Genetic and physiological analysis of tomato fruit weight and composition: influence of carbon availability on QTL detection

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Abstract
Throughout tomato domestication, a large increase in fruit size was associated with a loss of dry matter and sugar contents. This study aims to dissect the contributions of genetic variation and the physiological processes underlying the relationships between fruit growth and the accumulation of dry matter and sugars. Fruit quality traits and physiological parameters were measured on 20 introgression lines derived from the introgression of Solanum chmielewskii into S. lycopersicum, under high (HL, unpruned trusses) and low (LL, trusses pruned to one fruit) fruit load conditions. Inter- and intra-genotypic correlations among traits were estimated and quantitative trait loci (QTL) for size, composition, and physiological traits were mapped. LL increased almost all traits, but the response of sugar content was genotype-dependent, involving either dilution effects or differences in carbon allocation to sugars. Genotype x fruit load interactions were significant for most traits and only 30% of the QTL were stable under both fruit loads. Many QTL for fresh weight and cell or seed numbers co-localized. Eleven clusters of QTL for fresh weight and dry matter or sugar content were detected, eight with opposite allele effects and three with negative effects. Two genotypic antagonistic relationships, between fresh weight and dry matter content and between cell number and cell size, were significant only under HL; the second could be interpreted as a competition for carbohydrates among cells. The role of cuticular conductance, fruit transpiration or cracking in the relationship between fruit fresh weight and composition was also emphasized at the genetic and physiological levels.

Key words: Carbon allocation, fruit load, genetic variability, genotype x environment interaction, physiological processes, quality, QTL, Solanum lycopersicum, Solanum chmielewskii, sugar content.

Introduction
Plant domestication is the genetic modification of wild species to meet human needs (Doebley et al., 2006). In tomato, wild species originated in the Andes region where their tiny sweet fruits propagate the species. Tomato domestication dramatically increased fruit yield, and changes mainly occurred in fruit morphology or plant development. The most obvious evolution has been the massive increase in fruit size (Tanksley, 2004; Bai and Lindhout, 2007; Cong et al., 2008) which was associated with a reduction in sugar content and, subsequently, in sweet flavour. Soluble-solids content, mainly constituted by sugars, is high in wild tomato species such as Solanum pimpinellifolium or Solanum chmielewskii with more than 6% and 10% of the fruit fresh weight, respectively (Rick, 1974), whereas most of the fresh-market tomatoes contain less than 4% soluble solids. A negative relationship between fresh weight and soluble-solids content in the fruit (Goldenberg and von der Pahlen, 1966; Ibarbia and Lambeth, 1971)
hampers the transfer of high soluble-solids content from wild species into cultivated varieties. Several reviews summarize the numerous experiments of quantitative trait loci (QTL) mapping for tomato fresh weight and soluble solids content, and their co-localizations (Grandillo et al., 1999; Causse et al., 2006; Foolad, 2007). QTL for these two traits are frequently co-localized with opposite allele effects. Such QTL co-localizations can be due either to genetic linkage, and recombination could modify the relationships, or to fruit physiology and these relationships cannot be genetically modified. Yousef and Juvik (2001) identified chromosomal segments from *S. chmielewskii* that had a positive influence on fruit soluble solids while maintaining fruit size unaltered. Similarly, the alleles of *S. pennellii* at the QTL *Lin5* for soluble solids content increase sugar content without reducing total yield (Fridman et al., 2004).

In breeding programmes, interactions between genotype and environment limit the possibility to increase sugar content. These interactions were studied in wheat through comparisons of various trial locations (Robert, 1997; Matus-Cadiz et al., 2003) or through the impact of stresses (drought, salt) (Snape et al., 2007; Williams et al., 2008). In tomato, QTL detection under different saline conditions revealed a QTL specific to saline conditions (Villalta et al., 2007), indicating strong interactions between QTL and environment.

Understanding the relationship between fruit fresh weight and sugar content in tomato fruits requires identifying the key processes underlying this relationship, both from the genetic and the physiological points of view. The integration of physiological and genetic approaches allows a better dissection of the genetic basis of complex traits as well as their interactions with the environment. For instance, several co-localizations of QTL for fruit weight, fruit dry matter content or fruit sugar content and QTL for ecophysiological parameters were identified in peach (Quilot et al., 2005), suggesting which physiological processes were involved in the genetic variation.

Fruit weight and composition depend on the balance between inward and outward fluxes to/from fruit (mostly water and carbon), which involve many different processes. Transpiration leads to a water loss (Wu et al., 2003), and may decrease the fruit fresh weight and concentrate the soluble compounds. Cell division and cell expansion determine final fruit size and carbohydrate dilution within cells (Bohner and Bangerth, 1988; Ho, 1996). The number of cells influences the structural dry matter through the amount of cell wall. The size of cells mainly affects the capacity to store soluble dry matter. Finally, the number of seeds may interfere with cell division and cell expansion through the production of hormones (Rylski, 1979; Gillaspy et al., 1993). At the plant level, characteristics of the leaves (carbon source) could affect sugar production via photosynthesis. Carbon supply can be modified by environmental stresses or cultural practices. For instance, fruit thinning reduces the competition for carbon, and thus promotes fruit size and sugar content in several species, like peach fruits (Morandi et al., 2008), apple fruits (Link, 2000), mandarin fruits (Kubo et al., 2001), and papaya fruits (Zhou et al., 2000). In tomato, this treatment has previously been carried out, increasing in similar proportions fresh and dry weights (Heuvelink, 1997).

The aims of this study were first to determine and dissect the relative influence of genotype and fruit load on fruit weight and sugar content, then to identify which processes were underlying these traits and their relationships, at both the genetic and the physiological levels. For this purpose, a set of physiological, biochemical, and morphological parameters related to the main processes of fruit growth and plant development were measured in a population consisting of 20 introgression lines derived from a cross between a wild tomato species (*Solanum chmielewskii*) with small green fruits and a medium-sized cultivar (*Solanum lycopersicum* L.). QTL mapping and interactions between QTL and carbohydrate availability were examined over two years, by comparing plants under two contrasting fruit loads. One fruit per truss was the condition with no limitation for carbohydrate supply and corresponded to maximum genotypic potential. The second condition was similar to what is currently applied for genetic studies: a free load condition (without fruit pruning), with competition for assimilates among fruits.

**Materials and methods**

**Plant material**

The study was performed using the *Solanum lycopersicum* line ‘Moneyberg’ (hereafter referred to as M) and 20 indeterminate lines carrying single or multiple introgressions of the *Solanum chmielewskii* LA1840 in the background of Moneyberg, kindly provided by Keygene (The Netherlands). Each line was named by the chromosomal number and the location of the largest introgression. For instance, genotype C3a was the line that contained an introgressed fragment at the top of chromosome 3, while genotype C3d possessed an introgression at the bottom of chromosome 3.

**Growth conditions and experimental treatments**

Seeds were sown at the end of February, and a total of 400 plants were grown at a density of 3.6 plants m⁻² in a ground bed greenhouse in Avignon (Southern France) at day–night temperature set points of 24/16°C during spring 2006 (March–July) and 25/15°C during spring 2007 (March–July). Plants were randomly distributed in two blocks each containing 200 plants and facing, respectively, North and South. Plant nutrition and chemical pest and disease control followed commercial practices and plants were conducted on a single vine. Starting from anthesis of the first truss, flowers were pollinated with an electrical shaker every 2–3 d.

For each genotype, ten plants were randomly selected in the first block while nine plants were randomly selected in the second block. On 12 plants of each genotype, trusses
were pruned to one fruit (low fruit load, LL) while on seven other plants trusses were not pruned (high fruit load, HL). Under HL conditions, the average number of fruit sets per truss within the population was 5.3. On each inflorescence of the LL plants, all the flowers except the second one were removed just after fruit set. The fruit removal experiment concerned the first nine trusses. All the plants were stopped two leaves above the ninth truss.

Observations and measurements

Plant development: Anthesis time, achieved as the flower fully opened, was recorded three times a week in order to determine fruit age and fruit development duration (Dura expressed in days) considered as the time between anthesis and the red ripe stage. Plant development traits, used as indicators of plant vigour and carbohydrate supply, were measured on nine contrasted genotypes (C11b, C12d, C3a, C3c, C4c, C4d, C7a, C8e, and C9d) and M. For each genotype and treatment, four randomly selected plants (two per block) were measured for the number of leaves (LfN) until the ninth truss and the height of the fourth truss (H4t expressed in cm), at the end of the growing season. The area of five representative leaves were measured using a planimeter, and then the total leaf area (LfA expressed in cm² of five representative leaves were measured using a planimeter. Dry weight of the five leaves was estimated on five red ripe fruits, harvested for each genotype and treatment on five different plants randomly selected within the two blocks. In order to eliminate bias due to competition within and among trusses, only the second fruits of the fourth trusses were harvested. On each fruit, cheek, suture, and height diameters were measured assuming spherical form. The cuticular macro-crack area (FCr expressed as a percentage of cracked area relative to the total cuticle area) was calculated by drawing their outlines on tracing paper, cutting the area, and measuring it with a planimeter.

Fruit composition, cell number and size: The five red ripe fruits analysed for FCr were used for fruit composition, and cell measurements. Fruit fresh weight was measured (FW expressed in g/fruit), jelly and seeds were removed from the fruits and seeds were counted (SdN). Then, pericarp tissue including external, internal and transverse parts was weighted. One half of the fruit pericarps was ground in liquid nitrogen using a blender. Powders were freeze-dried and stored at -20 °C prior to sugar extraction. Pericarp dry weight (DW expressed in g) and dry matter content (DMC expressed in g/100 g FW) were measured after lyophilization of tomato powders. Sugars were extracted from the pericarp according to the method described in Gomez et al. (2002). The main sugar contents (glucose, fructose, and sucrose) were quantified by enzymatic assay in 96-well microplates, as detailed in Gomez et al. (2007). Sugar contents were expressed relative to the pericarp fresh weight (SUGfw in g/100 g FW) or to the pericarp dry weight (SUGdw in g/100 g DW). The pericarp structural carbon content (StrCfw) was estimated as follow:

\[
\text{StrCfw} = \text{DMC} - \text{SUGfw}
\]

where StrCfw, DMC, and SUGfw are expressed in g/100 g FW. This relationship was experimentally checked on 30 red ripe fruits, by the extraction of pericarp insoluble material after sugar eliminations from lyophilized powders.

On the second half of the fruit pericarp, cell division and expansion were evaluated by measuring the number (CIN) and mean size (CIS expressed in nl) of pericarp cells, according to the method described in Bertin et al. (2002).

DNA markers and assays

A set of PCR-based markers consisting of 130 Conserved Ortholog Set II (COSII) markers (Wu et al., 2006; http://www.sgn.cornell.edu/markers/cosii_markers.pl) and three Simple Sequence Repeats (SSR) (Frary et al., 2005), covering all 12 tomato chromosomes, were used to genotype the population of 20 S. chmielewskii LA1840 introgression lines (IL).

Genomic DNA of the two parent lines and of the 20 IL was extracted from leaf tissue of 3-week-old plants according to the protocol of Fulton et al. (1995).

The PCR of each marker was performed on both parents (Moneyberg and LA1840) in 25 μl reactions containing 50 ng of template DNA, 2.5 pmol of each forward and reverse primer, 1× Colorless GoTaq® Flexi Buffer (Promega), 0.2 mM dNTPs, and 0.2 U GoTaq® DNA Polymerase (Promega). The reactions were amplified using a DNA Engine (PTC-200) Peltier Thermal Cycler (Bio-Rad). Amplification consisted of an initial denaturation for 5 min at 94 °C, followed by 35 cycles of amplification with denaturation at 94 °C for 30 s, annealing at 55 °C for 45 s, and extension at 72 °C for 60 s, with a final cycle of 72 °C for 5 min. Following amplification, PCR products were analysed by electrophoresis on 1% agarose gels in 1× TAE buffer for 1–2 h at 100 V and room temperature. Direct fragment length polymorphism was detected for 12% of the COSII markers. In the other cases, the PCR products of the parent lines were digested with different frequent cutter restriction enzymes.
enzymes including TaqI, Hinfl, AluI, DraI, RsaI, and MseI, and electrophoresed through 2% agarose to identify polymorphisms. If no polymorphism was detected with these enzymes, then the PCR products of the two parent lines were sequenced. For this purpose, amplicons showing a single band on agarose gels were cleaned up from nucleotides and residual primers using 10 l of ExoSAP-IT®. The mixture was incubated at 37 °C for 1 h and then at 80 °C for 15 min. A 10 l sequencing reaction volume was prepared using 2 l of the cleaned PCR product, 1 l of either the forward or reverse primer, 1 l of 5× BigDye Buffer 3.1 and 1 l of either BigDye terminator v3.1 (Applied Biosystems). The sequencing PCR consisted of initial denaturation at 96 °C for 60 s and 25 cycles of 10 s at 96 °C, 5 s at 55 °C, and 4 min at 60 °C. The sequences were obtained through an ABI Prism 3100 Genetic Analyser automated sequencer (Applied Biosystems). Restriction maps were predicted using CAPS designer (http://www.sgn.cornell.edu/tools/caps_designer).

For some of the regions where polymorphic COSII markers were not found, SSR were surveyed in order to increase the map saturation. PCR reactions and thermocycling were as described for the COSII markers; PCR products were separated on 2.5% agarose gels in 1× TAE buffer for 1–2 h at 100 V and room temperature. Sequences of the primers used for the COSII and SSR assays are available on the SGN website (http://www.sgn.cornell.edu). The polymorphic COSII and SSR markers were then assayed on the 20 IL.

Statistical analyses

Altogether, data obtained in this study contained very few missing values, and all variables were normally distributed. After checking that block effect was not significant, the effects of year, genotype, fruit load, and their interactions on each trait were analysed using a three-way ANOVA. The linear model used was:

\[ Y_{ijkl} = \mu + \alpha_i + \beta_j + \delta_k + (\alpha \beta)_{ij} + (\alpha \delta)_{ik} + (\beta \delta)_{jk} + \epsilon_{ijkl} \]  

(2)

where \( Y_{ijkl} \) is the trait value for plant \( l \) on genotype \( i \), fruit load \( j \), and year \( k \); \( \mu \) is the general mean; \( \alpha_i \) is the effect of genotype \( i \); \( \beta_j \) is the effect of fruit load \( j \); \( \delta_k \) is the effect of year \( k \); \( (\alpha \beta)_{ij} \) is the effect of the interaction between genotype \( i \) and fruit load \( j \); \( (\alpha \delta)_{ik} \) is the effect of the interaction between genotype \( i \) and year \( k \); \( (\beta \delta)_{jk} \) is the effect of the interaction between fruit load \( j \) and year \( k \), and \( \epsilon_{ijkl} \) is the error term.

The percentage of variation due to each factor was then calculated as:

\[ V_i = \frac{SS_i \times 100}{\sum SS_i} \]  

(3)

where \( SS \) is the sum of squares of the factor \( i \). For each trait \( t \), the percentage of fruit load variation (\( \Delta_{FL} \)) from HL to LL was calculated following:

\[ (\Delta_{FL})_t = \frac{(\mu_{tLL} - (\mu_t)_HL)}{(\mu_t)_HL} \times 100 \]  

(4)

where \( (\mu_t)_HL \) and \( (\mu_t)_LL \) are the general means of the trait \( t \) under HL and LL, respectively.

For each genotype, the effect of fruit load on fruit fresh weight (FW), pericarp dry weight (DW), pericarp dry matter content (DMC), and pericarp sugar contents (SUGfw and SUGdw), was analysed by a two-way analysis of variance following this model:

\[ Y_{ijkl} = \mu + \beta_j + \delta_k + (\beta \delta)_{jk} + \epsilon_{ijkl} \]  

(5)

where \( Y_{ijkl} \) is the trait value for plant \( l \), fruit load \( j \), and year \( k \); \( \mu \) is the general mean; \( \beta_j \) is the effect of fruit load \( j \); \( \delta_k \) is the effect of year \( k \); \( (\beta \delta)_{jk} \) is the effect of the interaction between fruit load \( j \) and year \( k \), and \( \epsilon_{ijkl} \) is the error term.

Multivariate analyses were conducted using the MANOVA function in R (http://www.r-project.org). Genotypic and residual covariances were estimated for each trait pair under both fruit loads by pooling the two years and all genotypes as explained in Holland (2006). Covariance matrices were then used to calculate genotypic and residual correlation coefficients (hereafter called inter- and intragenotypic correlation coefficients).

QTL analysis was performed under each fruit load condition, first separately on both years by using a one-way ANOVA and then by pooling the two years in a two-way ANOVA. The within-genotype mean squares from these ANOVA were used to carry out Dunnett multiple comparison test (Dunnett, 1980) in SAS version 9.1.3 (SAS Institute, Inc.), to determine which genotypes were significantly different (at the 0.05 probability level) from the parent conferring the genetic background (Moneyberg), meaning which genotypes carried a QTL. The QTL effects are presented as percentages of difference from Moneyberg.

Results

Genotype and fruit load effect on fruit and plant trait variation

As individual sugar contents (glucose, fructose, and sucrose contents) were highly correlated together and to total sugar content (\( r \approx 0.8 \), data not shown), only the total pericarp sugar content was considered in the following analysis. Analysis of variance showed that the genotype significantly influenced all traits (Table 1), and that fruit load significantly influenced most of the traits, except seed number, cell size, leaf number, and specific leaf weight. Most of the traits showed higher average values under LL than under HL, except the sugar content (SUGdw), the cuticular conducance (CutC), and the fruit development duration (Dura). Fruit load mostly affected fruit cracking, pericarp dry weight, and fruit weight which increased by about 1000%, 87%, and 55%, respectively, under LL condition.
Table 1. Percentage of variation attributable to the effects of genotype (G), fruit load (FL), year (Y), genotype × fruit load interaction (G×FL), genotype × year interaction (G×Y), year × fruit load interaction (Y×FL) by analysis of variance.

When fruit load was significant, the percentage of variation from high load (HL) to low load (LL) (ΔHL) was calculated (equation 4 in the Materials and methods).

| Genotype× (G) | Fruit load× (FL) | ΔFL | Year× (Y) | G×FL | G×Y | Y×FL |
|---------------|-----------------|-----|-----------|-------|-----|------|
| Fruit weight and composition | | | | | | |
| Fruit fresh weight (g) | FW | 38*** | 52*** | +55% | 0 ns | 6*** | 2 ns | 1** |
| Dry weight of the pericarp (g) | DW | 25*** | 63*** | +87% | 3* | 1* | 3* | 5 ns |
| Dry matter content of the pericarp (g/100 g FW) | DMC | 43*** | 38*** | +17% | 14*** | 3*** | 3 ns | 0 ns |
| Sugar content of the pericarp (g/100 g DW) | SUGdw | 25*** | 1* | –1% | 45*** | 13*** | 14*** | 2** |
| Sugar content of the pericarp (g/100 g FW) | SUGfw | 53*** | 17*** | +17% | 6*** | 9*** | 10*** | 3** |
| Structural carbon content of the pericarp (g/100 g FW) | StrCw | 19*** | 19*** | +17% | 45*** | 6* | 8*** | 2** |
| Fruit physiology | | | | | | |
| Development duration (d) | Dura | 36*** | 9*** | –4% | 29*** | 7* | 19*** | 1* |
| Seed number | SnN | 55*** | 0 ns | ns | 27*** | 6 ns | 10* | 1 ns |
| Cell number of the pericarp | CIN | 60*** | 23*** | +42% | 0 ns | 12* | 3 ns | 1 ns |
| Cell size in the pericarp (nl) | CIS | 78*** | 0 ns | ns | 0 ns | 16* | 4 ns | 2 ns |
| Cuticular conductance (cm h⁻¹) | CutC | 26*** | 18*** | –25% | / | 49*** | / | / |
| Fruit cracking | FCr | 190*** | 26*** | +1000% | 17*** | 15*** | 9*** | 14*** |
| Plant development | | | | | | |
| Height of the 4th truss (cm) | H4t | 77*** | 1* | +4% | 19*** | 2 ns | 2 ns | 0 ns |
| Leaf number | LfN | 22*** | 0 ns | ns | 63*** | 4 ns | 9* | 2 ns |
| Specific leaf weight (g cm⁻²) | SLW | 18* | 1 ns | ns | 50*** | 19* | 19* | 0 ns |
| Total leaf area (cm²) | LfA | 52*** | 8*** | +43% | 5* | 24** | 10* | 1 ns |

ns, not significant; *, significant at the 0.05 probability level; **, significant at the 0.001 probability level; ***, significant at the 0.0001 probability level.

Genotype × fruit load interactions were also significant for all traits except the seed number, the height of the 4th truss, and the leaf number. Year effects and interactions between genotype, fruit load, and year were also found significant. Globally the percentages of variations due to interactions between year and genotype or between year and fruit load were lower than those of genotype or fruit load.

Fruit load effect was analysed for each genotype on fruit fresh weight, pericarp dry weight, dry matter content, and sugar contents (Fig. 1). Linear positive relationships were found between HL and LL conditions for fruit fresh weight, pericarp dry weight, and dry matter content. For sugar contents, the correlation between HL and LL values was lower (SUGfw) or non-significant (SUGdw). The fruit fresh weight and pericarp dry weight of all genotypes significantly increased from HL to LL, enlarging to twice their range of variation (Fig. 1B, C) and the dry matter content (DMC) significantly increased for all the genotypes except for C3a. Five groups of genotypes were identified according to their response to low fruit load. The first group contained two genotypes and was characterized by a significant increase in sugar contents (SUGdw and SUGfw). The second group was the most represented within this population as it contained 13 genotypes (including M): it was distinguished by an increase in SUGfw but no change in SUGdw. Groups 3, 4, and 5 (three, two, and one genotypes, respectively) showed no change in SUGfw, associated with a decrease (Gr 3) or no change (Gr 4 and Gr 5) in SUGdw. Belonging to these groups was not dependent on particular values of fruit fresh weight or sugar contents.

Inter- and intra-genotypic correlations among traits

Genotypic and residual correlations among traits were evaluated by analysing inter- and intra-genotypic correlation coefficients among variables, respectively (Table 2). Some correlations were common to inter- and intragenotypic levels and to both fruit loads. Fruit fresh weight was positively correlated to pericarp dry weight, seed number, and cell number. Pericarp dry weight was positively correlated to cell number. Dry matter content and sugar content (SUGdw) were positively correlated to SUGfw and positively or negatively to the structural carbon content, respectively.

Only few and low correlations were specific to the intragenotypic level (Table 2). More significant correlations occurred at the inter-genotypic level and one was common to HL and LL: the higher the structural carbon content, the lower the seed number. Antagonisms were found between fruit fresh weight and dry matter content or structural carbon content under HL. Dry matter content was positively related to fruit cracking and leaf number and negatively to the fruit development duration under HL. Dry matter content was also positively correlated to plant height under LL. The sugar content (SUGfw) was positively related to fruit cracking and leaf number under HL and to specific leaf weight under LL. It was also negatively linked to fruit development duration and to cell expansion via cell size under LL. Moreover, a significant negative correlation was found between cell number and cell size only under HL (r = −0.58, data not shown), suggesting that there was competition for assimilates among cells. Finally, the...
structural carbon content was negatively linked to fruit development duration and to cuticular conductance under HL while positively linked to leaf number under LL.

QTL for plant development, fruit weight, and composition traits

Linkage map of introgressions: The *S. chmielewskii* LA1840 population provided by Keygene had been developed using AFLP markers (http://www.keygene.com; unpublished data). In order to enhance the rate of introgression breeding, facilitate marker-assisted selection of new IL and comparisons between function maps of tomato and potato, within the framework of a large European project (http://www.eu-sol.net/), the *S. chmielewskii* IL population together with other four interspecific tomato mapping populations and one potato mapping population are being anchored to a common set of COSII markers. The other five mapping populations are: a potato diploid population F1840 (Gebhardt *et al.*, 2003), the *S. pennellii* LA716 IL.
Tables 3, 4, and 5 present QTL detected separately under each fruit load condition, and according to the model based on the two-year experiment. Positive or negative QTL correspond to a location where the allele of *S. chmielewskii* increased or decreased the trait, respectively, compared to Moneyberg. Excluding QTL for cuticular conductance which were only identified in 2007, 84 QTL were detected in 2006 versus 90 in 2007. Sixty-one QTL were common to both years. Sixty eight QTL were detected under HL versus 74 under LL. Only 30% of these QTL were detected whatever the fruit load and hereafter called ‘stable’. When stable, the sign of the QTL was the same under both fruit loads, except for QTL of cuticular conductance.

**QTL for fruit weight and composition traits**

Fourteen QTL were detected for FW, half being stable, the other half being detected only under LL (Table 3). All stable QTL were negative, with two genotypes (C11b and C3c) having a strong effect (fruits were 50% smaller than M). A multiple introgressed genotype (C5b) carried a positive QTL for FW under LL. Ten QTL were identified for DMC, all with positive effect and six were stable. Concerning sugar contents, six QTL for SUGfw were detected: two QTL were stable, and only two had negative effects. On the contrary, all the 11 QTL identified for SUGdw had low negative effects. They were twice more numerous under LL than under HL and C11b was the only genotype carrying a stable QTL whatever the fruit load.

**QTL for fruit physiological and plant developmental traits**

Five QTL with low effects were detected for fruit development duration and three of them were stable under both fruit loads (Table 4). Eight negative QTL for seed number were identified under HL, and half of them were

### Table 2. Inter-genotypic (Inter) and Intra-genotypic (Intra) correlation coefficients for traits relative to weight, composition, physiology of the fruit, and plant development, under high load (HL) and low load (LL).

Correlation coefficients significant at the 0.05 probability level were highlighted in grey.

| Traits   | FW | DW | DMC | SUGdw | SUGfw | StrCfw |
|----------|----|----|-----|-------|-------|--------|
|          | Inter | Intra | Inter | Intra | Inter | Intra | Inter | Intra | Inter | Intra | Inter | Intra |
|          | HL | LL | HL | LL | HL | LL | HL | LL | HL | LL | HL | LL | HL | LL | HL | LL | HL | LL | HL | LL |
| DW       | 0.90 | 0.04 | 0.91 | 0.89 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| DMC      | -0.58 | -0.31 | 0.06 | -0.10 | -0.14 | 0.03 | 0.44 | 0.54 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| SUGdw    | 0.23 | -0.21 | 0.05 | 0.03 | 0.28 | -0.30 | -0.01 | -0.09 | 0.04 | 0.05 | -0.12 | -0.25 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| SUGfw    | -0.29 | -0.44 | 0.12 | -0.06 | 0.06 | -0.16 | 0.35 | 0.19 | 0.77 | 0.86 | 0.64 | 0.58 | 0.66 | 0.46 | 0.49 | 0.63 | 1 | 1 | 1 | 1 | 1 | 1 |
| StrCfw   | -0.57 | -0.17 | 0.05 | -0.09 | -0.27 | 0.16 | 0.34 | 0.27 | 0.78 | 0.90 | 0.76 | 0.83 | -0.59 | -0.47 | -0.72 | -0.74 | 0.20 | 0.55 | -0.01 | 0.02 | 1 | 1 | 1 | 1 |
| Dura     | 0.21 | 0.10 | -0.08 | -0.02 | 0.11 | 0.14 | -0.13 | -0.02 | 0.47 | 0.26 | -0.06 | 0.02 | 0.23 | -0.65 | -0.07 | 0.02 | -0.30 | 0.48 | -0.14 | 0.05 | -0.48 | 0.04 | -0.01 | 0.02 | 1 | 1 | 1 | 1 |
| Sdn      | -0.49 | 0.42 | 0.39 | 0.37 | 0.31 | 0.26 | 0.31 | 0.37 | -0.43 | -0.34 | -0.06 | 0.11 | 0.46 | 0.36 | 0.14 | 0.05 | -0.01 | -0.16 | 0.07 | 0.12 | -0.63 | -0.45 | -0.13 | 0.07 | 1 | 1 | 1 | 1 |
| CIn      | 0.77 | 0.87 | 0.69 | 0.71 | 0.67 | 0.82 | 0.67 | 0.52 | -0.38 | -0.31 | 0.26 | -0.06 | 0.11 | 0.19 | -0.42 | 0.02 | -0.12 | -0.20 | 0.14 | 0.03 | -0.40 | -0.37 | 0.16 | 0.04 | 1 | 1 | 1 | 1 |
| CIS      | 0.02 | 0.40 | 0.13 | 0.00 | -0.02 | 0.37 | 0.01 | -0.05 | -0.09 | -0.38 | -0.15 | -0.15 | -0.03 | -0.42 | 0.05 | 0.00 | -0.11 | -0.53 | -0.03 | -0.20 | 0.01 | 0.03 | -0.15 | -0.15 | 1 | 1 | 1 | 1 |
| CutC     | 0.15 | -0.26 | -0.09 | 0.09 | 0.11 | -0.33 | -0.19 | -0.16 | 0.40 | 0.15 | -0.06 | -0.14 | 0.03 | 0.13 | 0.03 | 0.06 | 0.26 | 0.29 | 0.02 | -0.16 | 0.55 | -0.05 | -0.05 | -0.16 | 1 | 1 | 1 | 1 |
| FCr      | 0.00 | 0.04 | 0.32 | 0.31 | 0.43 | 0.20 | 0.25 | 0.58 | 0.10 | 0.10 | -0.01 | -0.12 | 0.25 | -0.24 | 0.05 | 0.01 | 0.62 | 0.03 | 0.02 | -0.10 | 0.28 | 0.25 | 0.04 | -0.07 | 1 | 1 | 1 | 1 |
| H4t      | 0.27 | 0.11 | 0.05 | 0.29 | 0.46 | 0.34 | 0.11 | 0.19 | 0.33 | 0.37 | 0.11 | 0.17 | 0.29 | 0.07 | -0.28 | -0.07 | 0.67 | 0.58 | -0.22 | 0.05 | 0.21 | 0.54 | 0.23 | 0.14 | 1 | 1 | 1 | 1 |
| LIn      | -0.55 | -0.42 | 0.09 | 0.09 | -0.44 | -0.34 | 0.15 | -0.02 | 0.82 | 0.01 | 0.23 | -0.07 | 0.06 | -0.73 | 0.18 | 0.00 | 0.07 | -0.10 | 0.13 | -0.30 | 0.60 | 0.93 | 0.22 | -0.10 | 1 | 1 | 1 | 1 |
| SLW      | 0.34 | 0.37 | -0.26 | -0.08 | 0.45 | 0.07 | -0.20 | 0.10 | -0.10 | -0.05 | 0.07 | 0.23 | -0.33 | 0.07 | 0.14 | 0.13 | -0.57 | 0.91 | 0.17 | 0.34 | 0.35 | 0.18 | -0.06 | 0.00 | 1 | 1 | 1 | 1 |
| LfA      | 0.04 | -0.20 | 0.61 | 0.17 | -0.18 | -0.32 | 0.57 | 0.15 | -0.25 | -0.10 | 0.01 | -0.16 | 0.02 | 0.46 | -0.15 | 0.21 | 0.02 | 0.53 | -0.11 | 0.00 | -0.02 | 0.01 | 0.06 | -0.19 | 1 | 1 | 1 | 1 |

a Traits for which correlation coefficients were calculated only among 10 genotypes.

(Eshed and Zamir, 1995), the *S. habrochaites* LA1777 IL (Monforte and Tanksley, 2000), the *S. neorickii* LA2133 backcross inbred lines (BIL) (Fulton et al., 2000), and the *S. cheesmaniae* LA483 recombinant inbred lines (RIL) (Paran et al., 1995).
QTL for cell traits (number and size) were mainly detected under HL (nine QTL under HL against three under LL), and a QTL for cell number was stable (C11b). All QTL for cell number had negative effects while for cell size, two positive and one negative QTL were identified. The cuticular conductance is the trait for which the number of detected QTL was the largest, but also the trait for which a surprising behaviour was observed between the two fruit loads. Under HL, all QTL had a negative effect (except C9c), while under LL all QTL had a positive effect, and nine stable QTL had opposite effects under HL and LL. This could be explained by the fact that Moneyberg had one of the highest values for conductance under HL, and the lowest under LL (data not shown). Concerning fruit cracking, C4d carried a stable positive QTL. The five other QTL were only detected under LL and had negative effects.

Only a few QTL were detected for plant development traits (from one to five QTL per trait) as QTL analysis was only carried out on ten genotypes (Table 5). Among them, less than half were stable.

Co-localizations between QTL for fruit weight and composition and QTL for fruit physiology or plant development: One objective of the present study was to look for co-localizations between QTL for fruit fresh weight and composition and QTL for physiological parameters under both fruit load conditions. In order to avoid additive or epistatic...
effects due to multiple introgressions, only QTL co-localizations found on genotypes carrying a single introgression were shown in Fig. 3. Eleven clusters of QTL for fruit fresh weight and composition traits were found. Five regions carrying QTL for fruit weight with negative effects of S. chmielewskii alleles also carried QTL for dry matter content with an opposite allele effect, in accordance with the inter-genotypic correlation. In the same way, three co-localizations between QTL for fruit fresh weight and sugar content (SUGfw) were identified with opposite allele effects, while two others were identified with the same negative allele effects. Finally, three co-localizations were identified between QTL for fruit fresh weight and QTL for sugar content (SUGdw), with the same negative allele effects. Several co-localizations between QTL for fruit fresh weight and QTL for cell number or for seed number (both three clusters) were detected with same sign effects. Co-localizations between QTL for sugar content (SUGfw) and QTL for cell size were expected according to correlations. A region located on the bottom of chromosome 9 carried such

Table 3. QTL characteristics for fruit weight and composition traits

Genotypes for which significant differences were detected at the 0.05 probability level in the model taking into account the two-year experiment. Chromosomes carrying introgressions are indicated for each genotype. Effects under HL or under LL are expressed as the average percentage of difference between the genotype and Moneyberg under high load and low load, respectively, over two years. Under each fruit load, the year when QTL was significant was indicated as ‘06/07’ when the QTL was detected whatever the year, ‘06’ or ‘07’ when it was significant only in 2006 or 2007, respectively.

| Trait | Genotype | Chr. | Effect under HL | Detection year under HL | Effect under LL | Detection year under LL |
|-------|----------|------|-----------------|-------------------------|-----------------|-------------------------|
| FW    | C3a      | 3    | –30             | 06/07                   | –17             | 06/07                   |
|       | C3c      | 2:3  | –41             | 06/07                   | –51             | 06/07                   |
|       | C3d      | 3    | ns              | –                       | –29             | 06/07                   |
|       | C4d      | 4    | ns              | –                       | –26             | 06/07                   |
|       | C5b      | 4;5;7;11 | ns  | –                  | 19              | 07                       |
|       | C6e      | 6    | ns              | –                       | –16             | 06/07                   |
|       | C7b      | 7    | –27             | 07                       | –27             | 06                       |
|       | C8a      | 8    | ns              | –                       | –23             | 07                       |
|       | C8c      | 8    | ns              | –                       | –19             | 06/07                   |
|       | C9a      | 7;9;11 | ns  | –                  | –16             | 07                       |
|       | C9d      | 9    | –30             | 06                       | –39             | 06/07                   |
|       | C10b     | 10   | –26             | 07                       | –22             | 06                       |
|       | C11b     | 11;12 | –49            | 06/07                   | –47             | 06/07                   |
|       | C12d     | 12   | –18             | 07                       | –24             | 06                       |
| DMC   | C1a      | 1    | 13              | 07                       | 10              | 06/07                   |
|       | C3a      | 3    | 11              | 06/07                   | ns              | –                       |
|       | C3c      | 2;3  | 23              | 06/07                   | 15              | 07                       |
|       | C3d      | 3    | 9               | 06/07                   | 12              | 07                       |
|       | C4d      | 4    | 27              | 06/07                   | 24              | 06/07                   |
|       | C5b      | 4;5;7;11 | ns  | –                  | 8               | 06/07                   |
|       | C7d      | 7    | 11              | 06/07                   | ns              | –                       |
|       | C8a      | 8    | 14              | 06                       | 15              | 07                       |
|       | C9d      | 9    | 19              | 06/07                   | 12              | 07                       |
|       | C11b     | 11;12 | 10              | 06/07                   | ns              | –                       |
| SUGfw | C3a      | 3    | 20              | 07                       | ns              | –                       |
|       | C3c      | 2:3  | 21              | 07                       | ns              | –                       |
|       | C4d      | 4    | 35              | 06/07                   | 19              | 07                       |
|       | C9d      | 9    | 20              | 06/07                   | 14              | 07                       |
|       | C10b     | 10   | –19             | 07                       | ns              | –                       |
|       | C12d     | 12   | ns              | –                       | –15             | 07                       |
| SUGdw | C1a      | 1    | ns              | –                       | –3              | 06/07                   |
|       | C5b      | 4;5;7;11 | ns  | –                  | –9              | 06/07                   |
|       | C6e      | 6    | ns              | –                       | –8              | 06/07                   |
|       | C7a      | 7    | ns              | –                       | –14             | 06                       |
|       | C7d      | 7    | ns              | –                       | –3              | 06/07                   |
|       | C8a      | 8    | –8              | 06/07                   | ns              | –                       |
|       | C8c      | 8    | –8              | 06/07                   | ns              | –                       |
|       | C9a      | 7;9;11 | ns  | –                  | –8              | 06/07                   |
|       | C10b     | 10   | –12             | 07                       | ns              | –                       |
|       | C11b     | 11;12 | –19            | 07                       | –6              | 06/07                   |
|       | C12d     | 12   | ns              | –                       | –3              | 06/07                   |

*a ns: The QTL was not significant.*
## Table 4. QTL characteristics for fruit physiological traits

Genotypes for which significant differences were detected at the 0.05 probability level in the model taking into account the two-year experiment. Chromosomes carrying introgressions are indicated for each genotype. Effects under HL or under LL are expressed as the average percentage of difference between the genotype and Moneyberg under high load and low load, respectively, over two years. Under each fruit load, the year when QTL was significant was indicated as ‘06/07’ when the QTL was detected whatever the year, ‘06’ or ‘07’ when it was significant only in 2006 or 2007, respectively.

| Trait | Genotype | Chr. | Effect under HL<sup>a</sup> | Detection year under HL<sup>b</sup> | Effect under LL<sup>a</sup> | Detection year under LL<sup>b</sup> |
|-------|----------|------|--------------------------|---------------------------------|--------------------------|---------------------------------|
| Dura  | C3a      | 3    | –8                       | 06/07                           | ns                       | –                               |
|       | C4d      | 4    | –6                       | 06/07                           | –6                       | 06/07                           |
|       | C7d      | 7    | ns                       | 10                               | –                        | 06/07                           |
|       | C9d      | 9    | –7                       | 07                               | –8                       | 07                               |
|       | C10b     | 10   | –8                       | 06/07                           | –7                       | 06/07                           |
| SdIn  | C1a      | 1    | –38                      | 07                               | ns                       | –                               |
|       | C3d      | 3    | –32                      | 06/07                           | ns                       | –                               |
|       | C5b      | 4;5;7;11 | –43                  | 07                               | –46                      | 07                               |
|       | C6e      | 6    | –49                      | 07                               | –45                      | 07                               |
|       | C8a      | 8    | –20                      | 06/07                           | ns                       | –                               |
|       | C9d      | 9    | –49                      | 06/07                           | –66                      | 06/07                           |
|       | C10b     | 10   | –42                      | 07                               | ns                       | –                               |
|       | C11b     | 11;12 | –71                    | 06/07                           | –50                      | 06/07                           |
| CIN   | C1a      | 1    | –19                      | 06                               | ns                       | –                               |
|       | C3a      | 3    | –38                      | 06/07                           | ns                       | –                               |
|       | C3c      | 2;3  | –32                      | 06/07                           | ns                       | –                               |
|       | C5b      | 4;5;7;11 | –28                  | 06/07                           | ns                       | –                               |
|       | C9a      | 7;9;11 | –28                  | 06/07                           | ns                       | –                               |
|       | C9d      | 9    | ns                       | –                                | –39                      | 06/07                           |
|       | C10b     | 10   | –42                      | 07                               | ns                       | –                               |
|       | C11b     | 11;12 | –56                    | 06/07                           | –48                      | 06/07                           |
|       | C12d     | 12   | –37                      | 06/07                           | ns                       | –                               |
| CIS   | C1a      | 1    | ns                       | –                                | 17                       | 06                               |
|       | C9d      | 9    | –12                      | 06                               | ns                       | –                               |
|       | C12d     | 12   | 32                       | 06                               | ns                       | –                               |
| CutC  | C1a      | 1    | ns                       | na                              | 52                       | na                               |
|       | C3a      | 3    | ns                       | na                              | 124                      | na                               |
|       | C3c      | 2;3  | –42                      | na                              | 189                      | na                               |
|       | C3d      | 3    | –49                      | na                              | 107                      | na                               |
|       | C4c      | 4    | –29                      | na                              | 40                       | na                               |
|       | C4d      | 4    | –48                      | na                              | 213                      | na                               |
|       | C5b      | 4;5;7;11 | –27                  | na                              | 187                      | na                               |
|       | C6e      | 6    | –45                      | na                              | 131                      | na                               |
|       | C7a      | 7    | ns                       | na                              | 123                      | na                               |
|       | C7b      | 7    | –42                      | na                              | 71                       | na                               |
|       | C7d      | 7    | ns                       | na                              | 66                       | na                               |
|       | C8a      | 8    | –41                      | na                              | ns                       | na                               |
|       | C8c      | 8    | ns                       | na                              | 107                      | na                               |
|       | C8e      | 3;8  | –45                      | na                              | 50                       | na                               |
|       | C9a      | 7;9;11 | ns                     | na                              | 90                       | na                               |
|       | C9c      | 1;7;9;11 | 59                    | na                              | ns                       | na                               |
|       | C9d      | 9    | –17                      | na                              | ns                       | na                               |
|       | C10b     | 10   | –50                      | na                              | 77                       | na                               |
|       | C11b     | 11;12 | ns                       | na                              | 184                      | na                               |
|       | C12d     | 12   | ns                       | na                              | 110                      | na                               |
| FCr   | C3a      | 3    | ns                       | –                                | –70                      | 07                               |
|       | C3c      | 2;3  | ns                       | –                                | –100                     | 07                               |
|       | C4d      | 4    | 741                      | 06/07                           | 182                      | 06/07                           |
|       | C7b      | 7    | ns                       | –                                | –74                      | 06/07                           |
|       | C9d      | 9    | ns                       | –                                | –58                      | 06/07                           |
|       | C11b     | 11;12 | ns                     | –                                | –63                      | 06/07                           |

<sup>a</sup> ns: The QTL was not significant.

<sup>b</sup> na: The QTL stability cannot be deduced as the cuticular conductance was only measured in 2007.
a co-localization with opposite allele effects (C9d). All QTL for fruit cracking co-localized with QTL for fruit fresh weight. Three of them had the same allele effects except on chromosome 4.

Some co-localizations between QTL for dry matter content and QTL for plant development did not always correspond to the direction of correlations (Table 2). For example, dry matter content was positively correlated to plant height at the inter-genotypic level and QTL analysis revealed one co-localization for these two traits with similar allele effects (C4d), and two others with opposite allele effects (C3a and C9d). Some co-localizations were also identified between QTL for sugar content (SUGfw) and QTL for specific leaf weight or leaf number (C3a and C4d).

## Discussion

### Relationships between fruit fresh weight and composition

The influence of carbon availability on the relationships between fruit weight and sugar content was studied via fruit thinning. In peach fruits (Morandi et al., 2008) or in apple fruits (Link, 2000), a lower fruit load increased simultaneously fruit fresh weight and sugar content. In tomato, some fruit thinning experiments were carried out and showed that fruit load reduction led to an increase in fruit fresh and dry weights (Gautier et al., 2001; Bertin, 2005; Baldet et al., 2006), but none of them has dealt with effects on fruit sugar content. In this tomato population, most of the genotypes (15 genotypes over 21) reacted to fruit thinning by increasing the dry matter content and, for only two of them, also by increasing the carbohydrate allocation to sugar metabolism. For the six other genotypes, sugar content relative to fresh weight was unchanged whatever the fruit load. Finally, in some cases, even if the dry matter content increased, the carbohydrate allocation to sugars was stable or decreased, leading to no change in sugar content. The only significant correlation between fruit fresh weight and composition was found at the inter-genotypic level, under high fruit load conditions (Table 1) and concerned the antagonism between fruit fresh weight and dry matter content, associated with a negative relationship between fruit fresh weight and structural carbon content, but not between fruit fresh weight and sugar content. From a genetic point of view, antagonism between fruit fresh weight and soluble solids content has been observed during tomato improvement under high load conditions, and is mainly due to co-localizations of QTL with antagonistic effects (Bernacchi et al., 1998; Chen et al., 1999; Saliba-Colombani et al., 2001; Lecomte et al., 2004). In the present population, markers used to locate the introgressed fragments were common to four tomato mapping populations. In this way, it was possible to compare QTL from the *S. chmielewskii* population with previous work. Co-localizations between QTL for fruit fresh weight and QTL for dry matter content or sugar content on fresh weight basis were detected with opposite effects (Fig. 3), and corresponded to regions that had already been identified in other progenies under high fruit load (Grandillo et al., 1999; Causse et al., 2006). These co-localizations of QTL for fruit fresh weight with QTL for dry matter content with antagonistic effects were common to both fruit loads (C9d), specific to high load (C3a), or specific to low load (C3d, C4d, and C8a) in the *S. chmielewskii* population. Moreover, two co-localizations were identified between QTL for fruit fresh weight and QTL for sugar content relative to fresh weight, with same negative allele effects under high load (C10b) and under low load (C12d). These regions could be involved in carbon allocation to cell structures or to sugar metabolism, because they also co-localized with QTL for sugar content relative to dry
weight. In this population, no stable QTL with positive effects for sugar content, which was not associated with a negative QTL for fruit fresh weight, was found.

Processes underlying fruit weight and composition

Cuticle properties are involved in water loss by transpiration (Schönherr, 1976; Becker et al., 1986; Kerstiens, 1996). Concerning fruit cracking, it usually occurs when fruit growth rate is high (Christensen, 1973). It was thus expected that under low fruit load, when fruit growth was faster, QTL for fruit fresh weight co-localized with QTL for fruit cracking. Genotype C4d showed an extreme phenotype even under HL and carried a major mutation for this trait. It probably corresponded to the mutation Cwp1 described by Hovav et al. (2007). Three other QTL for fruit cracking were mapped and co-localized with QTL for fruit fresh weight with similar effects (Fig. 3), while no such link was found between fruit cracking and fruit fresh weight through correlation analysis (Table 2). An increase in cuticular conductance or in fruit cracking was expected to increase the dry matter content or the sugar content (SUGfw). The hypothesis of a concentration of dry matter by water loss was confirmed at the inter-genotypic level under HL condition, as fruit cracking was positively correlated to dry matter content or sugar content. To avoid interaction with fruit cracking, measurement of cuticular conductance was performed 21 d after anthesis, during fruit cellular expansion, whereas all other variables were analysed at the red ripe stage. As cuticular conductance is known to decrease throughout fruit development (Gibert et al., 2005), conclusions may be biased. Numerous QTL for cuticular

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**Fig. 3.** Genetic map of the QTL detected on genotypes carrying a single introgressed fragment, and at least one QTL for fruit weight or composition. QTL for fruit weight and composition are circled; QTL only detected under high fruit load (HL) are on the left of the chromosome; QTL only detected under low fruit load (LL) are on the right of the chromosome; QTL detected whatever the fruit load are at the middle of the chromosome. (−) and (+) indicate if the S. chmielewskii alleles had negative or positive effects on the trait, respectively.
conductance were particularly susceptible to fruit load change as S. chmielewskii alleles carried negative effects under HL and positive effects under LL. This is probably linked to the extreme behaviour of Moneyberg changing from HL to LL. No other trait behaved similarly, making the interpretation of these co-localizations difficult.

Cell number is a determinant factor of fruit sink strength, usually determined during the early stages of tomato fruit development (Bohner and Bangerth, 1988; Joubes et al., 1999). In agreement with the literature (Higashi et al., 1999; Jullien et al., 2001; Bertin, 2005), fruit fresh weight was positively correlated with cell number and was present both at intra-genotypic and inter-genotypic levels whatever the fruit load (Table 2). This relationship was also confirmed by the numerous co-localizations under both fruit loads between QTL for fruit fresh weight and QTL for cell number, with similar effects (Fig. 3). The increase in fruit fresh weight and cell division in the absence of carbohydrate competition has also been described by Baldet et al. (2006) and was linked to the regulation of $fw2.2$, a cell cycle-regulated gene. Cell expansion was not directly linked to the fruit fresh weight as no significant correlation was found between cell size and fruit fresh weight and QTL co-localizations of these two traits were either with similar allele effects (C9d) or with opposite effects (C12d). Moreover, at the inter-genotypic level and under high fruit load condition, a negative correlation between cell number and cell size suggested the existence of competition for carbohydrates among cells. This competition may reduce the cell growth potential, resulting in smaller cells (Bertin, 2005; Tsukaya, 2006).

Positive correlations between fruit fresh weight and seed number were probably due to the effect of the latter on the sink strength of the fruit (Nitsch, 1970). QTL co-localizations of these two traits were similar to previous QTL mapping experiments carried out on a S. pimpinellifolium F$_2$ population (Van der Knaap and Tanksley, 2003) or on a S. peruviamum BC$_3$ population (Fulton et al., 1997). A co-localization was common to the S. pimpinellifolium F$_2$ population and to the present population at the bottom of chromosome 6. The role of seeds in the sink strength could be related to hormonal signalling, hormones being strongly implicated in the control of cell division rate and sustenance (Gillaspy et al., 1993).

Plant development traits are commonly described in ecophysiological studies, and were used here to estimate source strength. The main hypothesis was that the higher the number of leaves, or the leaf area, the higher the sugar production via photosynthesis, and thus the higher the fruit dry matter or sugar contents. Positive correlations between leaf number and dry matter or sugar content (SUGfw) comforted this hypothesis. A balance between plant vigour and distribution of assimilates to the fruit was thus found at the whole plant level, as already mentioned by Vaast et al. (2006). The hypothesis was also corroborated at the genetic level, as co-localizations between QTL for leaf area or leaf number and QTL for dry matter content or sugar content were identified with same allele effects (C4d and C9d).

**Conclusion**

The present paper aimed to assess the implication of various processes in the relationships between fruit weight and its composition. Our results suggested that these relationships could be mainly related to sink strength through cell division whose intensity was modulated by fruit load. An antagonism between fruit fresh weight and dry matter content was only detected at the inter-genotypic level, in conditions of competition for assimilates. This study also revealed different behaviours of genotypes with respect to changes in fruit load and it was consequently not possible to deduce a general scenario for the whole population. Moreover, a lot of QTL had different effects according to fruit load, suggesting that carbohydrate supply can strongly interact with the genome, probably via sugar or hormonal sensing. Although co-localizations of QTL can hide either pleiotropy or genetic linkage, this work could contribute in helping to choose candidate genes as physiological hypotheses linked to quality traits were formulated at the genetic level. QTL with similar behaviours under both fruit loads could also be interesting targets for breeding programmes as they are more likely to be stable under various environments.

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