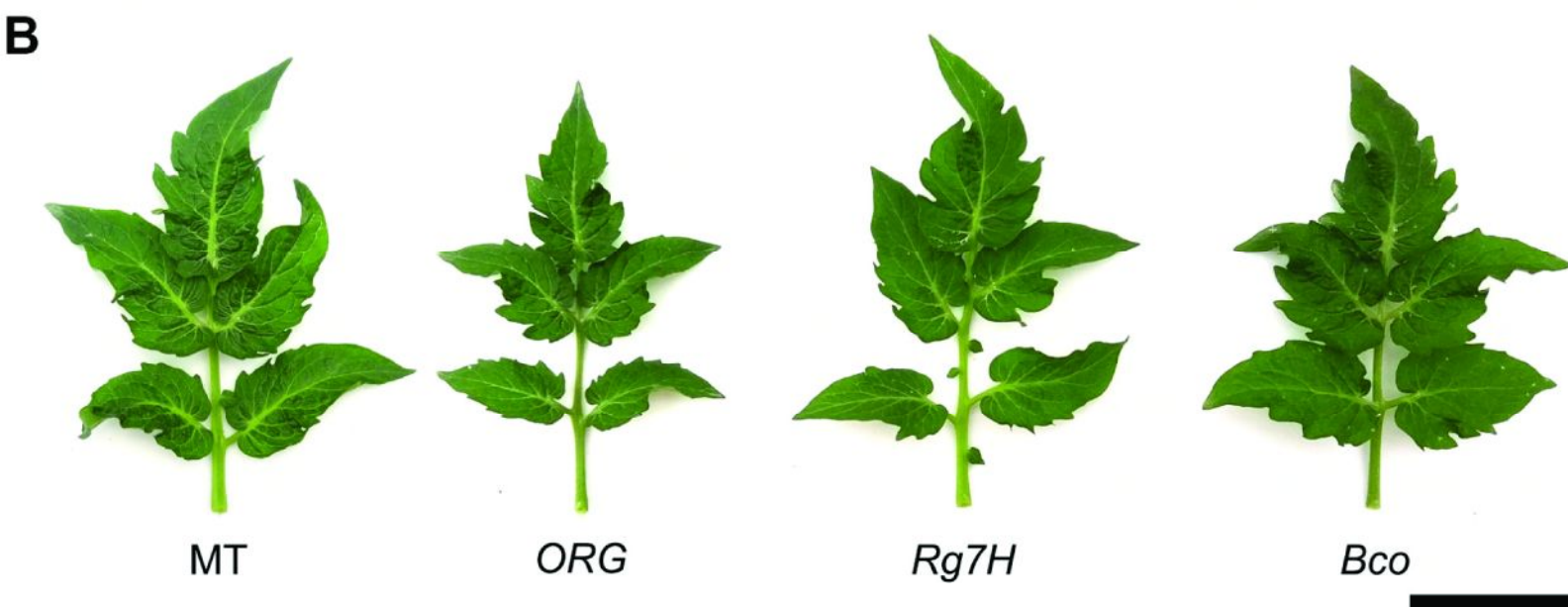
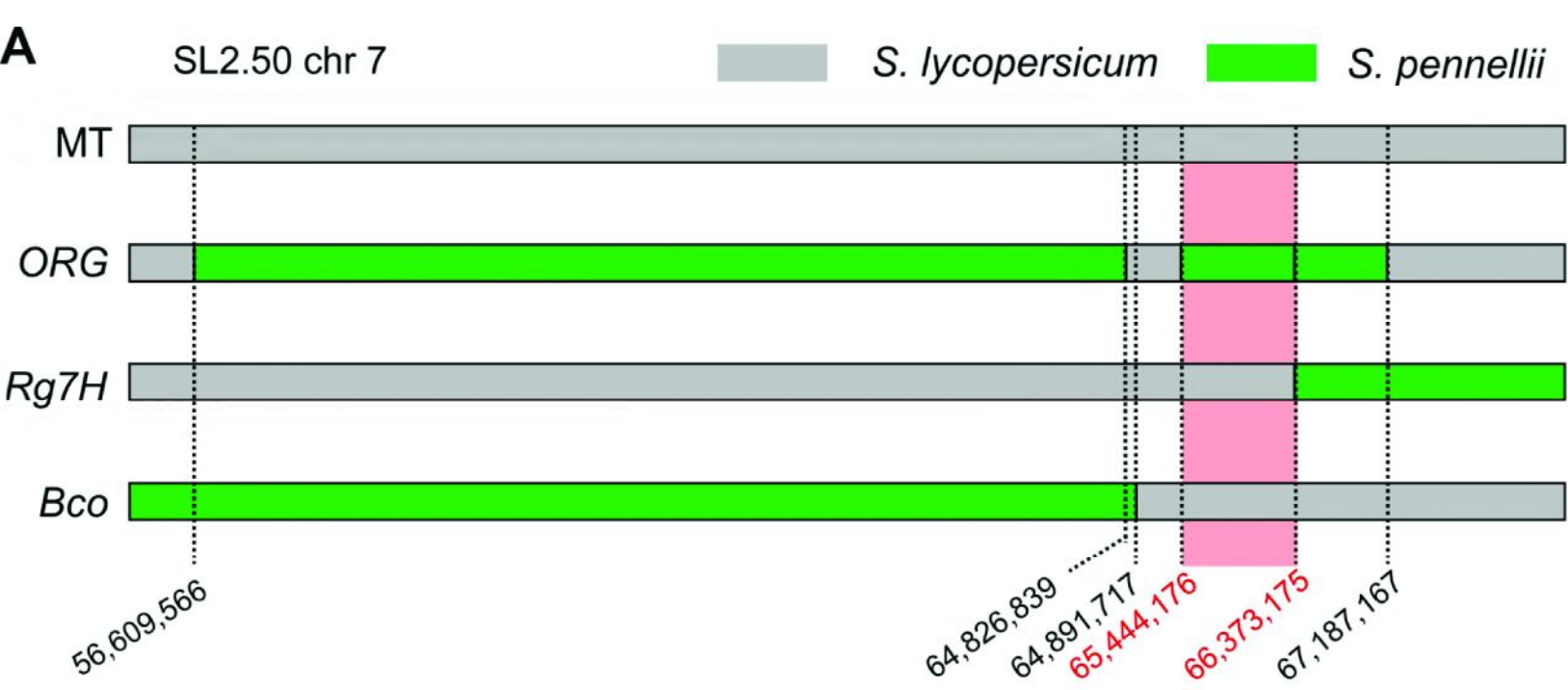


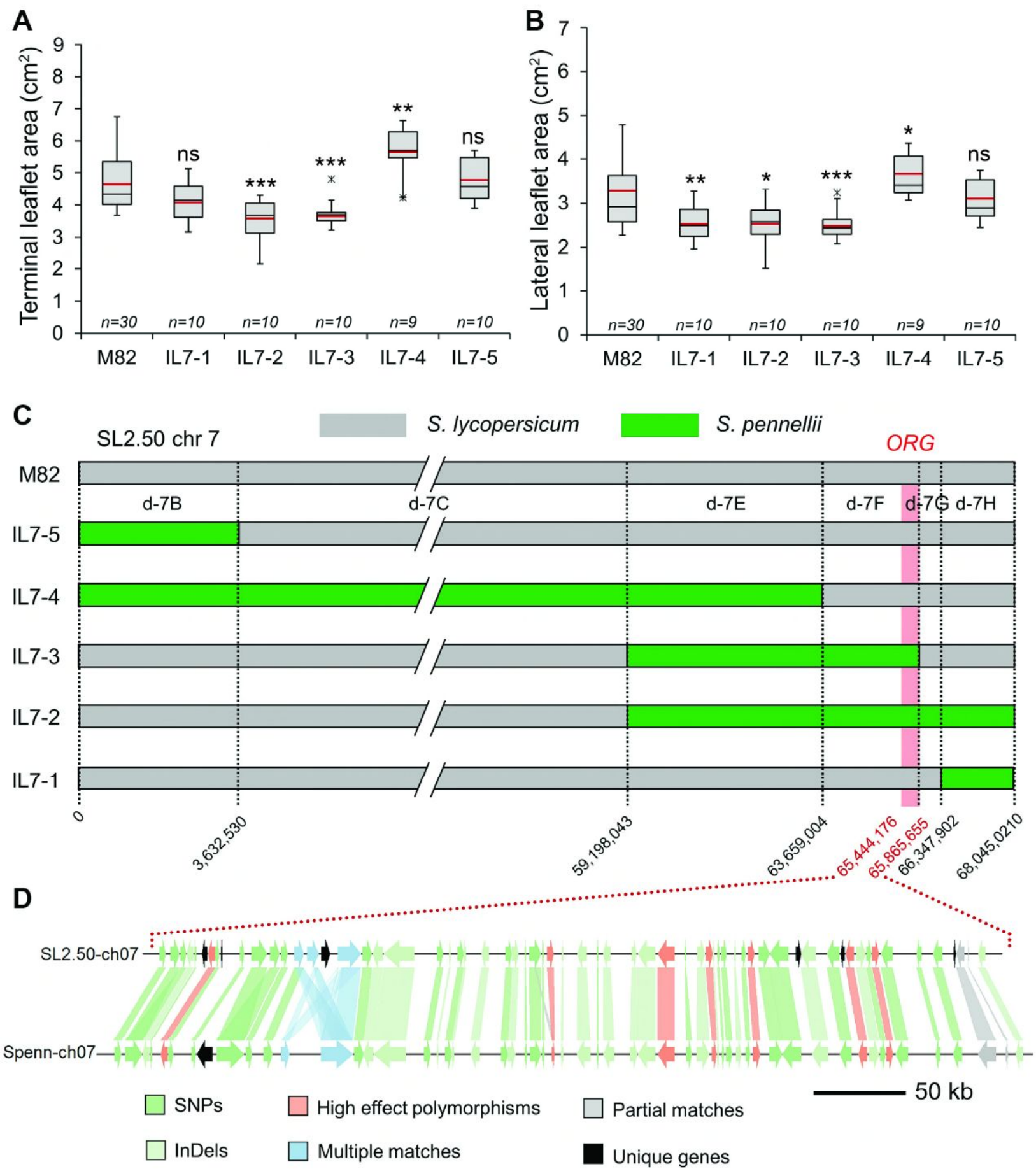
(a)



(b)







chr7



ORG
introgression

BIN

55.8 Mbp

d-7C

d-7E

d-7F

d-7G

d-7H

67.0 Mbp

Lin et al. 2014

Interval for
putative
domestication
genes

Interval for
putative
improvement
genes



Grandillo
et al., 1999

FW 7.2



van der
Knaap &
Tanksley,
2003

FW 7.2



Causse
et al., 2004

FW 7F



Barrantes
et al. 2016

FW 7.1



Approximate QTL location for fruit size

FW 7.3





DSPACE

<https://dspace.org/>

The ORGAN SIZE (ORG) locus modulates both vegetative and reproductive gigantism in domesticated tomato

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