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QTL analysis of morphological traits in eggplant and implications for conservation of gene function during evolution of solanaceous species

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Abstract An interspecific F_2 population from a cross between cultivated eggplant, *Solanum melongena*, and its wild relative, *S. linnaeanum*, was analyzed for quantitative trait loci (QTL) affecting leaf, flower, fruit and plant traits. A total of 58 plants were genotyped for 207 restriction fragment length polymorphism (RFLP) markers and phenotyped for 18 characters. One to eight loci were detected for each trait with a total of 63 QTL identified. Overall, 46% of the QTL had allelic effects that were the reverse of those predicted from the parental phenotypes. Wild alleles that were agronomically superior to the cultivated alleles were identified for 42% of the QTL identified for flowering time, flower and fruit number, fruit set, calyx size and fruit glossiness. Comparison of the map positions of eggplant loci with those for similar traits in tomato, potato and pepper revealed that 12 of the QTL have putative orthologs in at least one of these other species and that putative orthology was most often observed between eggplant and tomato. Traits showing potential orthology were: leaf length, shape and lobing; days to flowering; number of flowers per inflorescence; plant height and apex, leaf and stem hairiness. The functionally conserved loci included a major leaf lobing QTL (*llob6.1*) that is putatively orthologous to the potato leaf (*c*) and/or Petroselinum (*Pts*) mutants of tomato, two flowering time QTL (*dtf1.1*, *dtf2.1*) that also have putative counterparts in tomato and four QTL for trichomes that have potential orthologs in tomato and potato. These results support the mounting evidence of conservation of gene function during the evolution of eggplant and its relatives from their last common ancestor and indicate that this conservation was not limited to domestication traits.

Keywords Quantitative trait loci · Solanaceae · *Solanum melongena* · *Solanum linnaeanum* · Interspecific

Introduction

Eggplant (*Solanum melongena* L.) is an economically and nutritionally important crop, especially in developing countries where 94% of the world's supply is produced (FAO 2000). The species belongs to the Solanaceae, a family that also includes several other significant crops: potato, tomato and pepper. Of these solanaceous crops, the genome of eggplant is perhaps the least characterized, however, *S. melongena* has been the subject of several classical genetic analyses of both qualitative (Tigchelaar et al. 1968; Phatak et al. 1991) and quantitative traits (Baha-Eldin et al. 1967a, b). In the past, eggplant has also been used as a model for studies of heterosis (Kakizaki 1931; Odland and Noll 1948). Numerous wild relatives of cultivated eggplant have been collected and are being evaluated for their responses to biotic and abiotic stresses and their ability to hybridize with *S. melongena* (Daunay et al. 1999). In addition, because the taxonomy of the *Solanum* subgenus *Leptostemonum* is not clear, other studies have focused on the genetic relationships among eggplant and its wild and weedy relatives (Isshiki et al. 1994; Sakata and Lester 1994; Mace et al. 1999). Although some of these latter analyses have employed random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP) markers, the development of eggplant molecular genetics has been restricted by the lack of a genetic linkage map. The recent construction of a comparative molecular linkage map for *S. melongena* (Doganlar et al. 2002a) has opened the door

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to a diversity of molecular genetic studies centered around this crop and is an essential addition to the array of biotechnological tools that are currently available for eggplant (Collonnier et al. 2001).

The goal of the research reported here was to identify loci for leaf, flower, fruit and plant characteristics in an eggplant interspecific F_2 population. A previous study had examined the genetic control of domestication traits in the same population (Doganlar et al. 2002b). The use of interspecific F_2 and advanced backcross populations has proven to be an effective and efficient way of mapping agronomic and horticultural traits in eggplant's relatives: tomato, potato and pepper (e.g., Bonierbale et al. 1994; Tanksley et al. 1996; Ben Chaim et al. 2001). In addition to providing adequate phenotypic and DNA polymorphism which may be limiting in intraspecific eggplant populations (Nunome et al. 2001), interspecific populations can supply the starting material for the introgression of valuable traits from wild species into eggplant cultivars. In the current study, *S. linnaeanum* was used as the wild parent. This species is reported to be resistant to Verticillium wilt, black root rot (*Thielaviopsis basicola* and *Colletotrichum coccodes*), potato virus Y and salinity (Daunay et al. 1991). Therefore, populations derived from the cross between *S. linnaeanum* and *S. melongena* may be useful for the future mapping of disease resistance and abiotic stress loci and for transfer of these resistances to cultivated eggplant. The genomic locations of the morphological characteristics examined in this study were compared with those for similar traits in other solanaceous species to identify putative orthologs that may have been conserved during the evolution and domestication of eggplant, tomato, potato and pepper.

Materials and methods

Plant material

The mapping population consisted of 58 F_2 individuals derived from a cross made by MCD at INRA between *S. linnaeanum* MM195 and *S. melongena* MM738. The population was grown in the greenhouse in Ithaca, New York (NY) and was propagated by cuttings which were sent to Montfavet, France (FR) for field evaluations. Rooted cuttings were transplanted to the field on May 18, 2000. In most cases, two plants of each genotype were planted at a single stake, and stakes were separated by a row spacing of 1 m. Two replicates of the parental controls (four plants/replicate) were also included.

Trait evaluations

Individual greenhouse-grown F_2 plants were scored for three traits (leaf lobing, days to flowering and ovary hairs) in NY during spring 1999. The field-grown plants were scored for 16 traits in FR between July and October 2000. Five different leaf characters were measured. Leaf length (ll) and width (lw) were measured in centimeters (cm) for 12 leaves per genotype: six leaves were measured in September and six leaves were measured in October. Leaf shape (lsh) was calculated as the ratio between length and width (ll/lw). Leaf lobing (llob) was evaluated on a scale of 1 (very weak lobing) to 5 (very strong lobing) in both locations. Leaf surface appearance (lsur) was also measured on a scale of 1 to 5 (1 = smooth leaf, 5 = rugose, strongly wrinkled leaf). Four different flower traits were evaluated. Flower diameter (fld) was determined in millimeters (mm) for flowers harvested throughout the season (July to October). Only the main flower of each inflorescence was included and approximately 12 flowers were measured for each genotype. Flower shape (fls) was evaluated on a 1 (orbicular) to 5 (star-shaped) scale. Days to flowering (dtf) was determined only in NY as the number of days from transplanting to the greenhouse to the appearance of the first open flower. The number of flowers per inflorescence (fln) was measured at various times during the growing season and at various positions on the plant, and the mean fln for each genotype was used for analysis. Four fruit traits were also measured. Number of fruit per infructescence (ftn) was determined like fln, and the mean ftn for each genotype was used for analysis. Fruit set (fset) was an overall evaluation of plant fertility and was scored on a scale of 0 (no fruit) to 5 (many fruit on the plant). Fruit calyx size (cs) was expressed using a scale of 1 to 5 and was evaluated as the proportion of the fruit covered by the calyx (1 = very short calyx, <10% of fruit length; 5 = very long calyx, >75% of fruit length). Fruit glossiness (fglo) was measured on a scale of 1 (dull epidermis) to 3 (glossy epidermis). Five different plant traits were evaluated. Plant height (ht) was measured in centimeters during the middle of the growing season at the beginning of August. Hairiness was measured on a 0 (no hairs) to 5 (very many hairs) scale for the plant apex (ah), leaves (lh) and stem (sh). The presence or absence of ovary hairs (ovh) was also determined by microscopic examination of approximately three ovaries per genotype.

Genotyping and statistical analysis

Procedures for DNA extraction, restriction enzyme digestion and Southern blotting were as described for tomato by Bernatzky and Tanksley (1986). Marker analysis and map construction are detailed in Doganlar et al. (2002a). The 207 markers that mapped at LOD $\geq$ 3.0 were used for quantitative trait locus (QTL) analysis. Correlation coefficients were calculated by QGENE (Nelson 1997). QTL mapping was also performed by QGENE using simple linear regression. A significance threshold of $P \leq 0.01$ was used for QTL declaration. Estimates of magnitudes of effect (R^2 from QGENE), trait means and gene actions (*d*/*a*) were determined for the most significant marker for each QTL. Multiple regression analyses were performed in STATVIEW (SAS Institute, Raleigh, N.C.).

Results

Correlations between traits

Significant ($P < 0.05$) correlations were observed between several related traits (Fig. 1). The strongest correlations were between apex (ah), stem (sh) and leaf (lh) hairiness ($r = 0.71–0.85$). Leaf length (ll) and width (lw) were also positively correlated ($r = 0.68$) as were the yield traits, number of fruit per infructescence (ftn) and fruit set (fset) ($r = 0.61$). The correlations of numbers of flowers per inflorescence (fln) with ftn and fset were lower ($r = 0.46$ and 0.28, respectively) but still statistically significant. Fruit weight was not significantly associated with either fln or ftn and was positively correlated with fset ($r = 0.30$, data not shown).

Fig. 1 Significant ($P < 0.05$) correlations between traits in the *Solanum linnaeanum* × *S. melongena* F_2 population. For trait abbreviations see Materials and methods. – Not significant, *FR* Montfavet, France, *NY* Ithaca, N.Y.

Trait	LL	LW	LSH	LLOB FR	LLOB NY	LSUR	FLD	FLS	DTF	FLN	FTN	FSET	CS	FGLO	HT	AH	LH	SH
LW	0.68																	
LSH	-	-0.70																
LLOB.FR	-	-	-															
LLOB.NY	-	-	-	0.85														
LSUR	-	-	-	0.30	-													
FLD	-	-	-	-	-	-												
FLS	-	-	-	-	-	-	-											
DTF	-	0.34	-	-	-	-	-	-										
FLN	-	-	-	-	-	-	-	-	-									
FTN	-	0.29	-	-	-	0.38	-	-	-	0.46								
FSET	-	-	-	-	-	0.28	-	-	-	0.28	0.61							
CS	-	-	-	-	0.29	-	-	-	-	-	-	-						
FGLO	-	0.28	-0.49	-0.41	-0.52	-	-	-	-	-	-	-	-0.44					
HT	0.41	0.44	-	-	-	-	-	-	-	-	-	-	-	-				
AH	-	-	-	-	-	-	-	-	-	-	-	-	0.40	-0.39	-			
LH	-	-	-	-	-	-	-	-	-	-	-	-	0.43	-0.44	-	0.85		
SH	-	-	-	-	0.30	-	-	-	-	-	-	-	-	-0.50	-	0.78	0.71	
OVH	-	-	-	-	0.44	-	-	-	-	0.34	-	-	-	-	0.45	-	-	-

QTL detected for each trait

A total of 18 traits were evaluated, only one of which, leaf lobing, was measured in both locations. QTL were mapped to all 12 eggplant linkage groups and a total of 63 loci were identified. Figure 2 shows the map locations of these QTL. Because a relatively small population was used for mapping, it is likely that QTL of lesser significance and minor effects were not identified. Overall, the fewest QTL (two) were detected on linkage group 11, while the most (nine) were found on linkage group 3. For all but one of the traits that showed no variation in the two parents (apex hairs), allelic effects were predicted based on the phenotypes of *S. linnaeanum* and *S. melongena*. Of the 59 QTL for which a prediction could be made, 27 (46%) had allelic effects opposite to those expected. Such reverse QTL were identified for every trait except flower shape. Table 1 and the following sections summarize the QTL identified for each trait.

Leaf traits

Leaf length and width

Two leaf length (ll) QTL were identified on linkage groups 11 and 12. Both QTL were of approximately equal significance and magnitude of effect, however, for *ll11.1* the *S. linnaeanum* allele had an effect opposite to that expected and was associated with an increase in leaf length. Four QTL were significantly associated with leaf width (lw) and mapped to linkage groups 1, 3 (two QTL) and 7. The most significant QTL ($P = 0.002$), *lw3.1*, accounted for 22% of the phenotypic variation for the trait and behaved in an additive manner. Alleles for all but one locus, *lw7.1*, showed the expected effect as the *S. melongena* alleles were associated with increased leaf width.

Leaf shape

Leaf shape (lsh) was affected by four loci that mapped to linkage groups 1, 5, 7 and 8. The most significant QTL ($P < 0.0001$), *lsh1.1*, explained 40% of the variation for leaf shape and was the only QTL that had allelic effects opposite to those predicted from the parental phenotypes.

Leaf lobing

Two QTL were identified for leaf lobing, the only trait that was measured in both locations. The QTL on linkage group 6, *llob6.1*, was detected in both FR and NY, was highly significant ($P < 0.0001$) and accounted for 76% of the variation in leaf lobing. For this locus, the *S. linnaeanum* allele had the expected effect and was associated with increased lobing. The *S. linnaeanum* allele for the other QTL, *llob10.1*, had the opposite effect and was associated with decreased lobing.

Leaf surface

Only one QTL was identified for leaf surface appearance (lsur) which assessed whether the leaf was smooth or wrinkled. This QTL was located on linkage group 4 and explained 25% of the variation for the trait. The parental alleles for this locus had effects contrary to those predicted from the parental phenotypes. Thus, the *S. linnaeanum* allele was associated with a smoother, less rugose leaf surface.

Flowering traits

Flower diameter and shape

A single QTL for flower diameter (fld) was identified on linkage group 7. This QTL, *fld7.1*, explained 23% of the phenotypic variation for the trait, was additive and had allelic effects opposite to that expected as the *S. melongena* allele was associated with smaller flowers. Three QTL affecting flower shape (fls) were detected on linkage groups 1, 7 and 9. The most significant QTL ($P = 0.002$), *fls 7.1*, accounted for 27% of the variation in flower shape. For all of the QTL, homozygosity for the *S.*

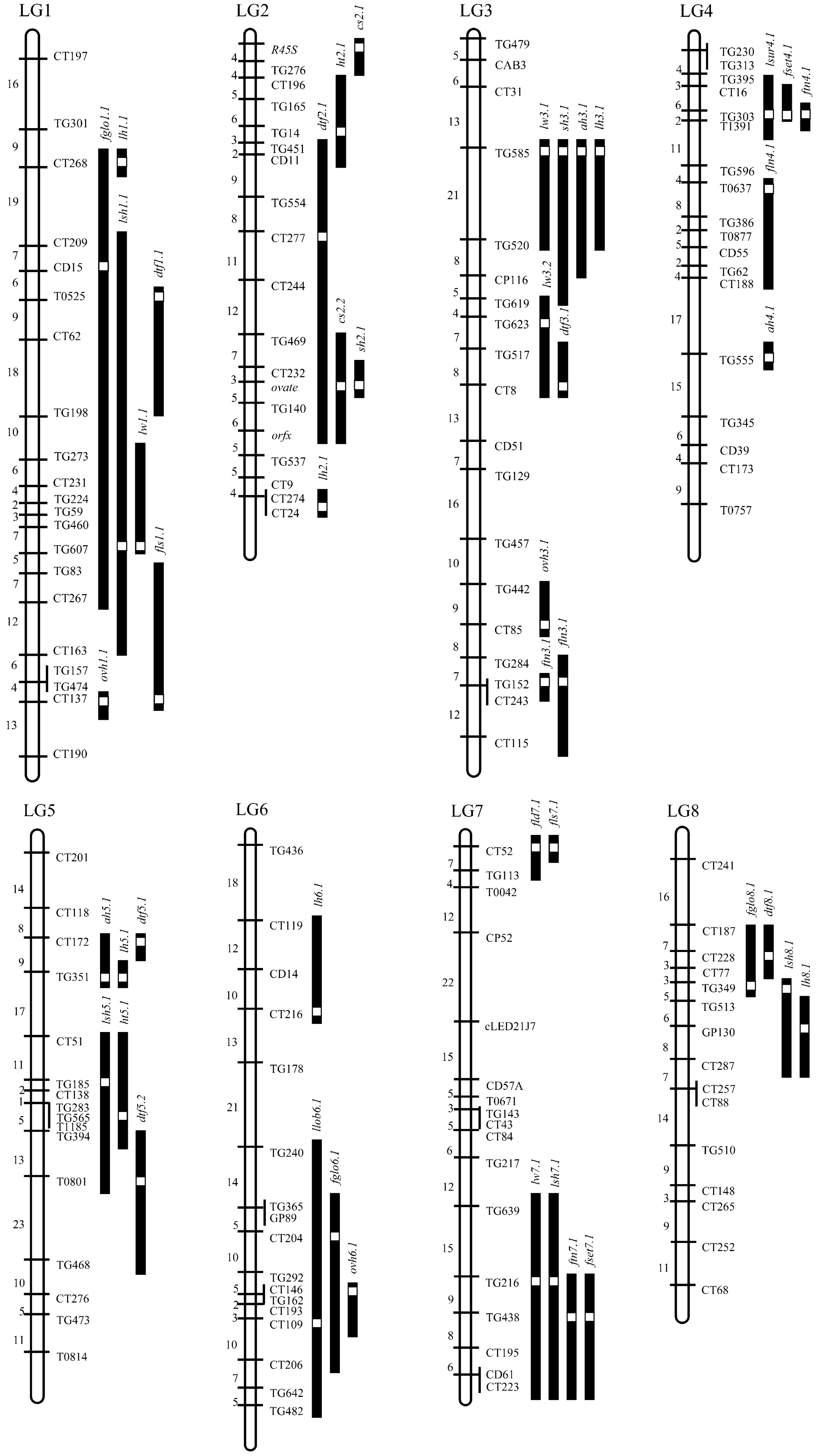
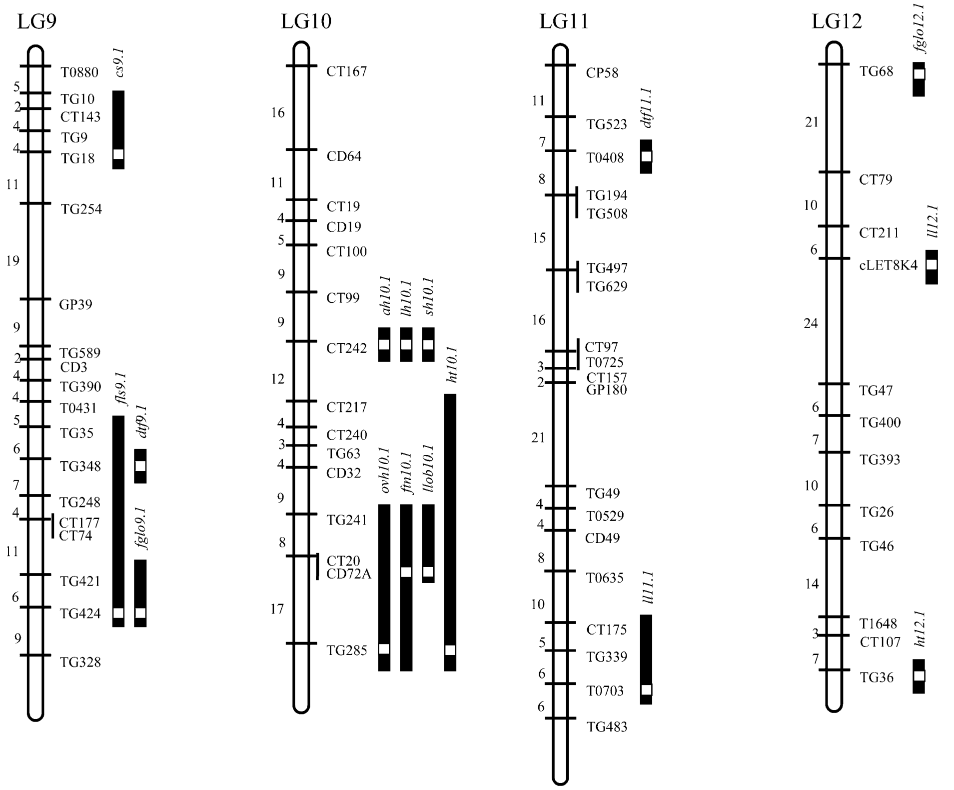


Fig. 2 Linkage map of the *S. linnaeanum* × *S. melongena* F_2 population showing positions of QTL. The numbers to the *left* of each chromosome indicate map distances (in centiMorgans) between linked markers. *Black bars* indicate significant marker trait associations ($P \leq 0.05$) based on single-point regression analyses. A *white box* indicates the marker with the most significant association with the trait ($P \leq 0.01$). Trait abbreviations are described in the Materials and methods

Fig. 2 (continued)



melongena alleles resulted in flowers that were slightly more star-shaped than orbicular.

Days to flowering

Of the 18 traits analyzed in this study, days to flowering (dtf) was controlled by the most QTL: eight QTL were identified on seven different linkage groups. The most significant (P = 0.0006), *dtf2.1*, was located on linkage group 2, explained 28% of the variation in flowering time and had additive gene action. When homozygous for the *S. melongena* allele of this QTL, plants flowered nearly 15 days earlier than individuals that were homozygous for the *S. linnaeanum* alleles. The *S. linnaeanum* alleles for only two QTL, *dtf1.1* and *dtf3.1*, had effects that were opposite to those predicted from the parental phenotypes and reduced days to flowering. Of these two QTL, *dtf3.1* had the most dramatic effect and decreased flowering time by 13 days when homozygous for the *S. linnaeanum* allele. Unfortunately, because this allele was recessive, earliness was not improved when the QTL was in the heterozygous condition, a fact that limits its usefulness for breeding of hybrid eggplant varieties.

Number of flowers per inflorescence

Two QTL were significantly associated with number of flowers per inflorescence (fln). The QTL on linkage group 4, *fln4.1*, was more significant (P = 0.002) and had a greater magnitude of effect (25%) than the one on linkage group 3. The *S. melongena* allele for *fln4.1* was associated with more flowers per inflorescence, an effect that was not expected from the parental phenotypes as the wild species bears more flowers per inflorescence than the cultivar.

Fruit traits

Number of fruit per infructescence

Four QTL for number of fruit per infructescence (ftn) were detected on linkage groups 3, 4, 7 and 10. The most significant QTL (P = 0.0007), *ftn10.1*, explained 26% of the phenotypic variation for the trait and appeared to be overdominant (d/a = –23.0). Two of the four QTL had allelic effects that were contrary to those expected. For both *ftn3.1* and *ftn4.1*, the *S. linnaeanum* alleles were associated with fewer fruit per infructescence.

Fruit set

Fruit set (fset) was affected by two QTL on linkage groups 4 and 7. Both QTL were of approximately the same significance and magnitude of effect, however, their *S. linnaeanum* alleles had opposite effects. The wild allele of *fset4.1* behaved as expected and, when homozygous, decreased the plant's fruit set. In contrast, the *S.*

Table 1 List of QTL detected for each trait. The QTL that explained the greatest percentage of phenotypic variation for each trait is underlined. A (–) after a QTL indicates that the parental alleles had effects opposite to those predicted by the parental phenotypes. The homoeologous tomato chromosome for each eggplant linkage group is included for reference purposes. Significant markers column includes the most significant marker ($P < 0.01$) linked to the trait (underlined) as well as flanking markers that were significant at $P < 0.05$. Statistics in remaining columns pertain to the underlined marker

Trait	QTL	Eggplant linkage group	Tomato chromosome	Location[a]	Significant marker(s)	*P*-value	Percentage PVE[b]	Trait means[c]			*d*/*a*[d]
								AA	Aa	aa	
Leaf length (ll)	*ll11.1* (–)	11	4S-11S	FR	CT175-T0703	0.007	19	14.5	15.5	16.0	–0.3
	ll12.1	12	11L-12S	FR	cLET8K4	0.006	20	15.8	14.6	15.6	–11.0
Leaf width (lw)	*lw1.1*	1	1	FR	TG273-TG607	0.004	21	11.1	11.3	10.2	1.4
	lw3.1	3	3	FR	TG585-TG520	0.002	22	11.6	10.7	9.8	0.0
	lw3.2	3	3	FR	TG619-TG623-CT8	0.007	20	11.0	10.7	7.6	0.8
	lw7.1 (–)	7	7	FR	TG639-TG216-CT223	0.004	23	10.5	10.3	11.5	1.4
Leaf shape (lsh)	*lsh1.1* (–)	1	1	FR	CT209-TG607-CT163	<0.0001	40	1.4	1.4	1.5	1.0
	lsh5.1	5	5L-12L	FR	CT51-TG185-T0801	<0.0001	36	1.5	1.5	1.3	1.0
	lsh7.1	7	7	FR	TG639-TG216-CT223	0.0002	33	1.5	1.5	1.3	1.0
	lsh8.1	8	8	FR	TG349-CT287	0.007	20	1.5	1.4	1.4	–1.0
Leaf lobing (llob)	*llob6.1*	6	6	FR	TG240-CT109-TG482	<0.0001	76	2.7	4.5	5.0	–0.6
		6	6	NY	TG240-CT109-TG482	<0.0001	76	1.8	3.7	4.8	–0.3
	llob10.1 (–)	10	10L-5S-12S	FR	TG241-CD72A	0.006	19	3.9	4.1	2.9	1.4
Leaf surface (lsur)	*lsur4.1* (–)	4	4L-10S	FR	TG395-TG303-T1391	0.001	25	3.6	2.2	2.9	–3.0
Flower diameter (fld)	*fld7.1* (–)	7	7	FR	CT52-TG113	0.005	23	40.3	43.0	45.6	0.0
Flower shape (fls)	*fls1.1*	1	1	FR	TG83-CT137	0.008	19	3.7	3.2	2.8	–0.1
	fls7.1	7	7	FR	CT52	0.002	27	3.5	2.8	3.0	–1.8
	fls9.1	9	9	FR	TG35-TG424	0.01	19	3.7	2.9	3.2	–2.2
Days to flowering (dtf)	*dtf1.1* (–)	1	1	NY	T0525-TG198	0.01	20	90.4	90.1	83.0	0.9
	dtf2.1	2	2	NY	TG451-CT277-*fw2.2*	0.0006	28	78.0	86.8	92.7	–0.2
	dtf3.1 (–)	3	3	NY	TG517-CT8	0.004	24	86.5	90.1	73.5	1.6
	dtf5.1	5	5L-12L	NY	CT172	0.005	20	84.0	90.5	92.9	–0.5
	dtf5.2	5	5L-12L	NY	TG394-T0801-TG468	0.002	23	84.5	88.2	94.8	0.3
	dtf8.1	8	8	NY	CT187-CT228-CT77	0.003	24	80.5	90.5	88.4	–1.5
	dtf9.1	9	9	NY	TG348	0.007	23	87.7	87.4	96.7	1.1
	dtf11.1	11	4S-11S	NY	T0408	0.005	20	82.6	91.0	90.9	–1.0
Flowers/inflorescence (fln)	*fln3.1*	3	3	FR	TG284-TG152-CT115	0.009	19	3.2	5.1	4.3	–2.5
	fln4.1 (–)	4	4L-10S	FR	T0637-CT188	0.002	25	6.1	4.3	3.8	–0.6
Fruit/infructescence (ftn)	*ftn3.1* (–)	3	3	FR	TG152	0.002	24	3.2	3.9	2.8	4.5
	ftn4.1 (–)	4	4L-10S	FR	TG303-T1391	0.004	21	4.5	3.3	3.4	–1.2
	ftn7.1	7	7	FR	TG216-TG438-CT223	0.003	23	2.6	3.4	3.9	–0.2
	ftn10.1	10	10L-5S-12S	FR	TG241-CD72A-TG285	0.0007	26	2.9	4.1	3.0	–23.0
Fruit set (fset)	*fset4.1*	4	4L-10S	FR	CT16-TG303	0.004	21	4.3	3.2	3.3	–1.2
	fset7.1 (–)	7	7	FR	TG216-TG438-CT223	0.003	23	2.6	3.4	3.9	–0.2
Fruit calyx size (cs)	*cs2.1*	2	2	FR	*R45S*-TG276	0.009	19	2.5	3.1	3.2	–0.7
	cs2.2 (–)	2	2	FR	TG469-*ovate fw2.2*	0.01	18	3.6	3.1	2.8	–0.2
	cs9.1 (–)	9	9	FR	TG10-TG18	0.003	23	3.1	3.3	2.6	1.8

Table 1 (continued)

Trait	QTL	Eggplant linkage group	Tomato chromosome	Location[a]	Significant marker(s)	*P*-value	Percentage PVE[b]	Trait means[c]			*d*/*a*[d]
								AA	Aa	aa	
Fruit glossiness (fglo)	*fglo1.1*	1	1	FR	CT268-CD15-CT267	0.0002	30	2.7	2.1	1.5	0.0
	fglo6.1	6	6	FR	TG365-CT204-CT206	<0.0001	40	2.8	1.8	1.9	–1.2
	fglo8.1 (–)	8	8	FR	CT187-TG349	0.007	20	1.5	2.3	2.4	–0.8
	fglo9.1	9	9	FR	TG421-TG424	0.005	22	2.1	2.5	1.6	2.6
	fglo12.1 (–)	12	11L-12S	FR	TG68	0.007	23	1.6	2.4	1.7	–15.0
Plant height (ht)	*ht2.1* (–)	2	2	FR	CT196-TG14-CD11	0.008	18	105.0	91.8	77.3	0.1
	ht5.1	5	5L-12L	FR	CT51-TG565-TG394	0.0006	28	64.0	90.9	81.6	–2.1
	ht10.1 (–)	10	10L-5S-12S	FR	CT217-TG285	0.001	26	85.3	89.3	65.8	1.4
	ht12.1 (–)	12	11L-12S	FR	TG36	0.008	18	83.1	89.6	70.4	2.0
Apex hairs (ah)	*ah3.1*	3	3	FR	TG585-CP116A	0.0004	28	2.3	3.3	4.1	–0.1
	ah4.1	4	4L-10S	FR	TG555	0.008	21	5.0	3.1	3.9	–2.5
	ah5.1	5	5L-12L	FR	CT172-TG351	0.002	25	2.5	3.1	4.1	0.3
	ah10.1	10	10L-5S-12S	FR	CT242	0.01	17	3.9	2.9	3.4	–3.0
Leaf hairs (lh)	*lh1.1*	1	1	FR	CT268	0.009	18	2.2	2.8	3.7	0.2
	lh2.1 (–)	2	2	FR	CT24	0.009	19	3.0	3.4	1.9	1.7
	lh3.1	3	3	FR	TG585-TG520	0.0005	28	1.6	3.1	4.0	–0.3
	lh5.1	5	5L-12L	FR	TG351	0.004	22	1.8	2.7	3.9	0.1
	lh6.1 (–)	6	6	FR	CT119-CT216	0.006	19	3.6	3.3	2.1	0.6
	lh8.1 (–)	8	8	FR	TG513-GP130-CT287	0.006	23	3.8	2.8	2.0	–0.1
	lh10.1 (–)	10	10L-5S-12S	FR	CT242	0.007	18	3.8	2.4	3.4	–6.0
Stem hairs (sh)	*sh2.1* (–)	2	2	FR	CT232-*ovate*	0.006	20	2.9	1.6	2.4	–4.2
	sh3.1	3	3	FR	TG585-TG619	0.0004	28	1.1	2.0	3.1	0.1
	sh10.1 (–)	10	10L-5S-12S	FR	CT242	0.003	21	2.8	1.6	2.0	–2.0
Ovary hairs (ovh)	*ovh1.1*	1	1	NY	CT137	0.007	28	0.2	0.7	0.9	–0.4
	ovh3.1 (–)	3	3	NY	TG442-CT85	0.001	35	0.6	0.9	0.3	3.0
	ovh6.1	6	6	NY	CT146-CT109	0.009	25	0.5	0.8	1.0	–0.2
	ovh10.1 (–)	10	10L-5S-12S	NY	TG241-TG285	0.0004	40	0.8	0.9	0.4	1.5

[a] FR, Montfavet, France; NY, Ithaca, N.Y.

[b] Percentage variation explained

[c] AA, Homozygous *Solanum melongena*; Aa, heterozygous; aa, homozygous *S. linnaeanum*

[d] *d*/*a*, Gene action

linnaeanum allele of *fset7.1*, was associated with improved fruit set.

Calyx size

Three QTL were detected for fruit calyx size (cs) on linkage groups 2 (two QTL) and 9. The most significant QTL was *cs9.1* ($P = 0.003$) and accounted for 23% of the variation in calyx size. For both *cs2.2* and *cs9.1*, the *S. melongena* alleles had the unexpected effect of increasing calyx size.

Fruit glossiness

Five QTL for fruit glossiness (fglo) were identified on linkage groups 1, 6, 8, 9 and 12. The most significant ($P < 0.0001$) QTL, *fglo6.1*, accounted for 40% of the variation in the trait. The other four loci had magnitudes of effect less than 30%. All but two of the QTL, *fglo8.1* and *fglo12.1*, had the allelic effects that were expected based on the parental phenotypes as the cultivated alleles were associated with glossier fruit.

Plant traits

Plant height

Four QTL were significantly associated with plant height (ht). These loci were located on linkage groups 2, 5, 10 and 12 and the most significant ($P = 0.0006$), *ht5.1*, explained 28% of the phenotypic variation in plant height. Interestingly, this was the only QTL for which the *S. linnaeanum* allele was associated with taller plants, the effect that was expected from the phenotypes of the parental lines. This locus appeared to be overdominant ($d/a = -2.1$) as individuals that were heterozygous for this QTL were taller than plants that belonged to the two parental genotypes.

Apex, leaf, stem and ovary hairs

Apex hairiness (ah) was found to be controlled by four QTL on linkage groups 3, 4, 5 and 10. *ah3.1* was the most significant of these QTL ($P = 0.0004$) and accounted for 28% of the variation in apex hairs. Because both the cultivated and wild parent had a similar number of apex hairs, it was impossible to predict the expected direction of allelic effects for this trait. Seven QTL for leaf hairs (lh) were identified on seven different linkage groups, with the most significant locus ($P = 0.0005$), *lh3.1*, located on linkage group 3. This QTL explained 28% of the variation in the trait and, like three other lh QTL, had the expected allelic effects as the *S. melongena* allele was associated with fewer leaf hairs. Stem hairiness (sh) was affected by three loci on linkage groups 2, 3 and 10. As with ah and lh, the most significant stem hair QTL ($P = 0.0004$) was located on linkage group 3 and explained 28% of the variation in stem hairiness. Four QTL were detected for ovary hairs (ovh) on linkage groups 1, 3, 6 and 10. The locus with the greatest magnitude of effect (40%) on the trait, *ovh10.1*, as well as *ovh3.1*, had allelic effects that were opposite to that predicted from the parental phenotypes. For these two QTL, the*S. melongena* alleles were associated with increased hairiness.

Discussion

Relationships between traits and co-localization of QTL

In general, traits with similar or related phenotypes had significant positive correlations. As expected, such correlations were observed between leaf length and width, flower number and fruit set and the amount of hairs on different plant tissues. Surprisingly, fruit weight was not significantly related to either flower or fruit number and was favorably correlated with fruit set. This result suggests that increased yield might be obtained by modification of flower number. The association between fruit weight and set might also be a consequence of partial sterility, which could limit overall fruit set and indirectly decrease fruit weight by reducing the number of fertilized ovules (seeds) per fruit. Thus, reduced fertility would be correlated with reduced fruit weight.

Related traits also tended to be co-localized within the genome. In many cases, this co-localization was probably the result of pleiotropic effects of a single gene or because the traits were not independent of each other. For example, both *lsh1.1* and *lsh7.1* co-localized with leaf width QTL, a result that was not unexpected as the leaf shape index was not independent of lw. Interestingly, none of the leaf lobing loci co-localized with leaf length, width or shape QTL, indicating that lobing is a distinct leaf character. Both flower shape and flower diameter loci mapped to the same region of linkage group 7, suggesting that pleiotropy may play a role in the expression of these two traits. In addition, fruit and flower number QTL mapped to a common region of linkage group 3. This was not unexpected because the number of fruit that can be set on an infructescence is, by necessity, correlated with the number of flowers on the inflorescence. Interestingly, however, *fln3.1* and *ftn3.1* had opposite allelic effects. If these two QTL are indeed the pleiotropic effects of a single locus, this result suggests that the expenditure of energy inherent to the production of more flowers per inflorescence is not necessarily rewarded by increased reproductive output. Both of the fruit set QTL identified in this study co-localized with fruit number loci. As the loci had the same general effects – that is, the alleles that increased ftn, also increased fset – it is likely that the two traits are the pleiotropic effects of the same loci on linkage groups 4 and 7. Perhaps the strongest evidence for pleiotropy was seen for the trichome traits. Three of the traits (ah, lh and sh) mapped to the same positions on linkage groups 3 and 10, and both ah and lh were localized to the same region of linkage group 5. In addition to their implications for pleiotropic control of the three traits, these results suggest that the shared loci may be controlling the presence/absence or degree of hairiness rather than the trait's tissue or organ-specific expression.

Implications for eggplant breeding

Six of the characters analyzed in this study are agronomically important traits: flowering time, flower and fruit number per inflorescence/infructescence, fruit set, calyx size and fruit glossiness. For these traits alone, 42% (10/24) of the QTL had wild *S. linnaeanum* alleles that were superior to the cultivated *S. melongena* alleles and were associated with an improvement in the trait. Thus, as has been found in several other plant species (Tanksley and McCouch 1997), the wild relatives of *S. melongena* promise to be a valuable source of germplasm for eggplant improvement. In the past, the use of such materials in eggplant has been limited to searches for disease and stress resistance (Daunay et al. 2001).

Conservation of eggplant QTL with loci from other solanaceous species

Several of the traits analyzed in this work have also been studied in other solanaceous crops. Comparison of the eggplant results with those from tomato, potato and pepper reveals that a number of eggplant loci have potentially orthologous counterparts in these other species. A locus was considered as a putative ortholog of an eggplant QTL if both loci were localized to syntenic map positions in the two species. The QTL with putative orthology are listed in Table 2 and discussed below.

Although 12 loci related to leaf size (length and width) and shape were detected in this study, QTL for leaf width (*lw1.1* and *lw7.1*) overlapped with leaf shape loci. Because leaf shape is a derived trait, it is likely that these lw and lsh QTL do not represent distinct loci. Therefore, for purposes of this discussion, it is assumed that ten, not 12, different leaf size and shape loci were identified in this work. Four of these ten QTL have putative orthologs in tomato. The position of the leaf length QTL *ll11.1* on eggplant linkage group 11 coincides with that of a leaf length locus on chromosome 4 identified by Paran et al. (1997) in a population of recombinant inbred lines derived from a cross between cultivated tomato and *Lycopersicon cheesmanii*. The two most significant eggplant leaf shape QTL, *lsh1.1* and *lsh5.1*, also have putative counterparts in tomato. The position of *lsh1.1* overlaps with *lr1a* and *lr1b* (lr = leaf ratio = ll/lw) and *lsh5.1* coincides with *lr5.1*. All three of these tomato QTL were identified in an *L. esculentum* × *L. pennellii* interspecific F_2 population (de Vicente and Tanksley 1993). In both the eggplant and tomato studies, the chromosome 1 QTL were the most significant loci and had the greatest effect on leaf shape phenotype. Together, *lsh1.1* and *lsh5.1* accounted for 48% of the variation for leaf shape in the eggplant population as determined by multiple regression analysis using the most significant marker for each QTL.

The locus *llob6.1* controls the majority of the phenotypic variation for leaf lobing in the eggplant F_2 and has two potential counterparts in tomato. Both *Pts*, Petroselinum, and *c*, potato leaf, have been mapped to the same genomic region as the eggplant QTL (Tanksley et al. 1992; Liharska et al. 1997). The Petroselinum mutation is incompletely dominant and mutant plants have highly compound leaves that resemble those of parsley (Rick 1980). The potato leaf mutation is recessive and is characterized by unlobed leaves that are less complex than wild-type ones because they have a reduced number of lateral leaflets (Hareven et al. 1996; Kessler et al. 2001). Histological analysis of this mutant indicates that it is defective in the delimitation of the leaf margin, a domain that is critical for leaf lobe production (Kessler et al. 2001). Thus, *c* reduces leaf complexity while *Pts* increases it by causing leaves to be subdivided to a third order (Hareven et al. 1996). Because both tomato mutants affect leaf morphology and have not, to our knowledge, been subjected to complementation analysis, it is possible that *c* and *Pts* are variant alleles of a single gene. Like the recessive alleles of *c* and *Pts*, the recessive *S. melongena* allele of *llob6.1* is associated with simpler leaves. Thus, without further analysis, it is not possible to determine whether *llob6.1* is orthologous to *c, Pts* or both. If *c* and *Pts* are indeed distinct loci, the greater similarity of the *c* and eggplant QTL phenotypes suggests that the potato leaf gene is the more likely ortholog.

Days to flowering is a trait that has been studied in several interspecific tomato populations. Of the eight dtf QTL identified in eggplant, two coincide with loci mapped in tomato. The strongest and most significant eggplant QTL, *dtf2.1*, co-localizes with flowering time loci detected in populations derived from *L. pennellii* (de Vicente and Tanksley 1993) and *L. pimpinellifolium* (Grandillo and Tanksley 1996). Eggplant *dtf1.1* is also potentially orthologous to chromosome 1 flowering time QTL identified in the same populations. Together, *dtf1.1* and *dtf2.1* explained 41% of the total variation for flowering time exhibited by the eggplant population. In tomato, these two QTL individually accounted for only 6 to 12% of phenotypic variation (de Vicente and Tanksley 1993; Grandillo and Tanksley 1996).

Number of flowers per inflorescence has not been examined in many tomato populations, however, Grandillo and Tanksley (1996) identified a locus on chromosome 3, *nflt3.1*, that maps to the same position as *fln3.1* in eggplant. One of the four eggplant plant height loci also has a putative ortholog in tomato: *ht2.1* seems to correspond to a height QTL identified by Paran et al. (1997). Neither *fln3.1* nor *ht2.1* was the most significant locus for its respective trait.

Although 18 QTL were detected for the four hairiness characteristics measured in eggplant, several of these loci

Table 2 Eggplant QTL with putative orthologs in related species. Putative orthologous loci are named according to references listed

Trait	Eggplant		Putative orthologous		Crop	Locus type	Mapping accuracy[a]	Reference
	Locus name	Linkage group name	Locus name	Chromosome				
Leaf length	*ll11.1*	11	leaf length QTL	4	tomato	QTL	***	Paran et al. 1997
Leaf shape	*lsh1.1*	1	*lra1a*	1	tomato	QTL	***	de Vicente and Tanksley 1993
			lra1b	1	tomato	QTL	***	de Vicente and Tanksley 1993
	lsh5.1	5	*lr5*	5	tomato	QTL	***	de Vicente and Tanksley 1993
Leaf lobing	*llob6.1*	6	*c*	6	tomato	morphological	***	Liharska et al. 1997
			Pts	6	tomato	morphological	*	Tanksley et al. 1992
Flowering time	*dtf1.1*	1	*dtf1.1*	1	tomato	QTL	***	de Vicente and Tanksley 1993
			dfl1.1	1	tomato	QTL	***	Grandillo and Tanksley 1996
	dtf2.1	2	*dftf2.1*	2	tomato	QTL	***	de Vicente and Tanksley 1993
			dfl2.1	2	tomato	QTL	***	Grandillo and Tanksley 1996
Flower number	*fln3.1*	3	*nflt3.1*	3	tomato	QTL	***	Grandillo and Tanksley 1996
Plant height	*ht2.1*	2	height QTL	2	tomato	QTL	***	Paran et al. 1997
Hairs	*ah3.1*[b]	3	*Ln*	3	tomato	morphological	*	Tanksley et al. 1992
	lh8.1	8	*Hr*	8	tomato	morphological	*	Tanksley et al. 1992
	ah10.1[c]	10	typeB trichome QTL	5	potato	QTL	***	Bonierbale et al. 1994
			TriV-1	5	tomato	QTL	***	Maliepaard et al. 1995
	ovh10.1	10	*h*	10	tomato	morphological	*	Tanksley et al. 1992

[a] *, Locus position deduced by comparison of classical and molecular markers; **, locus mapped but position on high-density map is approximate; ***, locus mapped relative to markers on high-density map

[b] *lh3.1* and *sh3.1* cosegregated with *ah3.1*

[c] *lh10.1* and *sh10.1* cosegregated with *ah10.1*

mapped to the same locations, suggesting that there may actually be only 13 different QTL (Fig. 2). Four of these 13 loci have putative orthologs in tomato or potato. The QTL located on linkage group 3 had the most significant association with the traits and the greatest effect on phenotypic variation for apex, leaf and stem hairs. This locus maps to a similar position as *Ln*, the Lanata mutant of tomato which has an excessively hairy phenotype (Tanksley et al. 1992). Unlike this mutation, which is dominant, the allele that conditions increased hairiness in eggplant is additive (Table 1).

A linkage group 8 leaf hairiness QTL, *lh8.1*, which did not map with the hairiness QTL for any other tissues, coincides with another tomato morphological gene, *Hr* (Tanksley et al. 1992). The *Hr* or Hirsute mutant is characterized by long hairs on the upper surface of the plant's leaves. The fact that both *lh8.1* and *Hr* have specific effects on only leaf trichomes provides additional support for their putative orthology. A cluster of eggplant hairiness loci on linkage group 10 also has potential counterparts in both tomato and potato. The map position of this cluster of apex, leaf and stem hairiness QTL corresponds to that of a type B trichome density QTL on chromosome 5 in potato (Bonierbale et al. 1994) and a type IV trichome density QTL on the same chromosome in tomato (Maliepaard et al. 1995). The densities of both type B and type IV trichomes have been associated with insect resistance in their respective crops. The relationship between hairs and insect resistance has not been extensively studied in eggplant. Therefore, the QTL identified in this study might provide a starting point for such work. The combined effects of this linkage group 10 locus and the one on linkage group 3 accounted for 28–38% of the phenotypic variation for apex, leaf and stem hairiness as determined by multiple regression analysis. Similarly, the three conserved loci for leaf hairiness (*lh3.1, lh8.1* and *lh10.1*) explained 35% of the variation for this trait.

The most significant ovary hairiness QTL, *ovh10.1*, is putatively orthologous to the hairs absent, *H*, locus on tomato chromosome 10 (Tanksley et al. 1992). This mutant is characterized by an absence of hairs on all plant parts except the hypocotyl and is incompletely dominant. Unlike the tomato mutation, the allele that conditions reduced hairiness in eggplant (from *S. linnaeanum*) is recessive to the allele that is associated with increased hairiness.

Several of the characteristics that were examined in eggplant have not, to our knowledge, been studied in the other Solanaceae. These traits include number of fruit per infructescence, calyx size and fruit glossiness. By eliminating the loci for these traits as well as those which mapped to overlapping positions (as discussed above for leaf shape and hairiness), it was determined that 44 different QTL were identified in eggplant for traits that have also been studied in other solanaceous crops. Overall, 12 (27%) of these 44 loci have putative orthologs in tomato or potato (Table 2). No orthologs to eggplant QTL were found in pepper probably because very few of the same traits were studied in this and the pepper work (Ben Chaim et al. 2001). An examination of the conservation of traits related to eggplant domestication revealed that 43% of the loci for fruit weight, shape and color have putative orthologs in tomato, potato and/or pepper (Doganlar et al. 2002b). These results indicate that gene function for such traits has been conserved during the evolution and domestication of the different solanaceous crops from their last common ancestor. The results of the work presented here suggest that this conservation has not been solely limited to characteristics related to domestication. Genes controlling phenotypes such as leaf shape, leaf lobing and plant hairiness, which presumably have not been the targets of intentional selection, have also been conserved during evolution of the Solanaceae.

As was discovered for traits related to eggplant domestication (Doganlar et al. 2002b), significant percentages of the phenotypic variations for several morphological traits were explained by the combined effects of conserved loci. For example, conserved QTL accounted for 35% of the total variation for leaf hairiness, 48% of the variation for leaf shape and 76% of the variation for leaf lobing. This finding as well as the fact that considerable proportions of loci for both morphological and domestication traits have been conserved suggests that the phenotypes of these traits are controlled by a limited number of genes with major effects. Thus, it is not a coincidence that the same gene targets have been repeatedly mutated during evolution and domestication of the different solanaceous species. Conservation of gene function among the Solanaceae also indicates that the wealth of knowledge that has accumulated from decades of genetic analysis of tomato, potato and pepper can be used as a springboard for the rapid advancement of eggplant genetics.

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