QTL analysis of plant development and fruit traits in pepper and performance of selective phenotyping

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QTL analysis of plant development and fruit traits in pepper using selective phenotyping.

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Abstract

A QTL analysis was performed to determine the genetic basis of 13 horticultural traits conditioning yield in pepper (*Capsicum annuum*). The mapping population was a large population of 297 recombinant inbred lines (RIL) originating from a cross between the large-fruited bell pepper cultivar 'Yolo Wonder' and the small-fruited chilli pepper 'Criollo de Morelos 334'. A total of 76 QTLs were detected for 13 fruit and plant traits, grouped in 28 chromosome regions. These QTLs explained together between 7% (internode growth time) and 91% (fruit diameter) of the phenotypic variation. The QTL analysis was also performed on two subsets of 141 and 93 RILs sampled using the MapPop software. The smaller populations allowed for the detection of a reduced set of QTLs and reduced the overall percentage of trait variation explained by QTLs. The frequency of false positives as well as the individual effect of QTLs increased in reduced population sets as a result of reduced sampling. The results from the QTL analysis permitted an overall glance over the genetic architecture of traits considered by breeders for selection. Colinearities between clusters of QTLs controlling fruit traits and/or plant development in distinct pepper species and in related solanaceous crop species (tomato and eggplant) suggests that shared mechanisms control the shape and growth of different organs throughout these species.

Key words: *Capsicum annuum*, QTL analysis, yield, fruit traits, plant growth, selective phenotyping

Introduction

All commercial cultivars result from long and intensive breeding efforts to improve multiple traits including resistance to diseases, fruit or grain characteristics and plant development, which determine adaptation to agro-climatic as well as market conditions. The favourable alleles for these traits are primarily dispersed in distinct individuals in plant germplasm and the selection of elite cultivars gathering these traits requires multiple crossovers within the genetic background. This is particularly true in pepper (*Capsicum annuum*) where disease resistance and adaptation to agroclimatic conditions have to be introgressed into large and sweet fruited cultivars from small-fruited and pungent accessions, which form the large majority of genetic resources. Multi-trait selection is often hampered by unfavourable genetic linkages. However, the genetic mapping of valuable traits should shed light on the genomic regions of economic interest and the loci where genetic recombination should result in more genetic gain. Two questions related to this stake will be addressed in this article. One generic question is: can we reduce the efforts developed in genetic mapping for multiple traits that requires repeated experiments of large progenies? The second and specific question is: what is the architecture of genes and QTLs of interest in the pepper chromosomes, and can the comparison with genomes from other species help in their genome localization and characterization?

The power of QTL detection is determined by many parameters, including the choice of the parental lines (the more the parental lines are genetically distant, the easier is the detection of QTLs) previously reported by Crepieux et al. (*2004*), the size of the segregating population and the magnitude of the experimental error (Hackett *2002*). Since large populations do allow for the identification of QTLs with weak effects (Tanksley *1993*; Haley and Andersson *1997*), the effort involved in the assessment of the phenotypes is large. Selective phenotyping has been proposed as a trade-off strategy to decrease phenotyping costs, and Brown and Vision (*2000*) developed the MapPop software which proposes to select a reduced subset of the most informative individuals, chosen from their genotype data. This reduced subset is further submitted to phenotyping, reducing the field experiments while losing as little information as possible. Such strategies where evaluated by Vales et al. (*2005*) and Birolleau-Touchard et al. (*2007*). They showed that the MapPop sampling method permits to select

population samples with balanced allele frequencies, and was superior to random sampling, particularly when QTL analysis has to be performed from unbalanced populations (doubled haploid or advanced backcross populations). However, performance in QTL detection remained affected by the population size, particularly for QTLs with low individual effects which are frequent for horticultural traits like fruit and plant growth traits in vegetables.

Considering pepper, gene and QTL mapping has been largely developed for disease resistance traits (Lefebvre *2005*; Djian-Caporalino et al. *2006*) and fruit traits, using both intraspecific (Ben Chaim et al. *2001*,*2006*) and interspecific crosses (Rao et al. *2003*; Zygier et al. *2005*; Ben Chaim et al. *2006*). Little information is available on QTLs controlling plant development traits: plant height and flowering time were investigated by Ben Chaim et al. (*2001*) and Rao et al. (*2003*), but primary components that determine plant growth and fruiting earliness, like the number of internodes on the primary stem, their length and growth speed, were not investigated. Considering fruit traits, results from Ben Chaim et al. (*2001*, *2006*), Rao et al. (*2003*) and Zygier et al. (*2005*) are strongly coherent and revealed clusters of QTLs on pepper chromosomes with tight linkage or pleiotropy between QTLs for fruit size, diameter, length and shape. Presence of QTL clusters on chromosomes P2, P3, P4 and P10 between distinct crosses attested the conservation of QTL effects for fruit traits. Moreover, relationships with other solanaceous crops were explored, particularly for genetics of fruit size and shape. In tomato, numerous QTL mapping studies on horticultural traits were carried out, mainly in interspecific crosses (De Vicente and Tanksley *1993*; Bernacchi et al. *1998*; Grandillo et al. *1999*; Ku et al.*1999*; Frary et al. *2004*; Barrero and Tanksley *2004*; Jiménez-Gómez et al. *2007*). QTL mapping research on horticultural traits was also performed to a more limited extent in eggplant and potato (Van Eck et al. *1994*; Doganlar et al. *2002*; Frary et al. *2003*). The large body of research concerned with trait inheritance in tomato has opened the way to the establishment of synteny (conservation of gene repertoire) and colinearity (conserved gene orders) among the *Solanaceae* (Tanksley et al. *1992*; Livingstone et al. *1999*; Ben Chaim et al. *2001*, *2003a*, *b*; Doganlar et al. *2002*; Rao et al. *2003*; Zygier et al. *2005*; Ben Chaim et al. *2006*; Paran and Van der Knaap *2007*).

In the current paper, we report the analysis of 13 horticultural traits including fruit traits

and plant development traits, in a large intraspecific recombinant inbred progeny (RILs) of pepper that was used by Barchi et al. (*2007*) to develop a high-resolution genetic linkage map. QTL detection was performed in the whole population including 297 RILs and compared with informative subsets of 141 and 93 RILs to test the advantage of selective phenotyping in this progeny. QTL analysis for multiple traits informed the relative position of QTL clusters and genetic linkages between loci determining traits of interest. It also delivered target QTLs that suggest syntenic relationships with known horticultural QTLs in other *Solanaceae* species.

Materials and methods

Plant material and trait evaluation

The plant material was developed from an intraspecific cross between the large-fruited inbred line 'Yolo Wonder' (YW) and a small-fruited pungent inbred line 'Criollo de Morelos 334' (CM334) issued from the Mexican landrace 'Criollo de Morelos'. The recombinant inbred line (RIL) population was based on a set of F_6derivatives, produced by self-pollination of the F5 RILs used to construct the genetic map (Barchi et al. *2007*). The horticultural traits of the parental lines, their F_1 hybrid and the RILs were measured in a single year experiment arranged in a randomized complete block design with three blocks of three individual plants (repeats) per genotype and block. The horticultural traits measured are included among the standard morphological descriptors for pepper (IPGRI *1995*). The fruit traits were measured from two individual fruits per plant, except the fruit weight measured as an average of 5–10 fruits per plant. These fruit traits were the log-transformed mean of the fruit weight (Lfw), the fruit length (Frl) measured as the distance (in mm) between the pedicel attachment and the fruit apex, the fruit diameter (Frd) measured as the maximum fruit width (in mm), the fruit shape (Frs) defined as the Frl:Frd ratio, the pericarp thickness (Pet) in mm, the pedicel length (Pel) in mm, the number of fruit locules (Nlo). The plant traits were measured from each individual plant: the flowering earliness (Flw), i.e., the number of days from sowing to the anthesis of the first flower, the primary axis length (Axl) defined as the length (in cm) of the primary axis from the cotyledons to the first branch, the number of leaves on the primary axis (Nle), the mean internode length (Inl) given by the ratio Axl:Nle in cm, the axis growth speed (Axs) given by the ratio Axl:(Flw - 15 days) in which the 15 days corresponding to the time of hypocotyl and cotyledons emergence after sowing were deduced to obtain the growth time of the axis = epicotyl, and the mean internode growth time (Int) given by the ratio (Flw - 15 days):Nle.

Data and QTL analyses

All statistical analyses were performed using R software (R Development Core Team *2006*). Analyses of variance (ANOVA) were applied to estimate genotypic/environmental effects according to the model $Y_{ij} = i + b_j + g_i + e_{ij}$, where i, b_j, g_i and e_{ij} represent, respectively, the overall mean, block effect, genotypic effect

and error effect. Broad-sense heritability (h_{BS}^2) values were calculated as $\sigma_G^2/(\sigma_G^2 + \sigma_E^2/n)$ where σ_G^2 is the genetic variance, σ_E^2 the environmental variance (including block, interaction and error effects) and n the number of blocks. Correlations between traits were estimated using Pearson's coefficient. The normal distribution of traits was assessed by using the Shapiro–Wilks test ($\alpha = 0.05$). Lines where declared transgressive when their value exceeded the highest parental value or were lower than the lowest parental value by more than the least significant difference (LSD) at $P < 0.05$.

QTL detection was based on the genetic map developed by Barchi et al. (*2007*), and made with QTL Cartographer software (Basten et al. *2002*), employing both interval (IM) (Lander and Botstein *1989*) and composite interval (CIM) (Zeng *1994*) mapping. For each population size, LOD thresholds at the 5% probability level were empirically established by applying 1,000 permutations for each trait and for both methods (Churchill and Doerge *1994*). The proportion of observed phenotypic variation attributable to an individual QTL was estimated by the coefficient of determination (R^2). The total phenotypic variation explained was estimated by fitting a linear model (multiple regression) including all the putative QTLs for the respective trait simultaneously. For each QTL, the marker with the highest LOD was chosen as the QTL-representative marker variable in the multiple regression. Epistatic interactions between all the 250 markers of the core map were tested using a two-way ANOVA model with interaction effect between all possible two-locus combinations of core map marker genotypes, as described by Lefebvre and Palloix (*1996*). With 250 core markers, 32,125 marker combinations per trait were tested (404,625 for 13 traits) and epistasis was inferred to be significant at $P < 10^{-5}$. Individual QTLs were named using the three-first letters to indicate the trait, followed by a number indicating the pepper chromosome (e.g. 1 for P1) or by the linkage group involved (e.g. LG13), and a second number defining the position within the chromosome/LG to which the QTL mapped (e.g. 1.1). IM or CIM were added when a QTL was detected with only one of the two methods. MapChart software (Voorrips *2002*) was used to produce visualisations of chromosomes carrying QTLs.

Choice of informative individuals

26 of the full set of 297 RILs were removed from the population because of their poor fertility resulting in a lack of seeds for further experiments. From the remaining 271 RILs, two subpopulations [‘A’ (141 RILs) and ‘B’ (93 RILs)] were selected using MapPop software (Brown and Vision *2000*), with the full linkage map as the input file. The selection criterion applied to identify the most informative individuals was the expected maximum bin length (eMBL), i.e. the expected maximum distance between two points subjected to recombination. As previously reported by Birolleau-Touchard et al. (*2007*), the best sample is the one with the most similar eMBL value compared to the original population obtained with a defined computational time and a chosen sample size. As a consequence, several iterations were run, until no further improvement in eMBL was achieved (data not shown).

Results

Phenotypic variation and trait correlations

The mean phenotypic values and estimated h_{BS}^2 for each trait are listed in Table 1. The parental lines displayed significant contrasted phenotypes (Table 1) for fruit traits, with a larger, heavier fruit, a thicker pericarp and a higher number of locules for YW compare to the small and elongated fruit of CM334 which showed a higher fruit shape ratio. The pedicel length was similar for the two cultivars. Considering the plant traits, the two parental lines also displayed contrasted phenotypes (Table 1), YW presenting a later flowering date, a shorter primary axis and internode length and a slower growth speed of the axis than CM334. However, the two parental lines were very close for the number of leaves on the axis and internode growth time. In the full RIL set, all the traits were normally distributed. The RIL progeny and F_1 hybrid displayed intermediate values between the parental lines for all the fruit traits, except the pedicel length (Pel) and the fruit length (Frl) where about 69% and 11.7% of the progeny displayed significant transgressive phenotypes with higher or lower values than the parental lines ($\alpha = 0.05$). Considering plant traits, for almost of them (except the flowering earliness) a large proportion (from 9.7% for Axs to 56% for Nle) of RILs displayed transgressive phenotypes; at the same time also the F_1 hybrid displayed higher (Axl, Inl, Axs) or lower (Flw, Nle) values than the parental lines.

Heritabilities were high for all the traits, ranging from 0.84 (Nlo) to 0.97 (Frd and Frs) (Table 1). Highly significant correlations were detected between fruit traits or between plant traits (Table 2). As a general feature, fruit weight, fruit diameter, locule number and pericarp thickness were positively correlated together but negatively correlated with fruit shape. Considering plant traits, the axis length increased with the number of leaves and the internode length. However, the growth speed of the axis (and of internodes) also increased with the axis length, so that flowering time (earliness) displayed a significant but weak correlation with Nle. Correlations between fruit and plant traits were either non-significant ($P > 0.05$) or weak (<0.3).

Trait means in the two subpopulations are listed in Table 1. In no case, a subpopulation mean differed significantly ($P < 0.05$) from the full population mean. The distribution of trait values was also very similar in both subpopulations and the full population for all the traits and the trait variances remained constant across subpopulations. Correlations

between traits were also comparable with those calculated for the full population (data not shown).

QTL detection in the full and partial RIL populations

Across the 13 traits, 76 QTLs were identified and grouped onto 28 genomic intervals distributed over 11 chromosomes and 14 small unassigned linkage groups (Fig. 1; Table 3). No significant epistatic interactions were identified between markers, even at higher *P* value ($P < 10^{-2}$). Clusters of QTLs governing 4–6 distinct fruit traits were mapped on chromosomes P2, P3, P4, P10, P11, P12 and small linkage groups LG 17, 24, 25 and 27. Considering plant developmental traits, only four tightly linked QTLs affecting four different traits were mapped on chromosome P2, with smaller clusters on chromosomes P1, P4 and P9. Depending on the traits, 2–12 QTLs were detected, with individual R^2 values ranging from 0.21 to 0.04. The total phenotypic variation explained by QTLs (global R^2) ranged from 0.07 to 0.91. Traits with the highest global R^2 were the fruit diameter (12 QTLs, $R^2 = 0.91$) followed by the fruit weight (7 QTLs, $R^2 = 0.48$), the number of locules (9 QTLs, $R^2 = 0.46$), the axis growth speed (4 QTLs, $R^2 = 0.44$) and the axis length (4 QTLs, $R^2 = 0.42$). The traits which variation was poorly explained by QTLs were the internode growth time (2 QTLs, $R^2 = 0.07$), the internode length (3 QTLs, $R^2 = 0.10$) and the flowering earliness (5 QTLs, $R^2 = 0.15$). For the fruit traits Lfw, Frd, Pet and Nlo, all the positive alleles were derived from the large-fruited parental line YW. For the fruit length (Frl) and shape (Frs), both parents contributed alleles at different QTLs that increased the trait value, that was expected since CM334 harbours long-shaped fruits. For the pedicel length (Pel) and all the plant traits, both parental alleles contributed to increase the trait.

In the subpopulations A (141 RILs) and B (93 RILs), 26 and 15 QTLs were detected respectively (Table 3). No significant epistatic interactions were identified in either subpopulation ($P < 10^{-6}$). The LOD scores associated to the QTLs were always much lower in the reduced subpopulations than in the full RIL population, and only the QTLs with the highest LOD scores remained significant. For example, *Frd11.1* QTL showing a LOD score greater than 11 was common to all three populations, while other Frd QTLs, with lower LOD scores were progressively lost in the A and B subpopulations. A contrario, their individual R^2 values where equal or higher in the subpopulations than in

the full RIL population. For example, the R^2 value for*LfwLG24.1* increased from 0.08 in the original population to 0.10 and 0.14 in the subpopulations A and B respectively, while for *Flw1.1*, the R^2 value increased from 0.10 (297 RILs) to 0.12 (A) and 0.17 (B). The total phenotypic variation explained by QTLs globally decreased with the population size, ranging from 0.91 to 0.07 in the whole population, from 0.36 to 0.08 in the A subpopulation and from 0.34 to 0.12 in the B subpopulation. This was spectacular for complex traits like Frd, which global R^2 decreased from 0.91 (297 RILs) to 0.36 (subpopulation A) and 0.21 (subpopulation B). Finally, the use of subpopulations led to detect new QTLs for Pel, Nle and Int in A subpopulation and two new QTLs for Frd and Flw in B subpopulation. These QTLs were not detected in the whole population even as putative (close to the LOD threshold) QTLs.

Discussion

The QTLs involved in the inheritance of 13 horticultural traits analysed provide a picture of the genetic complexity of these traits, and the location of the major loci should be informative for the genetic analysis and breeding of pepper. The mapping population was derived from an intraspecific cross between parental types widely used by pepper breeders. This choice serves both to maximise mapping precision by reducing the frequency of the skewed segregations commonly experienced in interspecific crosses, and to generate information with respect to QTL of relevance for genetic improvement within advanced germplasm.

General features of the data and QTL detection

Phenotypes were assessed in a single environment, that may affect portability of QTLs to different agro-climatic conditions. The plant environment may poorly affect the relative values for fruit shape and weight within a segregating progeny, and this is confirmed by the fact that the main QTLs for fruit weight and shape appeared conserved in these distinct studies. No previous experiments permit this comparison as regards growth and development traits. However, the axis length, the number of leaves on primary axis and the flowering date are known by breeders to be affected by environment × genotype interactions, despite these traits are very stable (genetically determined) in a constant environment (unpublished data). Thus, the results obtained here for plant traits may be relevant mainly in open field conditions in Mediterranean region. Nevertheless the high level of reproducibility between replicates resulted in high heritabilities of the traits in the tested environment. The heritability values were generally higher than those reported by Rao et al. (*2003*), but comparable to those estimated by Ben Chaim et al. (*2001*). The percentage of genetic variation explained by QTLs was highly trait-specific but not dependent on trait heritability. Frd was associated with the highestR^2 value (0.91) and Int with the lowest one (0.07) despite they displayed similar heritabilities (0.97 and 0.91 respectively). The highest percentage of variation explained by QTLs occurred when many QTLs with minor effects (e.g. Frd) were detected. Global R^2 depends on the accuracy of the linkage map as well as on the inter-marker distances (Jansen et al. *1995*). The genetic structure of the trait, the size of the mapping population (Melchinger et al. *1998*; Utz et al. *2000*), the genetic

background, the environment, and interactions between QTLs can all contribute to a failure to detect all the QTLs segregating in a population. In the present study, the limited percentage of variation explained for some traits, may indicate that the heritabilities were partially overestimated due to a single year and single environment experiment (the variation between lines would not reflect exclusively the genetic variations), but also suggests that some QTLs remain undetected, possibly because of their low individual effects.

Transgressive lines and contribution of parental alleles at the QTLs

Transgressive segregations in the RIL progeny were observed for many traits, particularly when parental values were similar (pedicel length, number of leaves). In every case, alleles from both parental lines were shown to contribute to increase (or decrease) the trait value. Transgressive genotypes were already known to result from the combination of alleles from both parents that have effect on the same direction (De Vicente and Tanksley *1993*). The effect of such allele combinations was tested regarding to the graphical genotypes at the detected QTLs of the three individuals with the highest and three individuals with the lowest values for the pedicel length (Fig. 2). The three transgressive individuals with the highest pedicel length were found to posses all the six alleles responsible for pedicel elongation (YW alleles at P1, P4 and LG42 and CM334 alleles at P2, P3 and P12), with the exclusion of one genotype, lacking one allele at *Pel12.1*. On the contrary, the three individuals with the shortest pedicel length possessed all the alleles which decreased the pedicel length, with the exclusion of one individual at *Pel2.1*. This result indicates that these six QTLs explain a major part (if not all) of the observed trait variation, and that the global R^2 of 0.37 is an underestimation, probably resulting from incomplete linkage (recombination rate) between the QTLs and the markers inferred in the multiple regression model.

Effect of selective sampling and reduced population size on QTL detection

The detection power increases as the population size is maximized (Charcosset and Gallais *1996*), an effect which is most severe for traits displaying lower levels of heritability (Gallais and Rives *1993*). However practical considerations, particularly with regard to phenotyping, dictate that population sizes should be minimised as far as

possible. Thus Charmet (*2000*) has shown that 100 doubled haploid (DH) lines appear to be the critical limit for detecting QTLs of traits with a heritability above 0.3, while about 1,000 individuals are needed to detect QTLs for a trait with a heritability of 0.25. The precision of QTL detection also depends on the sampling method, which can be either random or based on either selective genotyping or selective phenotyping. We have chosen the latter strategy to generate the two subpopulations, one of which is about half the size of the full set, and the other about one-third.

The use of subpopulations brought to the identification of fewer QTLs, characterised by a lower LOD score than those detected in the original population. In most cases, only QTLs with the highest LOD scores in the full population remained significant in the subpopulations. The reduction of the number of QTLs detected when reducing the number of individuals used was also observed by Vales et al. (*2005*) and Birolleau-Touchard et al. (*2007*) who compared different sampling procedures, including the MapPop approach. As an expected consequence of the reduction of the number of detected QTLs, the use of small subsets of individuals led in our analyses to the reduction of the global R^2 value for each trait. This result is in contrast with that reported by Vales et al. (*2005*) who obtained an increasing of global R^2 values as the population size decreased. This probably resulted from the decrease of the whole phenotypic variance in their reduced subpopulations, instead of the phenotypic variances of our subpopulations A and B remained similar to that of the whole population. On the other side, Vales et al. (*2005*) also found that the use of reduced populations overestimates the individual R^2 value of each QTL. The use of subpopulations also led to the detection of new QTLs, which were significant only in the smallest subpopulation B. The reduction in population size seemed to have generated unbalanced (skewed) samples which were responsible for detecting spurious QTLs (Birolleau-Touchard et al. *2007*). We previously showed in this progeny that selective genotyping was useful for the fast mapping of additional markers to enhance a pre-existing genetic map (Barchi et al. *2007*). In contrast, according to the results obtained, it seems that the selective phenotyping strategy performs poorly for traits governed by multiple genes with weak effects.

Genetic architecture of the QTLs determining fruit and plant traits

The analyses performed led to detect a total of 76 QTLs distributed over all the pepper chromosomes (with the exclusion of chromosome P5) and most unassigned linkage groups. All the traits are polygenically controlled, mainly by small effect QTLs as the R^2 values never overpassed 0.21 (Frl4.1). The fruit diameter was found to be controlled by 12 QTLs with individual R^2 ranging from 0.05 to 0.12 and distributed in 12 independent genomic regions.

QTLs controlling fruit traits were mainly concentrated on P2, P3, P4, P10, P11 and P12, with main effects on P4 for fruit weight and length, on P3 for fruit shape and length (upper arm) and for diameter and pericarp thickness (lower arm). Many fruit trait QTLs landed near the same chromosomal location, as a result of linkage, but also pleiotropy since alleles that affect fruit length or diameter will also affect fruit shape, and alleles affecting any fruit dimension (including pericarp thickness) will affect fruit weight. Clusters of QTLs for fruit traits were previously detected in colinear positions on P2, P3, P4, P10 in intra as well as interspecific crosses (Zygier et al. *2005*; Ben Chaim et al. *2001*, *2003a*), thus suggesting a conservation of alleles controlling these traits in both intra and interspecific germplasm. In the present study, we also detected a cluster on P11 of QTLs with minor effects for pericarp thickness, fruit weight, diameter and shape, linked to markers e41/m61_137c and e41/m61_270c that was also detected in interspecific crosses by Rao et al. (*2003*) but never reported in intraspecific crosses. Similarly, two QTLs for fruit shape were detected on P4, linked to markers p14/m39_417y and p25/m45_109y; fruit shape QTL clusters linked to these same markers were previously mapped in two separate interspecific crosses by Zygier et al. (*2005*). In addition, we detected a cluster of QTLs controlling the fruit weight, diameter, the number of locules and the pericarp thickness on chromosome P12 and linked to marker e44/m51_263c which was not previously detected. This probably resulted from allelic differences specific to the (YW × CM334) cross, displaying new alleles controlling the fruit parameters which could be potentially exploited in breeding programs. Co-localizations between fruit traits explain the correlations detected in the progeny, and suggest shared mechanisms between fruit components, i.e. pericarp thickness, fruit diameter and length that contribute to fruit weight of pepper.

Concerning the QTLs controlling plant growth, a tight co-localisation of four QTLs

affecting flowering earliness, axis length, axis growth speed and internode length was detected on chromosome P2. Additional clusters on chromosome P4 (flowering earliness, axis growth speed and internode growth time), on chromosome P9 (axis length and axis growth speed) and on LG47 (axis length, internode length and number of leaves) were also found. This clustering/co-localization of QTLs is in agreement with the correlations found between these traits. It may indicate linkage effects but also pleiotropic effects of genes on the morphology (internode length, number of leaves) or growth speed of vegetative organs. Co-localization between plant and fruit trait QTLs were detected on P2. A special interest should be brought on this chromosome where QTLs affecting the shape of several organs, i.e. the number of fruit locules, the fruit shape, the fruit diameter, the axis, internode and pedicel lengths, were tightly co-localized with overlapping LOD peaks. Only fine mapping would bring additional information on the linkage/pleiotropic determinism of these traits which all depend on cell division, elongation and regulation of the cell cycle. Several gene families involved in the cell cycle regulation were characterized for their functional role in plant growth and development (Goda et al. *2004*; Inzé *2005*). They may provide good candidates for further fine mapping these QTLs and looking for synteny relationships with *Arabidopsis* and solanaceous crops.

Potential orthologous QTLs with other Solanaceae species

Several studies revealed potential syntenies and colinearities among the *Solanaceae* species, in particular for fruit size and shape between pepper, tomato and eggplant (Tanksley et al. *1992*; Livingstone et al. *1999*; Ben Chaim et al. *2001*; Doganlar et al. *2002*; Rao et al. *2003*; Ben Chaim et al. *2003a*, *b*; Zygier et al. *2005*; Ben Chaim et al. *2006*; Paran and Van der Knaap *2007*). However, the lack of common markers used to map these loci in our progeny prevents further evidence of synteny between these species. The detection of QTL clusters for pepper fruit traits on chromosomes P2, P3, P4 and P10 only consolidates the previous analyses performed by the authors cited above. Some additional information was obtained regarding the fruit QTL cluster on P2. In tomato, several QTLs controlling fruit size were mapped in the colinear genomic region of chromosome T2. Ben Chaim et al. (*2001*) and Zygier et al. (*2005*) detected QTLs for fruit weight, shape and diameter in different crosses in pepper that were

suggested to correspond to the tomato genomic region of the QTL *fw2.1*, due to their tight linkage with the *ovate* sequence in both pepper and tomato. In our study, we detected again fruit diameter and fruit shape QTLs (*Frd2.1*, *Frs2.1*) in this same genomic region, but also a QTL for the locule number (*Nlo2.1*) that might correspond to the *lcn2.1* which also affects the number of locules in the tomato fruit (Lippman and Tanksley *2001*; Barrero and Tanksley *2004*). This last QTL in tomato, depending on the cross, explains 19 or 32% of the phenotypic variability, while in pepper, its effect seems lower with a R^2 of 5%. In pepper, fruit weight only depends on pericarp development, and fruit shape is mostly determined after fertilization, that suggests different mechanisms from tomato. However, co-localization of QTLs for the number of locules, the fruit diameter and shape and of the *ovate* gene strongly suggests synteny relationships of genes affecting cell division, elongation and polarity with colinearity relationships in tomato and eggplant. Additional candidate QTLs for synteny relationships include the QTL*Axl2.1* for height of the primary stem which has putative orthologues in both tomato chromosome T2 (Paran et al. *1997*) and eggplant chromosome E2 (Frary et al. *2003*.)

Further new QTLs which we identified and showing a putative synteny with other *Solanaceae* species are*pet10.1* (linked to marker e36/m47_145y with a confidence interval of 21 cM) affecting the pericarp thickness, which is a possible orthologue to tomato *pcp10.1* (Frary et al. *2004*) linked to TG52 marker. Finally, several QTLs were found in unassigned LGs and some of them (like *NloLG25.1* and *IntLG47.1*) explain a relatively high percentage of variation with individuals R^2 values of 0.13 and 0.11 respectively.

Results obtained from our and previous studies show that the main constraint in synteny analysis is due to the complex rearrangements between *Capsicum* and *Solanum* genomes. Fine mapping with shared markers will be required for identifying orthologous regions among these *Solanaceae* species. Moreover, Zygier et al. (*2005*) pointed out that the level of orthology between pepper and tomato chromosome T2 and T4 for QTL controlling fruit shape was limited as a consequence of the divergent selection that occurred during the domestication of these species. The divergent selection for horticultural traits in *Solanaceae* species may have conserved only a limited number of orthologous QTL thus allowing an explanation to the limited number

of shared QTLs found between pepper, tomato and eggplant.

Conclusions

Our results showed that fruit traits are mostly inherited independently from plant growth characteristics, except linkage relationships in chromosomes P2 and P4. This offers large degrees of freedom in breeding for plant and fruit ideotypes. Moreover, allelic diversity and contribution of alleles from distinct genotypes should increase the range of potential phenotypes. However, the clusters of QTLs for horticultural traits detected in chromosomes P4, P9 and P10 revealed linkage with previously mapped QTLs or major genes for resistance to major pepper diseases including *P. capsici*, tospoviruses and potyviruses on chromosomes P4 and P10, nematodes on chromosome P9 (for review see Djian-Caporalino et al. *2006*). Selection of recombination events in these chromosomes have to be facilitated by a marker-assisted strategy, and markers localized in the chromosome regions where recombinant individuals have to be selected need to be further developed. The linkage between markers and QTLs for horticultural important traits may therefore represent a valuable tool for multi-trait marker-based breeding strategy in pepper.

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Table 1: Trait means, standard deviation (SD) and heritabilities for the horticultural traits measured in the parental lines, the F1 hybrid, the RIL population of pepper (n=297) and the sub-populations A (n=141) and B (n=93) issued from selective genotyping.

Trait	code	Yolo Wonder	Criollo de Morelos 334	Significant mean difference among parental values (t test)	F1	F6	Sub-population A	Sub-population B	Heritability
Logarithm of fruit weight	Lfw	5.38±0.12	1.83±0.08	Yes: $p<10^{-6}$	3.27±0.11	3.33±0.37	3.33±0.41	3.27±0.39	0.96
Fruit length (mm)	Frl	91.47±12.70	58.83±5.22	Yes: $p<10^{-6}$	81.88±12.63	77.8±14.70	78.05±14.25	76.53±12.985	0.96
Fruit diameter (mm)	Frd	90.43±8.44	18.54±1.56	Yes: $p<10^{-6}$	37.57±3.36	36.98±6.52	36.98±7.34	36.36±7.18	0.97
Fruit shape	Frs	1.02±0.19	3.17±0.27	Yes: $p<10^{-6}$	2.20±0.38	2.19±0.57	2.21±0.58	2.55±0.58	0.97
Pericarp thickness (mm)	Pet	7.45±0.66	2,48±0.25	Yes: $p<10^{-6}$	3.64±0.63	4.06±0.65	4.12±0.66	4.06±0.65	0.92
Number of locules	Nle	4.02±0.98	2.29±0.46	Yes: $p<10^{-6}$	2.46±0.51	2.85±0.37	2.83±0.40	2.82±0.38	0.84
Pedicel length (mm)	Pel	40.67±6.41	38.23±4.24	No: p=0.67	49.94±5.63	47.63±8.17	46.75±6.94	46.37±6.53	0.95
Flowering (days)	Flw	60.96±3.19	53.07±3.07	Yes: $p<10^{-6}$	52.73±2.51	56.62±2.26	56.61±2.23	56.48±2.21	0.88
Axis length (cm)	Axl	18.01±2.42	22.92±3.67	Yes: $p<10^{-6}$	25.1±2.7	22.06±3.66	21.96±3.75	21.85±3.37	0.94
Number of leaves	Nle	12.12±1.56	12.50±1.91	No: p=0.47	11.26±1.42	11.56±1.47	11.59±1.52	11.44±1.57	0.92
Internode length (cm)	Inl	1.49±0.16	1.85±0.24	Yes: $p<10^{-6}$	2.25±0.32	1.93±0.28	1.91±0.27	1.93±0.26	0.91
Internode growth time (days)	Int	3.86±0.59	3.09±0.42	Yes: $p<10^{-6}$	3.39±0.37	3.68±0.48	3.67±0.44	3.71±0.45	0.90
Axis growth speed (mm/day)	Axs	3.93±0.55	6.01±1.00	Yes: $p<10^{-6}$	6.66±0.68	5.32±0.84	5.82±0.84	5.27±0.74	0.93

Table 2. Pearson correlations between traits assessed in the F6YC RIL population. The traits analysed were Lfw (logarithm of the mean fruit weight), Frl (fruit length), Frd (fruit diameter), Frs (fruit shape), Pet (pericarp thickness), Nlo (number of fruit locules), Pel (pedicel length), Flw (earliness), Axl (axis length), Nle (number of leaves), Inl (mean internode length), Int (mean internode growth time), Axs (axis growth speed). Coloured boxes indicate significant correlations ($p<0.05$).

Trait	Lfw	Frl	Frd	Frs	Pet	Nlo	Pdl	Flw	Axl	Nle	Inl	Int
Frl	0.41											
Frd	0.87	0.06										
Frs	-0.31	0.69	-0.64									
Pet	0.73	0.06	0.68	-0.43								
Nlo	0.23	-0.29	0.36	-0.46	0.17							
Pdl	0.14	0.40	-0.02	0.30	-0.04	-0.22						
Flw	0.23	0.03	0.26	-0.14	0.20	0.03	0.25					
Axl	-0.09	0.03	-0.11	0.08	-0.03	0.02	0.08	0.26				
Nle	-0.16	-0.11	-0.13	0.01	-0.10	0.06	-0.13	0.34	0.50			
Inl	0.05	0.14	0.00	0.09	0.06	-0.05	0.21	0.01	0.66	-0.30		
Int	0.28	0.12	0.27	-0.09	0.20	-0.05	0.26	0.12	-0.39	-0.88	0.34	
Axs	-0.17	0.03	-0.20	0.14	-0.10	0.01	-0.01	-0.08	0.94	0.40	0.68	-0.45

Table 3: QTLs detected in the whole F5YC RIL population, the sub-populations A and B obtained by selective genotyping. For each trait the LOD significance threshold at p=0.05 determined after 1000 permutations is indicated. The closest marker to the QTL and the direction of the QTL (i.e., which parent contributes positively to the trait) are indicated, along with the LOD value of the QTL, the determination coefficient of the individual QTL and for the whole trait. IM, CIM: QTLs detected only with Interval mapping or Composite interval mapping.

	QTL	Marker	Direction	LOD	Variation explained		Heritability	Additive
					Locus	Trait		
Logarithm of fruit weight Lod>3.08	Lfw3.1	e40/m49_198y	Yolo Wonder	5.14	0.11			0.12
	Lfw4.1	p17/m32_240c	Yolo Wonder	9.63	0.15			0.15
	Lfw11.1	e41/m61_137c	Yolo Wonder	4.61	0.07			0.1
	Lfw12.1 CIM	e44/m51_263c	Yolo Wonder	4.22	0.05			0.09
	LfwLG15.1	e38/m60_224y	Yolo Wonder	5.03	0.08			0.1
	LfwLG24.1 IM	e41/m54_184y	Yolo Wonder	4.49	0.08			0.11
	LfwLG45.1	Epms_402	Yolo Wonder	4.01	0.08	0.48	0.96	0.1
Fruit length Lod>3.12	Frl3.1	e36/m52_158y	Criollo de Morelos	7.26	0.1			-3.9
	Frl4.1	e38/m60_109y	Yolo Wonder	17.16	0.21			6.5
	Frl7.1	e41/m61_140c	Yolo Wonder	5.53	0.1			3.43
	FrlLG22.1	e34/m53_181c	Yolo Wonder	5.99	0.1	0.39	0.96	3.95
Fruit diameter Lod>3.15	Frd2.1 CIM	e36/m52_116c	Yolo Wonder	4.73	0.12			2.23
	Frd3.1	p14/m39_221y	Yolo Wonder	3.72	0.11			2.17
	Frd4.1	e41/m48_078y	Yolo Wonder	4.63	0.05			1.46
	Frd8.1 CIM	p11/m49_274c	Yolo Wonder	3.23	0.06			1.38
	Frd10.1	e36/m47_145y	Yolo Wonder	3.32	0.07			1.73
	Frd11.1	e41/m61_137c	Yolo Wonder	11.27	0.13			2.34
	Frd12.1 IM	e44/m51_263c	Yolo Wonder	3.43	0.06			1.65
	FrdLG15.1	e38/m60_224y	Yolo Wonder	7.64	0.1			2.06
	FrdLG17.1	e38/m61_144y	Yolo Wonder	4.74	0.06			1.57
	FrdLG24.1 IM	e41/m54_184y	Yolo Wonder	4.57	0.08			1.85
	FrdLG25.1	p15/m40_091c	Yolo Wonder	6.09	0.07			1.7
	FrdLG37.1	p15/m40_319c	Yolo Wonder	3.94	0.06	0.91	0.97	1.56
Fruit shape Lod>3.12	Frs2.1 CIM	e36/m52_116c	Criollo de Morelos	3.24	0.04			-0.11
	Frs3.1	e43/m54_256y	Criollo de Morelos	11.75	0.15			-0.22
	Frs4.1	p14/m39_417y	Yolo Wonder	4.01	0.05			0.11
	Frs4.2CIM	p25/m45_109y	Yolo Wonder	3.83	0.08			0.16
	Frs10.1	e38/m60_117c	Criollo de Morelos	4.68	0.06			-0.14
	Frs11.1	e41/m61_270c	Criollo de Morelos	4.41	0.07			-0.13
	FrsLG17.1	e40/m47_239y	Criollo de Morelos	5.21	0.07			-0.14
	FrsLG25.1	e41/m54_351c	Criollo de Morelos	3.79	0.06	0.31	0.97	-0.12
Pericarp thickness Lod>3.06	Pet3.1	PG101	Yolo Wonder	5.15	0.14			0.24
	Pet6.1 IM	p25/m45_185y	Yolo Wonder	3.59	0.05			0.15
	Pet10.1	e36/m47_145y	Yolo Wonder	6.87	0.09			0.19
	Pet11.1 IM	e41/m61_270c	Yolo Wonder	3.69	0.06			0.15
	Pet12.1CIM	e44/m51_263c	Yolo Wonder	3.31	0.04			0.13
	PetLG15.1	e38/m60_224y	Yolo Wonder	7.82	0.1			0.2
	PetLG24.1IM	e41/m54_184y	Yolo Wonder	4.27	0.07			0.18
	PetLG27.1	e40/m49_305c	Yolo Wonder	5.75	0.08	0.31	0.92	0.18
Number of locules Lod>3.00	Nlo2.1 CIM	e36/m47_146c	Yolo Wonder	3.42	0.05			0.08
	Nlo8.1	Hpms1_214	Yolo Wonder	3.83	0.06			0.09
	Nlo12.1	e44/m51_263c	Yolo Wonder	4.08	0.05			0.08
	Nlo12.2	e36/m47_237c	Yolo Wonder	4.88	0.1			0.08
	NloLG17.1 IM	e38/m61_144y	Yolo Wonder	4.06	0.08			0.1
	NloLG22.1CIM	e34/m53_181c	Criollo de Morelos	3.13	0.04			-0.07
	NloLG25.1	p15/m40_091c	Yolo Wonder	8.12	0.13			0.12
	NloLG30.1	e44/m51_376c	Yolo Wonder	8.12	0.11			0.12
	NloLG39.1	TntC07y	Yolo Wonder	5.72	0.1	0.46	0.84	0.1
Pedicel length Lod>3.03	Pel1.1 CIM	e41/m61_199y	Yolo Wonder	3.48	0.04			1.58
	Pel2.1	e36/m52_116c	Criollo de Morelos	9.04	0.1			-2.61
	Pel3.1 IM	e34/m53_077c	Criollo de Morelos	5.48	0.12			-2.79
	Pel4.1	e41/m48_078y	Yolo Wonder	5.68	0.07			2.05
	Pel12.1	p25/m45_087c	Criollo de Morelos	7.2	0.12			-2.83
	PelLG42.1	p25/m45_335c	Yolo Wonder	6.14	0.08	0.37	0.95	2.15
Flowering earliness Lod>3.07	Flw1.1	e34/M53_233c	Yolo Wonder	8.04	0.1			0.72
	Flw2.1	Epms409	Criollo de Morelos	6.64	0.1			-0.7
	Flw4.1 CIM	e38/m61_168c	Yolo Wonder	3.34	0.05			0.49
	FlwLG15.1	e38/m60_224y	Yolo Wonder	4.83	0.07			0.58
	FlwLG17.1	p14/m33_851c	Yolo Wonder	4.19	0.07	0.15	0.88	0.59
Axis length Lod>3.02	Axl2.1	e36/m47_146c	Criollo de Morelos	4.65	0.07			-0.96
	Axl6.1 IM	p14/m41_060y	Yolo Wonder	3.29	0.05			0.83
	Axl9.1	e37/m54_92c	Criollo de Morelos	3.83	0.08			-0.98
	AxlLG24.1 IM	Epms376	Yolo Wonder	3.53	0.06			0.88
	AxlLG47.1	p14/m33_311c	Yolo Wonder	6.15	0.1	0.42	0.94	1.18

Number of leaves	Nle3.1 IM	e40/m49_198y	Criollo de Morelos	3.29	0.06			-0.36
Lod>3.17	NleLG38.1 CIM	p17/m32_344c	Criollo de Morelos	3.3	0.04			-0.31
	NleLG45.1 IM	Epms_402	Criollo de Morelos	3.08	0.05			-0.33
	NleLG47.1	p14/m33_311c	Yolo Wonder	6.31	0.11	0.25	0.92	0.49
Internode length	Inl1.1	e36/m52_190y	Yolo Wonder	4.22	0.06			0.07
Lod>3.13	Inl2.1	e36/m47_146c	Criollo de Morelos	6.25	0.11			-0.08
	InlLG28.1 IM	e41/m54_221c	Yolo Wonder	5.1	0.08	0.1	0.91	0.08
Internode growth time	Int4.1IM	e42/M48_116y	Yolo Wonder	3.47	0.05			0.1
Lod>3.00	IntLG47.1	p14/m33_311c	Criollo de Morelos	4.86	0.11	0.07	0.9	-0.14
Axis growth speed	Axs2.1 CIM	e36/m47_146c	Criollo de Morelos	6.27	0.1			-0.26
Lod>3.05	Axs2.2 CIM	p25/m42_268c	Yolo Wonder	3.69	0.05			0.18
	Axs4.1	e38/m61_168c	Criollo de Morelos	4.48	0.07			-0.2
	Axs9.1	CT145	Criollo de Morelos	4.46	0.09	0.44	0.93	-0.24

Subpopulation A

	QTL	Marker	Direction	LOD	Variation explained		Additive
					Locus	Trait	
Logarithm of fruit	Lfw3.1	P14/m39_221y	Yolo Wonder	5.14	0.13		0.12
weight	Lfw4.1	p17/m32_240c	Yolo Wonder	4.56	0.15		0.16
Lod>3.03	LfwLG24.1 CIM	EPMS_376	Yolo Wonder	3.57	0.1	0.31	0.13
Fruit length	Frl4.1	e38/m60_109y	Yolo Wonder	3.86	0.12		5.7
Lod>3.06	FrlLG22.1	P17/m32_155c	Yolo Wonder	3.86	0.1	0.24	5.07
Fruit diameter	Frd11.1	e41/m61_137c	Yolo Wonder	5.96	0.14		2.89
Lod>3.21	FrdLG15.1	e38/m60_224y	Yolo Wonder	4.55	0.12		2.60
	FrdLG17.1	P14/m33_851c	Yolo Wonder	4.55	0.12		2.57
	FrdLG24.1 IM	P11/m49_197y	Yolo Wonder	3.86	0.12	0.36	2.66
Fruit shape	Frs3.1	E34/m53_077c	Criollo de Morelos	4.1	0.13		-0.21
Lod>3.18	Frs11.1 CIM	e41/m61_270c	Criollo de Morelos	3.3	0.06		-0.15
	FrsLG17.1	e40/m47_239y	Criollo de Morelos	3.37	0.11	0.36	-0.19
Pericarp thickness	Pet3.1 IM	PG101	Yolo Wonder	3.33	0.14		0.25
Lod>3.10	Pet10.1	e36/m47_145y	Yolo Wonder	5.42	0.15		0.24
	PetLG15.1	e38/m60_224y	Yolo Wonder	3.44	0.11	0.16	0.21
Number of loges	NloLG17.1 IM	e38/m61_144y	Yolo Wonder	3.86	0.15		0.15
Lod>3.21	NloLG25.1	p15/m40_091c	Yolo Wonder	8.42	0.21	0.22	0.21
Pedicel length	Pel2.1 CIM	e36/m52_116c	Criollo de Morelos	4.40	0.1		-2.29
Lod>3.18	Pel4.1 IM	P17/m32_240c	Yolo Wonder	3.18	0.1		2.31
	Pel4.2 CIM	E42/m48_116hy	Yolo Wonder	3.32	0.07	0.19	1.94
Flowering earliness	Flw1.1	e34/M53_233c	Yolo Wonder	5.42	0.12		0.79
Lod>3.16	FlwLG15.1	e38/m60_224y	Yolo Wonder	5.61	0.13	0.29	0.85
Axis length	Axl9.1	e37/m54_92c	Criollo de Morelos	3.43	0.12		-1.3
Lod>3.09						0.12	
Number of leaves	Nle11.1 CIM	EPMS_410	Yolo Wonder	3.20	0.08		-0.44
Lod>3.00						0.08	
Internode growth time	Int9.1CIM	E44/m61_515c	Criollo de Morelos	4.06	0.09	0.09	-0.14
Lod>3.18							
Axis growth speed	Axs9.1 CIM	CT145	Criollo de Morelos	3.66	0.13	0.13	-0.31
Lod>3.12							

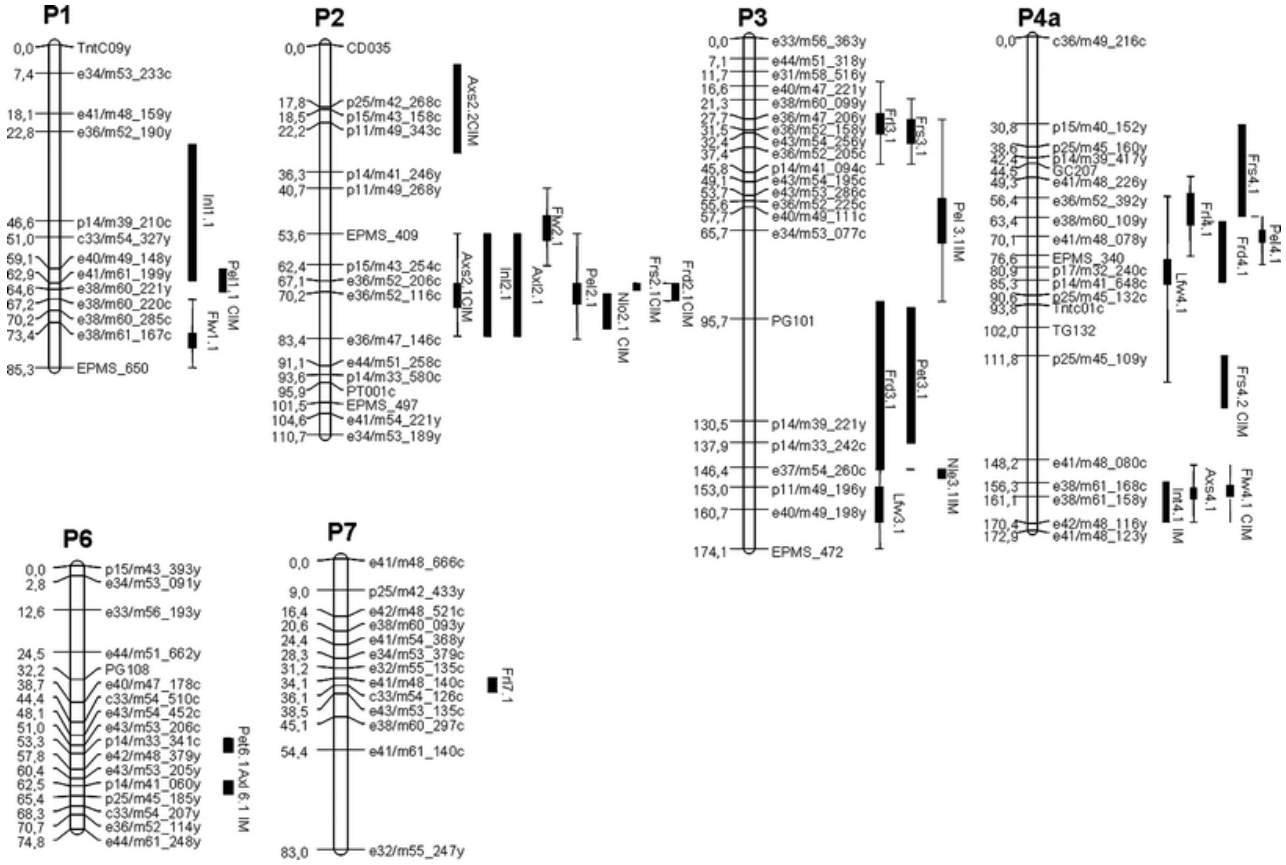
Subpopulation B

	QTL	Marker	Direction	LOD	Variation explained		Additive
					Locus	Trait	
Logarithm of fruit	Lfw4.1	P14/m41_648c	Yolo Wonder	4.74	0.17		0.18
weight	LfwLG24.1 CIM	EPMS_376	Yolo Wonder	3.27	0.14		0.15
Lod>3.24						0.13	
Fruit length	Frl4.1	P17/m32_240c	Yolo Wonder	7.16	0.2	0.2	6.7
Lod>3.16							
Fruit diameter	Frd1.1 CIM	E38/m60_221y	Yolo Wonder	4.13	0.1		2.43
Lod>3.36	Frd4.1 CIM	E38/m60_109y	Yolo Wonder	5.74	0.16		3.03
	Frd11.1	e41/m61_137c	Yolo Wonder	6.72	0.17	0.21	2.96
Pericarp thickness	Pet10.1	E38/m60_117c	Yolo Wonder	3.3	0.16	0.16	0.27
Lod>3.29							
Pedicel length	Pel12.1 IM	E36/m47_237c	Criollo de Morelos	3.51	0.18	0.18	-2.83
Lod>3.28							
Flowering earliness	Flw1.1CIM	TntC09y	Yolo Wonder	4.31	0.17		0.93
Lod>3.26	FlwLG15.1IM	e38/m60_224y	Yolo Wonder	3.60	0.17		0.93
	FlwLG24.1IM	E41/m54_184y	Yolo Wonder	3.88	0.19	0.34	0.97
Internode length	Inl1.1	C33/m54_327y	Yolo Wonder	4.99	0.12		0.11
Lod>3.27	Inl2.1IM	Ee44/m51_258c	Criollo de Morelos	3.28	0.17	0.12	-0.11
Axis growth speed	Axs2.1	EPMS_497	Criollo de Morelos	3.22	0.12		-0.25
Lod>3.19	Axs2.2CIM	P15/m43_153	Yolo Wonder	3.95	0.14	0.32	0.29

Legend for figures :

Figure 1. Map positions of the significant QTLs on each chromosome or LG.

The length of the vertical bars represents the confidence interval of the QTL (LODmax – 1 interval). Lfw (logarithm of the mean fruit weight), Frl (fruit length), Frd (fruit diameter), Frs (fruit shape), Pet (pericarp thickness), Nlo (number of fruit locules), Pel (pedicel length), Flw (earliness), Axl (axis length), Nle (number of leaves), Inl (mean internode length), Int (mean internode growth time), Axs (axis growth speed).



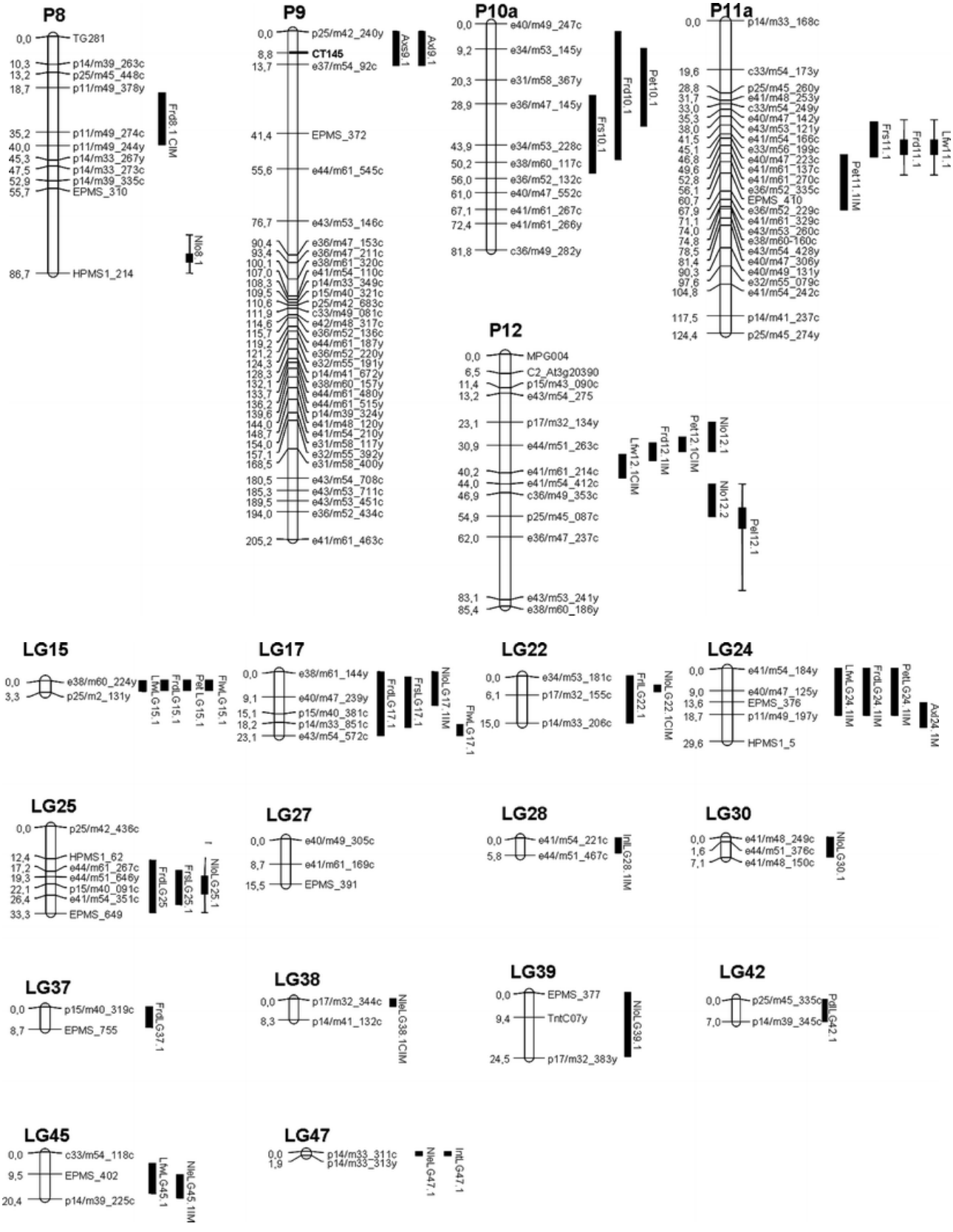

P8
0,0 TG281
10,3 p14/m39_263c
13,2 p25/m45_448c
18,7 p11/m49_378y
35,2 p11/m49_274c
40,0 p11/m49_244y
45,3 p14/m33_267y
47,5 p14/m33_273c
52,9 p14/m39_335c
55,7 EPMS_310
86,7 HPMS1_214
Frd8.1CIM
Nlo8.1
P9
0,0 p25/m42_240y
8,8 CT145
13,7 e37/m54_92c
41,4 EPMS_372
55,6 e44/m61_545c
76,7 e43/m53_146c
90,4 e36/m47_153c
93,4 e36/m47_211c
100,1 e38/m61_320c
107,0 e41/m54_110c
108,3 p14/m33_349c
109,5 p15/m40_321c
110,6 p25/m42_683c
111,9 c33/m49_081c
114,6 e42/m48_317c
115,7 e36/m52_136c
119,2 e44/m61_187y
121,2 e36/m52_220y
124,3 e32/m55_191y
128,3 p14/m41_672y
132,1 e38/m60_157y
133,7 e44/m61_480y
136,2 e44/m61_515y
139,6 p14/m39_324y
144,0 e41/m48_120y
148,7 e41/m54_210y
154,0 e31/m58_117y
157,1 e32/m55_392y
168,5 e31/m58_400y
180,5 e43/m54_708c
185,3 e43/m53_711c
189,5 e43/m53_451c
194,0 e36/m52_434c
205,2 e41/m61_463c
Axs9.1
Axl9.1
P10a
0,0 e40/m49_247c
9,2 e34/m53_145y
20,3 e31/m58_367y
28,9 e36/m47_145y
43,9 e34/m53_228c
50,2 e38/m60_117c
56,0 e36/m52_132c
61,0 e40/m47_552c
67,1 e41/m61_267c
72,4 e41/m61_266y
81,8 c36/m49_282y
Frs10.1
Frd10.1
Pet10.1
P11a
0,0 p14/m33_168c
19,6 c33/m54_173y
28,8 p25/m45_260y
31,7 e41/m48_253y
33,0 c33/m54_249y
35,3 e40/m47_142y
38,0 e43/m53_121y
41,5 e41/m54_166c
45,1 e33/m56_199c
46,8 e40/m47_223c
49,6 e41/m61_137c
52,8 e41/m61_270c
56,1 e36/m52_335c
60,7 EPMS_410
67,9 e36/m52_229c
71,1 e41/m61_329c
74,0 e43/m53_260c
74,8 e38/m60_160c
78,5 e43/m54_428y
81,4 e40/m47_306y
90,3 e40/m49_131y
97,6 e32/m55_079c
104,8 e41/m54_242c
117,5 p14/m41_237c
124,4 p25/m45_274y
Frs11.1
Frd11.1
Lfw11.1
Pet11.1IM
P12
0,0 MPG004
6,5 C2_At3g20390
11,4 p15/m43_090c
13,2 e43/m54_275
23,1 p17/m32_134y
30,9 e44/m51_263c
40,2 e41/m61_214c
44,0 e41/m54_412c
46,9 c36/m49_353c
54,9 p25/m45_087c
62,0 e36/m47_237c
83,1 e43/m53_241y
85,4 e38/m60_186y
Lfw12.1CIM
Frd12.1IM
Pet12.1CIM
Nlo12.1
Nlo12.2
Pet12.1
LG15
0,0 e38/m60_224y
3,3 p25/m2_131y
LMxLG15.1
FrdLG15.1
PetLG15.1
FlwLG15.1
LG17
0,0 e38/m61_144y
9,1 e40/m47_239y
15,1 p15/m40_381c
18,2 p14/m33_851c
23,1 e43/m54_572c
FrdLG17.1
FrsLG17.1
NloLG17.1IM
FlwLG17.1
LG22
0,0 e34/m53_181c
6,1 p17/m32_155c
15,0 p14/m33_206c
FrdLG22.1
NloLG22.1CIM
LG24
0,0 e41/m54_184y
9,0 e40/m47_125y
13,6 EPMS_376
18,7 p11/m49_197y
29,6 HPMS1_5
LMxLG24.1IM
FrdLG24.1IM
PetLG24.1IM
Axl24.1M
LG25
0,0 p25/m42_436c
12,4 HPMS1_62
17,2 e44/m61_267c
19,3 e44/m51_646y
22,1 p15/m40_091c
26,4 e41/m54_351c
33,3 EPMS_649
FrdLG25
FrsLG25.1
NloLG25.1
LG27
0,0 e40/m49_305c
8,7 e41/m61_169c
15,5 EPMS_391
LG28
0,0 e41/m54_221c
5,8 e44/m51_467c
IrdLG28.1IM
LG30
0,0 e41/m48_249c
1,6 e44/m51_376c
7,1 e41/m48_150c
NloLG30.1
LG37
0,0 p15/m40_319c
8,7 EPMS_755
FrdLG37.1
LG38
0,0 p17/m32_344c
8,3 p14/m41_132c
NleLG38.1CIM
LG39
0,0 EPMS_377
9,4 TntC07y
24,5 p17/m32_383y
NloLG39.1
LG42
0,0 p25/m45_335c
7,0 p14/m39_345c
PdlLG42.1
LG45
0,0 c33/m54_118c
9,5 EPMS_402
20,4 p14/m39_225c
LMxLG45.1
NleLG45.1IM
LG47
0,0 p14/m33_311c
1,9 p14/m33_313y
NleLG47.1
IrdLG47.1

Figure 2: Allelic combination of the RIL individuals with extreme phenotypes for the pedicel length.

On the left, chromosomes location of QTLs controlling pedicel length are presented. A, B and C indicate the three individuals with the highest pedicel value, while D, E and F refer to individuals having the shortest pedicel. On the right, the table shows the allele constitution of the six individuals analyzed. The “plus” refers to the allele responsible for increasing the pedicel length at that QTL, and vice versa the “minus” refers to the allele responsible for decreasing the pedicel length at that QTL for each individual. The bar-graphic below the chromosomes represents the phenotypic value of the six extreme individuals.