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ORIGINAL PAPER

Identification of fruit yield loci controlling the salt tolerance conferred by solanum rootstocks

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Abstract The rootstock effect on the fruit yield of a grafted tomato variety was genetically analyzed under salinity using as rootstock two populations of F_9 lines developed from a salt sensitive genotype of *Solanum lycopersicum* var. cerasiforme, as female parent, and two salt tolerant lines, as male parents, from *S. pimpinellifolium*, the P population (123 lines), and *S. cheesmaniae*, the C population (100 lines). There were rootstock lines from the two populations (up to 65% in the P population) that raised the fruit yield of the commercial hybrid under saline conditions. It is shown that this salt tolerance rootstock effect is a heritable trait (h^2 near 0.3), governed by at least eight QTLs. The most relevant component was the number of fruits. Thus most detected QTLs correspond to this component. In general, QTL gene effects are medium-sized, with contributions from 8.5 up to 15.9% at most, and the advantageous allele comes from the wild, salt tolerant species. Only two fruit yield QTLs on chromosomes P9 and C11 might correspond to fruit yield QTLs of the non-grafted lines indicating their root system dependence. A fruit yield QTL on chromosome 3 is acting epistatically in both populations. The epistatic interactions found were dominant and they were unveiled using the associated marker as cofactor in the composite interval mapping methodology. Therefore, an efficient and profitable utilization of wild germplasm can be carried out through the improvement of rootstocks that confer salt tolerance in terms of fruit yield to the grafted variety.

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Introduction

Tomato is one of the most important horticultural crops. In terms of human health, tomato fruit is a major component of daily meals in many countries and constitutes an important source of minerals, vitamins, and antioxidant compounds; however, the areas for tomato optimal growing conditions are becoming narrower around the world. About 20% of irrigated agricultural land and 2% of dryland agriculture are affected by salinity (Yeo et al. 1999). Since salt tolerance, such as tolerance to any abiotic stress, means adaptation, breeding for salt tolerance should take advantage of the evolution of *Solanum* species occurred through adaptation to marginal environments. In this sense, two tomato wild species have been considered as possible donors of salt tolerance: *Solanum pimpinellifolium* L. (Bolarin et al. 1991; Cuartero et al. 1992; Asins et al. 1993; Foolad and Lin 1997) and *S. cheesmaniae* (L. Riley) Fosberg (Rush and Epstein 1976; Tal and Shannon 1983; Mahmoud et al. 1986; Asins et al. 1993).

Efforts on salt tolerance dissection using tomato experimental populations have been carried out taking into account different kind of traits; however, in the case of crop plants, it is ultimately the yield under specific field conditions that will determine whether or not a gene or combination of genes (or QTLs) is of agronomic importance. Salt tolerance in terms of fruit yield has been studied by QTL analysis using two solanum populations (Villalta et al. 2007). Contrary to expected, it was found that the wild allele (i.e. from the wild salt tolerant genotype) was

advantageous only at one total fruit yield QTL on chromosome 10 (*tw10.1*, near the salt specific *fn10.1*). In fact, they found that the advantageous allele at all fruit weight QTLs came from the cultivated, salt sensitive, species. Therefore, other approaches in raising tolerance to salt using wild germplasm need to be considered.

The grafting technique has been used in agriculture since ancient time to improve horticultural crops. Nonetheless, the mechanism by which the rootstock affect the scion trait remains elusive. The tomato is an ideal research material for physiological, cellular, biochemical, and molecular genetic or genomic investigations. It is easy to cultivate, has a short life cycle and is amenable to varied horticultural manipulations including grafting. In the past, grafting was used widely with tomato to limit the effects of fusarium wilt (Scheffer 1957; Lee 1994) but the reasons for grafting, as well as the kinds of vegetables grafted, have increased dramatically over the years. In relation to salinity, Estañ et al. (2005) showed that grafting raised fruit yield of a tomato hybrid variety under salinity. The objectives of the present study are: (1) to evaluate the salt-tolerance improvement strategy of grafting using two populations of RILs developed from salt tolerant wild species (Villalta et al. 2005) as rootstock, (2) to estimate the heritability of the rootstock effect on the salt tolerance of the grafted variety in terms of fruit yield (3) to detect the QTLs involved in both the populations, (4) to analyze their gene effects and interactions for a more efficient utilization of wild tomato germplasm, and (5) to compare the results of this QTL analysis to that reported for the same populations without grafting (Villalta et al. 2007).

Materials and methods

Two populations of F_9 lines were developed from a salt sensitive genotype *Solanum lycopersicum* var. cerasiforme (formerly *L. esculentum*) as female parent. Male parents were two salt-tolerant lines from *S. pimpinellifolium* L. (formely *L. pimpinellifolium*), for the P population, and *S. cheesmaniae* (L. Riley) Fosberg (formerly *L. cheesmanii*), for the C population, respectively. Both populations were developed by single seed descent from 300 to 400 individual plants of the P and C F_2 progenies, respectively (Monforte et al. 1997) after seven selfings, with no conscious selection at any generation, under greenhouse or screenhouse conditions. A total of 123 F_9 P lines and 100 F_9 C lines were used for the salinity-tolerance experiments reported here.

The commercial tomato hybrid *S. lycopersicum* cv. Boludo (Bol) was used as scion, and plants from the P and C populations were used as rootstocks. Boludo (the scion) was also grafted onto roots derived from a different plant of the same genotype (Bol/Bol). Bol and Bol/Bol, non-grafted and self-grafted, plants were included as controls. Bol/Bol plants were used to evaluate any physiological change that could be induced by the grafting process per se.

Seeds were germinated in a growth chamber under controlled conditions (28°C and 90% relative humidity in darkness). Grafting was performed when seedlings had developed 3–4 true leaves, seedlings were cut over the cotyledons, using the shoot as scion and the remaining plant part as rootstock. Grafts were made immediately after cutting the plants and grafting clips were used to adhere the graft union. After grafting, seedlings were grown in the same growth chamber, where the environmental conditions were optimized for the growth of grafted plants: 25/18°C, 70 and 90% relative humidity in light (16 h) and dark conditions, respectively; during the light period, the irradiance changed trying to simulate the natural diurnal changes, being the maximum and minimum photosynthetic photon flux density at plant level of 385 and 135 μmol m^{-2} s^{-1} (400/700 nm), except for the first day in which the grafted plants remained in dark condition.

Six plants per line were transferred to a polyethylene greenhouse, in Murcia Spain, after the grafts had established (2 weeks after grafting). Plants were grown in fiber-coconut coast, using a drip irrigation system, with 4 l h^{-1} drippers, and normal fertilization for tomato culture (Cadahia 1995). The plants were cultivated to only one stem, eliminating all axillary bud. The growing period was February–July.

The water of irrigation used in both experiments comes from Transvase Tajo-Segura, CE = 0.85 dS m^{-1}. The salt treatment applied to the first population, C, was 75 mM NaCl (CE = 8.6 dS m^{-1}) and to the second, P, 125 mM NaCl (13.7 dS m^{-1}). The salt treatments were applied from 15 days after transplant to the end of the experiment (120 days).

The ripe fruits were collected weekly for 3 months, and the weight (gFW) and fruit number (gFN) were recorded.

Broad sense heritability (h_S^2) was calculated for traits measured in both populations assuming individuals from the ninth self-pollination generation were nearly homozygous for all loci. Heritability was calculated as reported previously by Villalta et al. (2007), using the formula: $h_S^2 = V_g/(V_g + V_e)$ where V_g and V_e are the estimates of genotype and environmental variance, respectively, by minimum variance quadratic unbiased estimator (MIVQUE).

Pearson's correlation coefficients were calculated for each trait combination in both populations. Fruit yield and physiological traits previously evaluated in the P and C populations under saline (Villalta et al. 2007, 2008, respectively) have also been taken into account in correlation and QTL analysis.

Marker analyses and linkage maps used for the QTL analysis have been previously reported by Villalta et al. (2005) and updated in Villalta et al. (2007, 2008). Two additional salt-tolerance candidate genes have been added to those maps for the present study: *NHX4* and *XTH9* (DY523676 in Ouyang et al. 2007). The tomato sequence DY523676 is available at National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov/), and was used for primer design. The position of introns in the genomic sequence of the tomato *NHX4* was obtained from the *Arabidopsis* likely ortholog (gene ID: 819811) through the NCBI gene tool (http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=gene). The identity of the polymorphic amplification products were checked by sequence analysis. Other two tomato genes reported by Ouyang et al. (2007) as salt tolerance candidates, namely DY523893 (encoding AGP) and DY523762 were tried but no polymorphism was found between lines of the P and C populations. A total of 156 markers were genotyped for the P population and 134 markers for the C one using DNA pools of six plants per line. New linkage analyses were calculated using Joinmap 3.0 software for Windows (Van Ooijen and Voorrips 2001). A minimum LOD of 3, recombination fraction of 0.5 and Kosambi as the mapping function (Kosambi 1944) were used for linkage analysis. QTL analyses were carried out using interval mapping procedure using MapQTL (Van Ooijen and Maliepaard 1996), and by linear regression and by interval mapping using QTL-Cartographer (Basten et al. 2002). Permutation tests were used to obtain an overall 5% significant level for each linkage group. Consequently, only LOD values $\geq$1.88 are reported. For a more accurate positioning of QTLs, composite interval mapping methodology was tried using both the programs and one or two QTL-linked markers as cofactors. Epistatic interactions between SSR24_250 and QTL-linked markers were tested by two-way ANOVA.

Results

The cumulative distribution of fruit yield traits in Fig. 1 clearly shows that a certain proportion of RILs, depending on the family, increased tomato yield under salinity. This proportion was the largest one when using the P population as rootstock, thus 65% of its lines increased Boludo TW (gTW) in comparison to the controls, although the level of salinity was higher than when using the C population. Only in the C population, some lines (3) were found to significantly ($P < 0.05$) reduce gTW.

Another difference between the populations concerned the traits previously evaluated under salinity (Villalta et al. 2007; Villalta et al. 2008), that are significantly ($P < 0.05$) correlated to the fruit yield of the grafted variety. These traits are leaf sodium concentration (LNC) and transported sodium (TN) in the P population, and leaf area (LA) and dry leaf weight (DLW) in the C population (Table 1).

As shown in Fig. 2, *sensu lato* heritability of fruit yield of the grafted variety (gTW) is much lower than that of the RIL population itself, particularly for fruit weight within the P family. However, when comparing families, similar heritability estimates for total fruit weight (TW) were obtained for the non-grafted C family and the P family used as rootstock (grafted P) pointing this strategy (rootstock utilization of P lines) as the most likely profitable one to improve the salt tolerance of tomato varieties.

Eight different QTLs governing total fruit yield of the grafted variety have been detected in the P (5) and the C (3) populations (Table 2). In agreement with correlation analysis, most gTW QTLs corresponded to gFN QTLs (Fig. 3). Only one gFW QTL has been detected (*gfw9.1* on chromosome P9). In general, individual contributions of the reported QTLs were medium-size (individual contributions from 8.5 up to 15.9% at most) and the advantageous allele came from the wild, salt tolerant, species. None of the salt tolerance candidate genes, including *NHX4* that mapped on chromosome 1 (position 45.164 on P1b) nor *XTH* that mapped on chromosome 12 (positions 12.931 on P12 or 16.452 on C12), co-located with any of the fruit yield QTL of the grafted, or non-grafted RILs (Villalta et al. 2007).

Increased LOD values were obtained for *gfn6.1* using composite interval mapping methodology and the QTL-associated markers SSRW12_220, SSR11_490, CT283_700, SSR24_250 or, particularly, SSR223_508 (LOD 3.57) as individual cofactors in the P population. The LOD scores of *gfn3.1*, *gtw3.1*, *gtw6.1* and *gtw9.1* also increased up to 5.8, 5.4, 2.91 and 2.64, respectively, when SSR24_250 was used as cofactor. This marker was used as cofactor in the P population because its effects as cofactor on the significance of QTLs of the C population, making unlinked QTL disappear (Table 3). Given this unexpected result, it was hypothesized that SSR24_250 would be involved in epistatic interactions with yield QTLs in the C population. Figure 4 shows the three epistatic interactions found between SSR24_250 and SSRW104_560 ($P = 0.0295$), and TG16_800 ($P = 0.0162$), both for gFN, and TG16_800 ($P = 0.0349$) for gTW in the C population. Another epistatic interaction between SSR24_250 and SSR21_900 for gFW was detected in the P population where SSR24_250 is not significantly associated with any QTL.

Discussion

Previous studies aimed at increasing salt tolerance in tomato using grafting indicated that the rootstock can

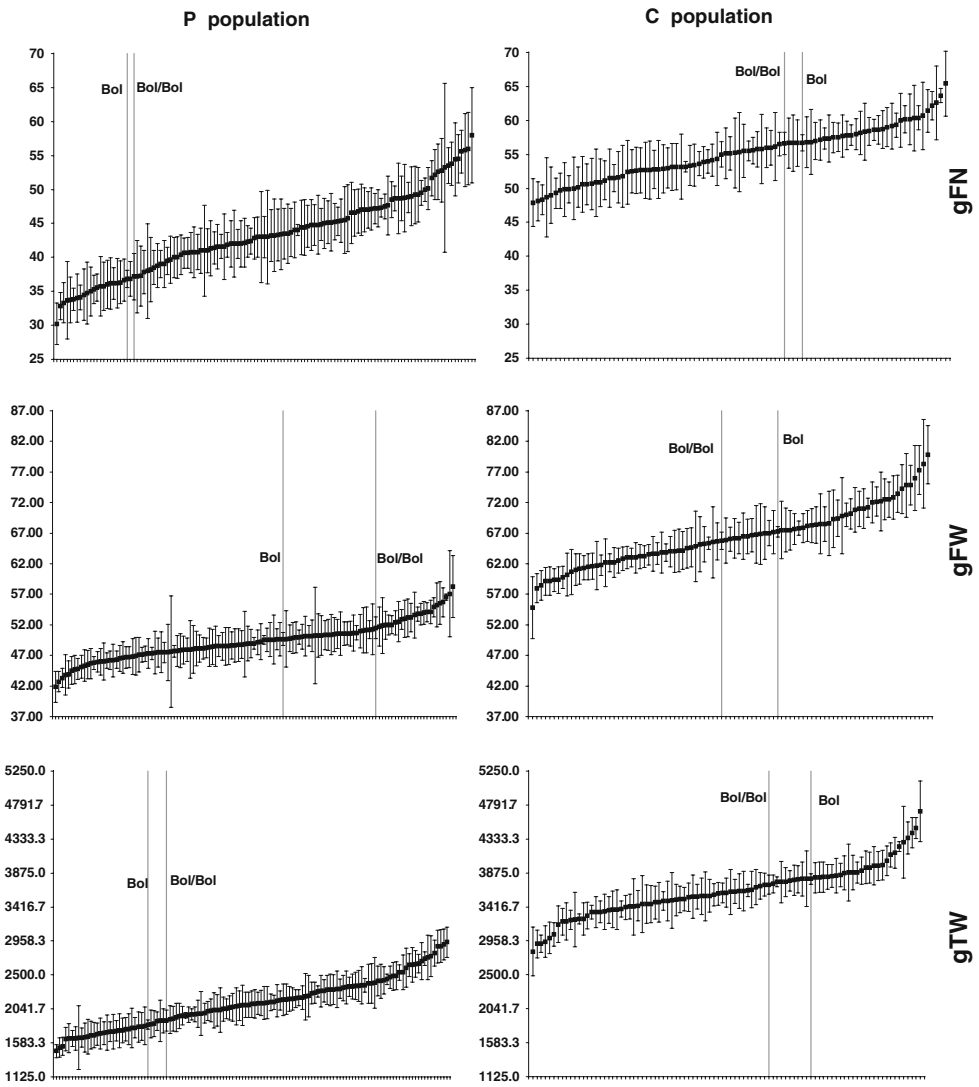

Fig. 1 Ordered means and standard errors for the fruit yield traits of Boludo (*gFN*, *gFW* and *gTW*) using the lines of the P and the C populations as rootstock in comparison to the controls, non-grafted and self-grafted Boludo plants (Bol and Bol/Bol). *Vertical bars* indicate the relative position of these controls

Table 1 Significant correlations between traits in the P and C populations

Pop	Trait	Probability			Correlation coefficient		
		gFW	gFN	gTW	gFW	gFN	gTW
P	LNC		0.02	0.01		0.22	0.22
P	TN		0.03			0.2	
P	gFW		0.02	2.00E-11		0.21	0.56
P	gFN			<5.00E-12			**0.92**
C	DLW	0.02		0.04	0.25		0.21
C	LA	2.70E-03		0.01	0.3		0.25
C	gTW	5.90E-12	<5.00E-12		0.62	**0.7**	

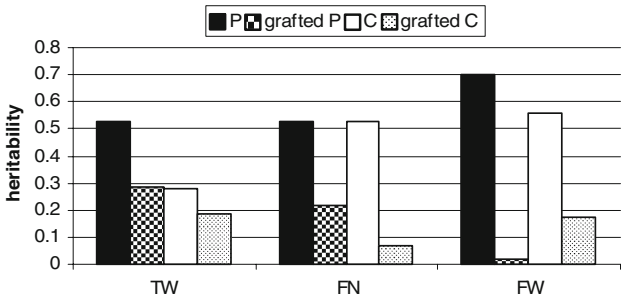

Fig. 2 Comparison of *sensu lato* heritability estimates of total fruit weight (*TW*), and number (*FN*) and weight (*FW*) of fruits for the two populations (*P* and *C*) of lines, grafted and non-grafted

improve the salt tolerance of tomato plants on the basis of fruit yield (Estañ et al. 2005; Martinez-Rodriguez et al. 2008). Here, we corroborate the positive effect of the rootstock on the fruit yield, as in the two populations there were rootstock lines that raised the fruit yield of the commercial hybrid under saline conditions, showing that this salt tolerance rootstock effect is a heritable trait, governed by at least eight QTLs.

The salt tolerance effect conferred by the rootstock might be enhanced when increasing the salinity level, as previ-

Table 2 List of fruit yield QTLs detected by using interval mapping procedure and MapQTL (Van Ooijen and Maliepaard 1996) when Boludo is grafted on the P or the C populations

Pop	Trait	Chr	Markers	Position	LOD	QTL	*a*	PEV
P	gFW	P9	SSRW19_220	24.4	2.81	*gfw9.1*	0.968	10.1
P	gFN	P3	SSRW223_508	53.2	4.59	*gfn3.1*	−2.329	15.9
P	gFN	P5a	SSR21_900	33.9	2.91	*gfn5.1*	1.928	10.5
P	gFN	P6	CT283_500	0	1.96	*gfn6.1*	−1.587	7.1
P	gFN	P6	SSRW11_490-CT283_700	32.7	2.52	*gfn6.2*	−2.059	12
P	gTW	P3	TG134_118	49.9	4.29	*gtw3.1*	−130.157	14.9
P	gTW	P5a	SSR21_900	33.9	3.36	*gtw5.1*	118.528	12
P	gTW	P6	TG16_380	3.8	2.15	*gtw6.1*	−97.189	7.8
P	gTW	P6	SSRW11_490-CT283_700	27.7	2.57	*gtw6.2*	−124.961	13.3
P	gTW	P9	SSR30_450	26	2.58	*gtw9.1*	102.923	9.3
C	gTW	C3	SSR24_250	16.3	2.01	*gtw3.2*	−130.126	9.3
C	gTW	C11b	TG30_320-SSRW104_560	28.4	2.09	*gtw11.2*	−143.588	14
C	gTW	C11b	TG16_800	49.5	2.05	*gtw11.1*	−112.732	9.3
C	gFN	C11b	SSRW104_560	32.1	2.04	*gfn11.2*	−1.414	10
C	gFN	C11b	TG16_800	49.5	1.88	*gfn11.1*	−1.227	8.5

The position in the solanum P or C chromosomes (Chr) (Villalta et al. 2008) is also indicated in cM. The estimated additive value is *a* and the percentage of explained variance, PEV

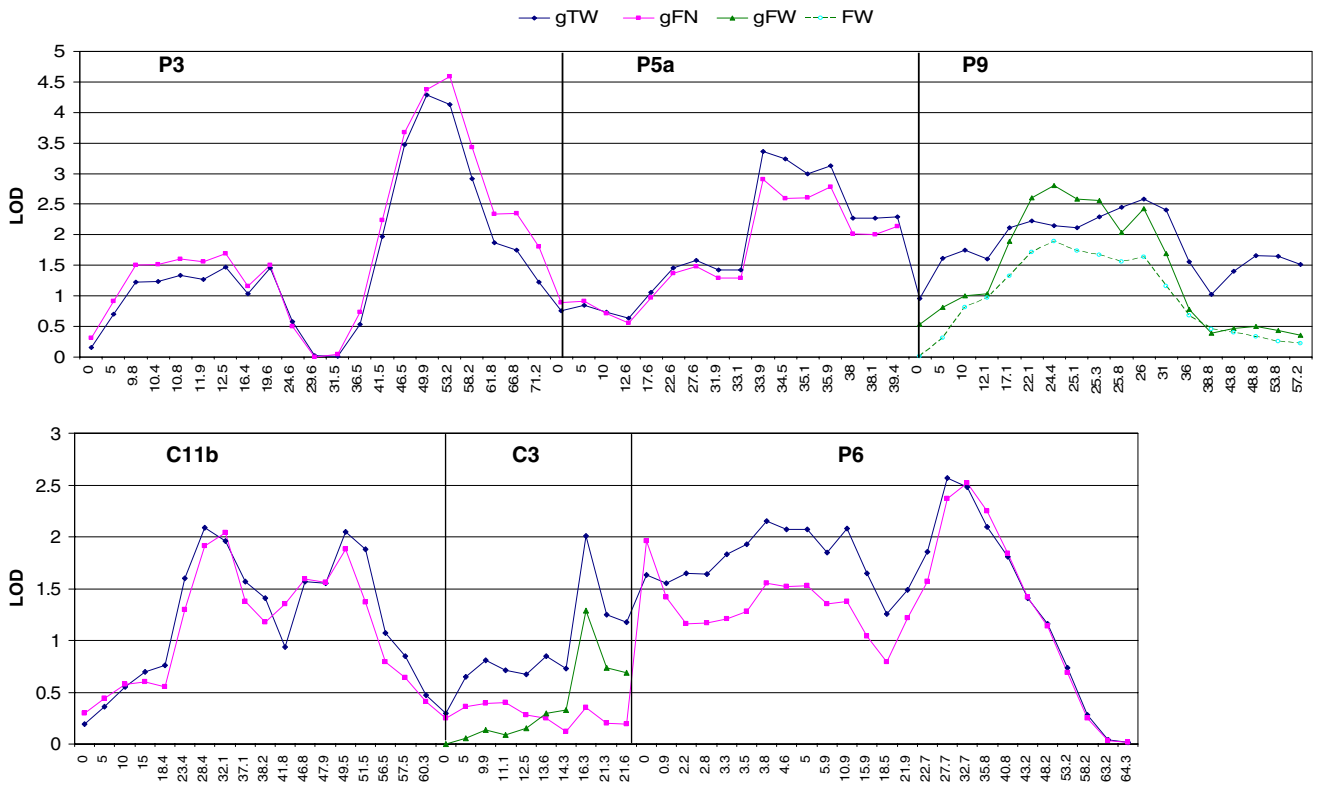

Fig. 3 LOD function along the linkage groups (*C3*, *C11b*, *P3*, *P5a*, *P6* and *P9*) containing the fruit yield QTLs here reported by using interval mapping procedure and MapQTL (Van Ooijen and Maliepaard 1996). Map positions in cM are indicated at the *X* axis. FW and gFW traits correspond to the fruit weight of the non-grafted and the grafted RIL plant, respectively

ously reported by Estañ et al. (2005). Thus, the number of rootstock lines increasing fruit yield, with respect to the commercial hybrid, was significantly higher in the population P (grown at 125 mM NaCl) than in the population C (grown at 75 mM NaCl). Similarly, the heritability of gTW (and its main component, gFN) and the number of the

Table 3 Effect of the composite cofactor chosen on the significance and position of the maximum significance (PMS) of the fruit yield QTLs for the grafted C population

Cofactor[a]	QTL	Cartographer PMS	MapQTL PMS	Cartographer LR	MapQTL LOD (LR)
–	*gtw3.2*	16.33	16.3	9.26	2.01 (9.26)
–	*gtw11.2*	28.44	28.4	9.65	2.09 (9.62)
–	*gtw11.1*	49.48	49.5	9.40	2.04 (9.39)
1	*gtw3.2*	16.33	–	9.25	–
1	*gtw11.2*	28.44	–	–	–
1	*gtw11.1*	51.48	–	–	–
2	*gtw3.2*	16.33	–	–	–
2	*gtw11.2*	28.44	37.1	9.64	2.07 (9.53)
3	*gtw3.2*	16.33	–	–	–
3	*gtw11.1*	49.48	49.5	9.40	2.23 (10.27)
1 + 2	*gtw3.2*	16.33	–	–	–
1 + 2	*gtw11.2*	32.15	37.1	7.94	1.52 (7.00)
1 + 3	*gtw3.2*	16.33	–	–	–
1 + 3	*gtw11.1*	51.48	49.5	6.63	1.74 (8.01)
2 + 3	–	–	–	–	–
–	*gfn11.2*	32.15	32.1	9.41	2.04 (9.39)
–	*gfn11.1*	49.48	49.5	8.60	2.05 (9.44)
1	*gfn11.2*	32.15	–	7.94	–
1	*gfn11.1*	51.48	–	–	–
2	*gfn11.2*	32.15	37.1	9.40	1.77 (8.15)
3	*gfn11.1*	49.48	49.5	8.60	2.23 (10.27)
1 + 2	*gfn11.2*	32.15	37.1	7.94	1.52 (7.00)
1 + 3	*gfn11.1*	49.48	49.5	7.46	1.65 (7.60)

[a] Cofactor 1: SSR24_250, linked to *gtw3.2*; cofactor 2: SSRW104_560, linked to *gfn11.2*; cofactor 3: TG16_800, linked to *gfn11.1*

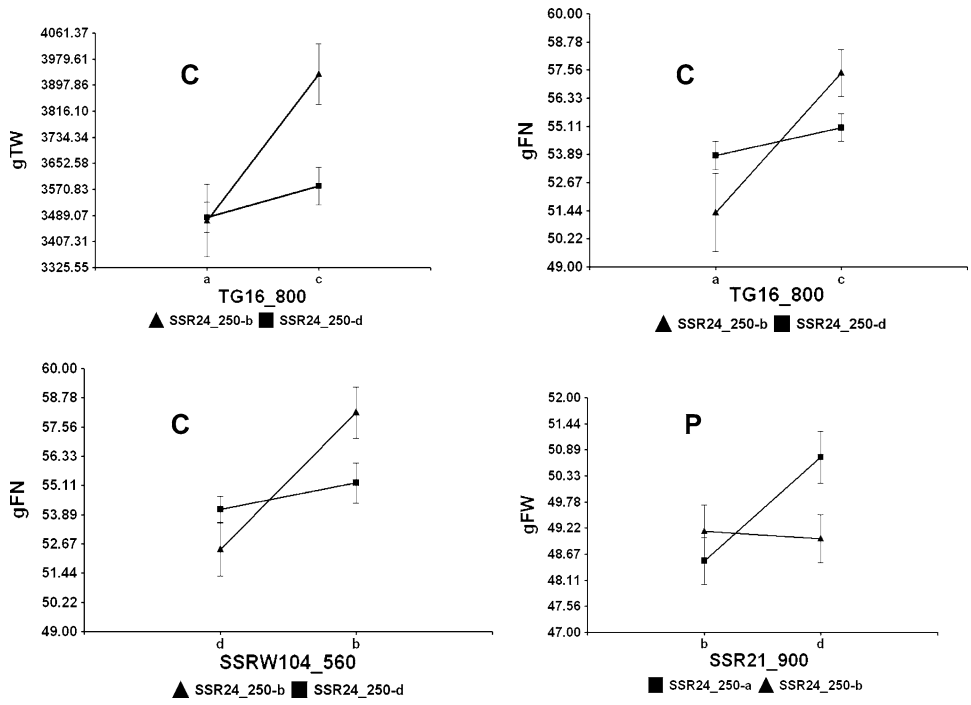

Fig. 4 Epistatic interactions affecting gTW, gFN and gFW in the *C* and *P* populations. All of them involve SSR24_250

QTLs detected for these traits were higher in the P than in the C population. Besides, the C population is worse than the P population when their lines are used as rootstock because three lines significantly reduced Boludo fruit yield under salinity (8.6 dS m^{-1}). Why does the P population seem to be better for conferring salt tolerance as rootstock

to the cultivated species? Villalta et al. (2007) reported that high salinity (15 dS m^{-1}) made the heritability of fruit yield traits change in opposite directions depending on the population: increasing in the P population, while decreasing in the C population. The larger genetic distance between *S. cheesmaniae* and *S. lycopersicum*, in comparison to that between *S. pimpinellifolium* and *S. lycopersicum* (Bretó et al. 1993), might hypothetically translate into a less fine regulation between cheesmaniae and lycopersicum genes, leading to a higher proportion of loci with segregation distortion (Villalta et al. 2005), and more developmental errors that would inflate the environmental variance reducing heritability particularly in grafting experiments. Nevertheless, as shown in Fig. 1, mean standard errors are not remarkably different between populations, suggesting that the bad behavior of the C population is more likely due to its genetic composition and/or the lower salinity level used (75 vs. 125 mM NaCl) rather than to a larger environmental component of variance.

In a previous study of salt tolerance in terms of fruit yield using the same populations without grafting, Villalta et al. (2007) reported that the contribution of fruit weight component to the total yield was clearly larger than that of the number of fruits since most of the total weight QTLs co-located with fruit weight QTLs. Present results show that the major fruit yield component involved in the benefices of using salt tolerant rootstocks in tomato involve the fruit number component. Thus, the correlation coefficient between gFN and gTW reaches 0.92 in the P population. This result agrees with high similar LOD curves obtained for most gTW and gFN QTLs (Fig. 3). Is it due to differences in the level of salinity? At relatively low salinity, the main reduction in yield involves FW (Van Ieperen 1996) but this cannot explain the scarceness of gFW QTLs because the level of salinity in the experiment of the grafted C population (8 dS m^{-1}) is nearly half of the non-grafted C population (15 dS m^{-1}) where six FW QTLs were detected. Therefore, the effect of the rootstock over the salt tolerance of the grafted variety is more related to the fruit number than to the fruit weight, in general. This observation is in agreement with the differences in the estimated heritabilities for both traits between grafted and non-grafted lines (Fig. 2).

No common QTL has been found between the P and the C populations when grafted in contrast to the non-grafted RILs. In this situation, Villalta et al. (2007) found that three chromosomes (1, 2 and 8) showed common QTLs: *fn1.2*, *fw2.1-tw2.1* and *fw8.1-tw8.1*, and the first two were significant under both control and salinity conditions. Therefore, these important QTLs are not acting through the root system. Fruit yield of grafted tomato plants seems to be a new trait governed by genes, in general different from those controlling the yield of non-grafted ones. This is also supported by the lack of significant correlation found between the fruit yield traits of the grafted and non-grafted RILs (Table 1). Additionally, no negative correlation has been found between gFW and gFN as it was found between FW and FN (Villalta et al. 2007). In spite of these differences in the genetic control of the fruit yield of the grafted and non-grafted RIL, the same physiological traits that were significantly correlated to the fruit yield depending on the population are maintained (Villalta et al. 2008): LNC and transported sodium in the P population, and LA and DLW in the C population. Thus, the strong association found between LA and FW might be explained just by a limiting effect of the carbohydrate source (the LA) over the fruit weight (carbohydrate sink). Since the same association is observed when the leaves belong to a grafted variety, we must infer that the root system of the RILs is the primary cause, likely acting through the LA. Therefore, each population as a whole is keeping its own and peculiar relationship between physiological and yield traits just by maintaining its root system, although different sets of QTLs are detected.

Only two out of eight QTLs detected for fruit yield of the grafted RILs (*gfw9.1* and *gtw11.1* in the P and C populations, respectively) might correspond to fruit yield QTLs of the non-grafted RILs: *fw9.1* and *tw11.1* under salinity (Villalta et al. 2007). Therefore, *fw9.1* and *tw11.1* might be related to the root system. In the case of *gfw9.1*, the position of the maximum LOD score points exactly the same maker, SSRW19_220, at 24.4 cM. Moreover, the LOD curve of *gfw9.1* along the P9 chromosome perfectly matches that of *fw9.1* (Fig. 3-P9) although they have been detected in two completely different experiments. It is important to point out that *fw9.1* was not reported previously by Villalta et al. (2007) because its LOD score was under 2.0. Since the maximum LOD score position is particularly relevant for the identification of the QTL correspondent gene (Price 2006), this marker has been investigated. It corresponds to a SSR primer pair available from the International Solanaceae Genomics Network (SGN) website database (http://www.sgn.cornell.edu/). The correspondent EST trace is SGN-E116243 that has given rise to COSII marker C2-Atg51880 on chromosome 9. *Arabidopsis* single At3g51880 on TAIR encodes a protein belonging to the subgroup of HMGB (high mobility group B) proteins that have a distinctive motive, the HMG-box domain which confers non-sequence specific interaction with linear DNA and structure-specific binding to distorted DNA sites. This gene and their neighbors will be further investigated as candidate genes for *fw9.1* and *gfw9.1*.

Also considering the position of maximum significance, we have seen that using composite interval mapping procedure, some previously detected QTL using interval mapping may unexpectedly disappear (particularly when using

MapQTL software) or slightly change their position (Table 3). In this sense, the analysis of QTL by composite interval mapping has so unveiled three epistatic interactions in the C population and another involving the same marker in the P population. All four are similar to Mendelian dominant epistasis in which one locus (SSR24_250) suppresses the allelic effects of a second locus or QTL (Fig. 4). Such epistasis often leads to individual QTLs having small average differences among genotypes and therefore not being detected unless epistasis is incorporated into the analysis (Carlborj and Haley 2004). These epistatic interactions should be considered when pyramiding QTLs into a line, otherwise the observed value of the cumulating line will be lower than expected, as reported by Causse et al. (2007).

Up to our knowledge, this is the first QTL analysis of the rootstock effect on the scion fruit yield. It is shown that the salt-tolerance alleles from wild species can be more easily used to improve salt tolerance of the cultivated species through their utilization in tomato rootstock breeding programs since the salinity tolerance so conferred to the hybrid variety in terms of fruit yield (mostly the fruit number component) is a heritable trait controlled by at least eight QTLs of medium size effects where the advantageous allele usually comes from the wild allele.

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