# Conservation of Gene Function in the Solanaceae as Revealed by Comparative Mapping of Domestication Traits in Eggplant

**Sami Doganlar,*[,1,2] Anne Frary,*[,1,2] Marie-Christine Daunay,[†] Richard N. Lester[‡] and Steven D. Tanksley*[,3]**

**Department of Plant Breeding and Department of Plant Biology, Cornell University, Ithaca, New York 14853, [†]INRA, Unité de Génétique et Amélioration des Fruits et Légumes, 84143 Montfavet Cedex, France and [‡]University of Birmingham Botanical Gardens, Birmingham, B15 2RT, United Kingdom*

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ABSTRACT

Quantitative trait loci (QTL) for domestication-related traits were identified in an interspecific $F_2$ population of eggplant (*Solanum linnaeanum* × *S. melongena*). Although 62 quantitative trait loci (QTL) were identified in two locations, most of the dramatic phenotypic differences in fruit weight, shape, color, and plant prickliness that distinguish cultivated eggplant from its wild relative could be attributed to six loci with major effects. Comparison of the genomic locations of the eggplant fruit weight, fruit shape, and color QTL with the positions of similar loci in tomato, potato, and pepper revealed that 40% of the different loci have putative orthologous counterparts in at least one of these other crop species. Overall, the results suggest that domestication of the Solanaceae has been driven by mutations in a very limited number of target loci with major phenotypic effects, that selection pressures were exerted on the same loci despite the crops' independent domestications on different continents, and that the morphological diversity of these four crops can be explained by divergent mutations at these loci.

DOMESTICATION of many of today's crop plants occurred ~10,000 years ago with the beginning of agriculture (Harlan 1992). The earliest farmers intentionally and unintentionally selected for and affected a wide array of morphological and physiological traits that distinguish cultivated crops from their wild ancestors. Such characteristics include changes in plant architecture (*e.g.*, maize), gigantism (*e.g.*, tomato), and morphological diversity (*e.g.*, the cultivar groups of *Brassica oleracea*: broccoli, cauliflower, cabbage, and brussel sprouts) in the consumed portion of the plant, and reduced seed dispersal (nonshattering, *e.g.*, common bean and cereals). Research has revealed that a relatively small number of qualitative and quantitative trait loci with major effects control domestication-related traits in crops such as maize (Paterson *et al.* 1995; Doebley *et al.* 1997), rice (Paterson *et al.* 1995; Xiong *et al.* 1999), sorghum (Paterson *et al.* 1995), pearl millet (Poncet *et al.* 2000), tomato (Alpert *et al.* 1995; Grandillo *et al.* 1999), and common bean (Koinange *et al.* 1996). In addition, comparative mapping of some of these major domestication trait loci in the cereals indicates that seed size, seed dispersal, and day-length-insensitive flowering loci are shared by three different members of the Poaceae: maize, rice, and sorghum (Paterson *et al.* 1995). The convergent evolution of these independently domesticated cereals supports the hypothesis that relatively few genes were involved in the dramatic morphological and physiological changes associated with the domestication process.

Eggplant (*Solanum melongena*) is a member of the Solanaceae, a large, diverse plant family containing 18 different domesticated species (Harlan 1992). Other prominent solanaceous crops are potato (*S. tuberosum*), tomato (*Lycopersicon esculentum*), and pepper (Capsicum spp.). Unlike these other crops, which were domesticated in the New World, *S. melongena* is an Old World species that was domesticated in the region of Asia encompassed by China, India, and Thailand (Daunay *et al.* 2001). The wild forms of eggplant are prickly and have small, bitter fruit; however, selection during domestication resulted in cultivated types with large, palatable fruit and fewer prickles (Choudhury 1995). The crop was brought from Southeast Asia and distributed to western and northern Africa, the Mediterranean basin, and eventually Europe during the Arab incursions into those regions starting in the seventh century (Daunay *et al.* 2001). Today, eggplant continues to be an economically and nutritionally important species in Asian and Mediterranean countries (Fao 2000).

In the Solanaceae, tomato, potato, and pepper have all been the subject of extensive classical and molecular genetic research including the development of high density, molecular marker-based linkage maps (Tanksley *et al.* 1992; Livingstone *et al.* 1999) and numerous

[1]These authors contributed equally to this work.

[2]*Present address:* Department of Molecular Biology, Izmir Institute of Technology, Gulbahce Campus, Urla 35437, Izmir, Turkey.

[3]*Corresponding author:* 246 Emerson Hall, Cornell University, Ithaca, NY 14853. E-mail: sdt4@cornell.edu

qualitative and quantitative trait mapping studies (*e.g.*, Bonierbale *et al.* 1994; Maliepaard *et al.* 1995; Grandillo and Tanksley 1996; Bernacchi *et al.* 1998; Ben Chaim *et al.* 2001). Eggplant has also been the focus of classical genetic analyses including studies on qualitative (Tigchelaar *et al.* 1968; Phatak *et al.* 1991) and quantitative (Gotoh 1953; Baha-Eldin *et al.* 1967a,b) traits and heterosis (Kakizaki 1931; Odland and Noll 1948). In contrast, the molecular genetics of eggplant has remained unexplored because, until recently, a molecular linkage map of the species was not available. The availability of such a map (Doganlar *et al.* 2002), constructed using single-copy cDNA, genomic DNA, and conserved orthologous set (COS) restriction fragment length polymorphism (RFLP) markers from tomato, opens the door to the mapping, tagging, and isolation of qualitative and quantitative trait loci in eggplant, as well as comparative mapping with other solanaceous species.

To date, comparative mapping in the Solanaceae has been rather limited in scope and has usually involved comparisons across pairs of species (*e.g.*, pepper and tomato; Ben Chaim *et al.* 2001). Notable exceptions are studies that examined the comparative genetics of disease resistance (Grube *et al.* 2000) and the carotenoid biosynthetic pathway (Thorup *et al.* 2000) in tomato, potato, and pepper. The addition of an eggplant linkage map to the repertoire of tools available in the Solanaceae allows comparisons encompassing all four economically important species of the family. Because eggplant was domesticated in Asia and tomato, potato, and pepper were domesticated in the Americas, the inclusion of *S. melongena* in comparative mapping studies also provides a snapshot of domestication spanning two different continents.

The objectives of this study were to map traits related to domestication in an interspecific $F_2$ population derived from a cross between the cultivated eggplant *S. melongena* L. and the wild species *S. linnaeanum* Hepper & Jaeger (= *S. sodomaeaum* auct. non L.) and to compare these results with similar studies in the other solanaceous crop species. Three categories of characteristics were examined: color traits, fruit traits, and plant prickliness. The color traits encompassed several plant tissues and organs, namely the stem, leaves, flower, fruit, and prickles. The fruit traits included fruit weight and locule number as well as fruit shape parameters such as ovary and fruit length and diameter. Similar to the color traits, plant prickles were also evaluated for individual organs including stem, leaf, and flower and fruit calyxes. The choice of these traits was based on a single criterion: They are all obvious targets for selection during the domestication of a fruit crop like eggplant. Moreover, with the exception of prickliness, all of these traits have been studied to some degree in the other Solanaceae, with the most extensive and intensive analyses done for fruit weight (Alpert and Tanksley 1996; Frary *et al.* 2000) and shape (reviewed in Grandillo *et al.* 1999; Ku *et al.* 2001) in tomato. Thus the Solanaceae is an excellent system for comparative mapping of domestication traits in related crop species.

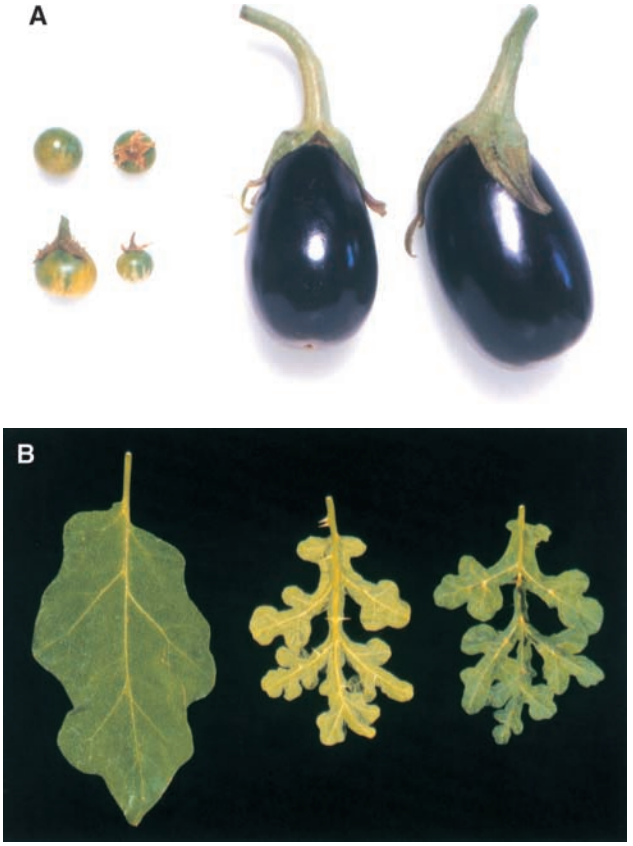


Figure 1.—Fruit and leaf phenotypes of the parental lines. (A) Fruit of *S. linnaeanum* MM195 (left) and *S. melongena* MM738 (right). (B) Leaves of *S. linnaeanum* MM195 (right and middle) and *S. melongena* MM738 (left).

## MATERIALS AND METHODS

**Plant material:** The $F_2$ mapping population used in this study was produced by M.-C. Daunay at the Institut National de la Recherche Agronomique, Montfavet, France and consisted of 58 individuals derived from a cross between *S. linnaeanum* MM195 (the female parent) and *S. melongena* MM738. Native to South Africa, *S. linnaeanum* is a prickly wild relative of cultivated eggplant and bears small, green, striped, round fruit. MM738 is a commercial-type line, is not prickly, and bears large, purple, unstriped, oblong fruit (Figure 1). The $F_2$ population was grown in the greenhouse in Ithaca, New York and was propagated by cuttings. Rooted cuttings were sent to Montfavet for field assessment. In most cases, two plants of each genotype were transplanted to the field on May 18, 2000: Both individuals were planted at the same stake and each genotype was separated by a row spacing of 1 m. Two replicates of the parental controls (four plants/replicate) were also included.

**Phenotyping:** Individual greenhouse-grown $F_2$ plants and controls were scored for 18 traits in Ithaca, New York (NY) during spring 1999. The field-grown plants were scored for 18 traits in Montfavet, France (FR) between July and October

2000. In general, secondary fruits were excluded from the analysis for fruit characteristics. Fruit weight (fw) was determined in grams for the five heaviest fruits in both NY and FR. The length (fl) and diameter (fd) of these fruits were also measured (centimeters) in both locations. Fruit shape (fs) was calculated as fl/fd. Thus, round fruit had an fs index of 1, oblate fruit had an index <1, and oblong fruit had an index >1. Ovary length (ovl), diameter (ovd), and shape (ovs) were determined only in NY by analyzing longitudinal sections of ovaries harvested at anthesis. In most cases, three ovaries were measured for each genotype. Measurements were in millimeters. Transverse sections of approximately three ovaries/genotype were also examined to determine ovary locule number (oln).

Fruit color was assessed in three ways at both locations. Fruit anthocyanin presence (fap) recorded whether the fruits were green or purple (presence/absence of anthocyanin). Fruit anthocyanin intensity (fai) measured the intensity of the anthocyanin for purple fruit on a scale of 1 (light purple) to 3 (dark purple). Thus, green fruits were excluded from the analysis of fai. Fruit color (fc) assessed both the hue and intensity of overall fruit color for both purple and green fruits. This trait was scored on a 1 to 5 scale in NY (1, light green; 3, light purple; 5, dark purple) and a 1 to 6 scale in FR (1, light green; 4, light purple; 6, dark purple). The anthocyanin contents of other tissues/organs were measured on a 1 (green) to 3 (dark purple) scale in NY and a 0 (green) to 5 (dark purple) scale in FR. The anthocyanin content of leaf lamina (lla), stem (sa), and prickle (pa) was evaluated in both locations. Leaf rib (lra) and flower corolla anthocyanin (ca) was determined only in FR. Fruit stripe (fst) or secondary color repartition of the fruit was measured as a presence/absence trait in NY and on a 1 to 3 scale in FR (1, no stripes; 2, irregular striping; 3, uniform reticulate striping).

Prickliness of various plant tissues/organs was evaluated on a 1 to 5 scale in NY (1, no prickles; 5, many prickles) and a 0 to 5 scale in FR (0, no prickles; 5, many prickles). Leaf prickle (lp), stem prickle (sp), and fruit calyx prickle (ftcp) were determined in both locations while flower calyx prickle (flcp) and petiole prickle (pp) were measured only in FR.

**Genotyping:** Molecular marker analysis and map construction for the population are described in the accompanying article (Doganlar *et al.* 2002, this issue). Only the 207 framework markers with LOD ≥ 3.0 were used for the statistical analysis.

**Statistical analysis:** Correlation coefficients were determined by the QGene computer program (Nelson 1997). QTL mapping was performed by single-point linear regression as implemented by QGene. A significance level of $P \leq 0.01$ was used as the type I locus-wise threshold for QTL declaration. Estimates of percentage phenotypic variation explained (% PVE, $R^2$ from QGene analysis) and gene action (*d/a*, dominance deviation/additivity) were determined by simple linear regression analysis for the most significant marker for each QTL. To confirm QTL identified by linear regression, simple interval analyses were performed with QGene using a significance threshold of LOD ≥ 2.4. Multiple regression analyses to determine the combined effects of multiple QTL on each trait were done in StatView (SAS Institute).

## RESULTS

**Correlations between traits:** In general, traits with similar or related phenotypes showed significant positive correlations at $P \leq 0.05$. Fruit color traits such as fap and fc were highly correlated ($r = 0.87$ in NY and 0.88 in FR) and there were significant positive correlations between the anthocyanin contents of various plant tissues. For example, fruit, stem, leaf rib, leaf lamina, and leaf prickle anthocyanin were all positively correlated ($0.41 \leq r \leq 0.82$). Fruit weight, length, and diameter were also highly correlated with the strongest correlation between fw and fd ($r = 0.95$ in NY and 0.97 in FR). Prickliness of various plant tissues (lp, sp, ftcp) was also strongly correlated ($0.75 \leq r \leq 0.88$). These significant positive correlations between related traits suggest that they may be controlled by the same loci with pleiotropic effects. Surprisingly, the ovary shape traits (ovl, ovd, ovs) were not significantly positively correlated with the fruit shape traits (fl, fd, fs). For every trait, correlations between the data collected in NY and FR were significant with the strongest correlations observed for fruit shape ($r = 0.96$) and its components, fruit length ($r = 0.94$) and fruit diameter ($r = 0.92$). These results indicated good correspondence between the two data sets.

**Summary of QTL detected:** Both single-point linear regression ($P \leq 0.01$) and interval analysis (LOD ≥ 2.4) were used for QTL detection. Only QTL that were statistically significant for both analyses are reported in this work. Because of the relatively small population size and the purposes of this research, comparatively lenient significance levels were used as the type I (locus-wise) thresholds for declaring QTL. For example, with the linear regression analysis, a given QTL has a <0.01 probability of being a false positive (Churchill and Doerge 1994). However, across all chromosomes and traits, there is a significant possibility that one or more of the reported loci are spurious. Because the primary purpose of this study was to determine whether common QTL control similar domestication traits in eggplant, tomato, and other solanaceous species, it was deemed more desirable to identify as many valid eggplant loci as possible, even at the risk of reporting a few false positives. The alternative was to use very high locus-wise thresholds to reduce the number of false positives at the expense of not reporting many valid QTL shared by eggplant and its related species. In addition, although the population used for this study was relatively small (58 individuals), population size does not affect the type I error rate; instead it increases the probability of not detecting true QTL (type II error). Thus, although the small population size may have prevented the detection of every locus affecting a trait, it does not nullify the validity of the QTL that were detected. As the scientific deductions derived from this work are not based on the detection of a single locus but instead on the larger picture that emerges by considering all QTL, the overall conclusions of this work should not be impaired.

A total of 22 traits were examined. Fourteen of these traits were measured in both locations while the remaining 8 were measured in either NY or FR. More specifically, 4 ovary traits were evaluated only in NY and four anthocyanin and prickle characters were deter-

**TABLE 1**

**List of QTL detected for each domestication trait**

| Trait | QTL | Eggplant linkage group | Tomato chromosome | Location | Significant marker(s) | *P* value | % PVE | *d/a* |
|---|---|---|---|---|---|---|---|---|
| Fruit weight (fw) | *fw2.1* | 2 | 2 | FR | TG469-*orfx* | 0.002 | 23 | −0.8 |
| | *fw9.1* | 9 | 9 | NY | TG589-TG35 | 0.005 | 44 | −0.1 |
| | *fw11.1* | 11 | 4S–11S | FR | TG523 | 0.009 | 19 | −7.3 |
| Fruit length (fl) | *fl2.1* | 2 | 2 | NY | TG469-*orfx*-CT9 | 0.002 | 23 | −0.3 |
| | | 2 | 2 | FR | TG469-*orfx*-CT24 | 0.0004 | 29 | −0.4 |
| | *fl9.1* | 9 | 9 | NY | TG589-CD3 | 0.0008 | 27 | −0.1 |
| | | 9 | 9 | FR | TG589-CD3 | 0.002 | 24 | −0.2 |
| | *fl11.1* | 11 | 4S–11S | FR | TG523-T408 | 0.004 | 22 | −3.5 |
| Fruit diameter (fd) | *fd1.1* | 1 | 1 | FR | TG273-TG607 | 0.002 | 23 | 0.8 |
| | *fd11.1* | 11 | 4S–11S | FR | TG523 | 0.01 | 19 | −6.0 |
| Fruit shape (fs) | *fs2.1* | 2 | 2 | NY | TG140-CT9-CT274 | 0.002 | 22 | −1.0 |
| | | 2 | 2 | FR | TG140-CT9 | 0.006 | 19 | −1.0 |
| | *fs7.1* | 7 | 7 | NY | TG639-TG216-CT195 | 0.0008 | 29 | 1.0 |
| | | 7 | 7 | FR | CT84-TG216-CT195 | 0.0009 | 29 | 1.0 |
| Ovary length (ovl) | *ovl1.1* (−) | 1 | 1 | NY | TG224-TG83-CT163 | 0.0008 | 35 | −0.3 |
| Ovary diameter (ovd) | *ovd4.1* (−) | 4 | 4L–10S | NY | CD55-TG62 | 0.003 | 29 | −7.0 |
| | *ovd9.1* (−) | 9 | 9 | NY | TG390 | 0.003 | 31 | −0.8 |
| | *ovd9.2* (−) | 9 | 9 | NY | TG35-CT74 | 0.0008 | 35 | −2.3 |
| Ovary shape (ovs) | *ovs4.1* | 4 | 4L–10S | NY | TG596-TG386-TG62 | 0.0009 | 36 | −3.0 |
| Ovary locule number(oln) | *oln5.1* | 5 | 5L–12L | NY | CT118-CT172 | 0.003 | 29 | −1.2 |
| Fruit anthocyanin presence (fap) | *fap10.1* | 10 | 10L–5S–12S | NY | CT100-CT240-CT20 | <0.0001 | 86 | 1.0 |
| | | 10 | 10L–5S–12S | FR | CT100-CT240-TG285 | <0.0001 | 93 | 1.0 |
| Fruit anthocyanin intensity (fai) | *fai1.1* (−) | 1 | 1 | NY | TG607-TG83 | 0.01 | 34 | −0.3 |
| | *fai10.1* | 10 | 10L–5S–12S | NY | CT242-TG241 | 0.003 | 42 | −0.1 |
| | *fai12.1* | 12 | 11L–12S | NY | CT79 | 0.001 | 48 | −5.4 |
| Fruit color (fc) | *fc8.1* (−) | 8 | 8 | NY | TG510-CT148 | 0.006 | 28 | −0.1 |
| | *fc10.1* | 10 | 10L–5S–12S | NY | CT99-CT240-TG285 | <0.0001 | 76 | 0.5 |
| | | 10 | 10L–5S–12S | FR | CT99-CT240-TG285 | <0.0001 | 81 | 0.7 |
| Leaf lamina anthocyanin (lla) | *lla2.1* | 2 | 2 | NY | *ovate-orfx* | 0.005 | 20 | −4.3 |
| | *lla6.1* (−) | 6 | 6 | NY | TG178-CT204-CT109 | 0.0003 | 27 | −0.2 |
| | | 6 | 6 | FR | TG240-GP89 | 0.005 | 22 | −0.2 |
| | *lla9.1* | 9 | 9 | NY | TG421-TG424 | 0.002 | 22 | 76.0 |
| | *lla10.1* | 10 | 10L–5S–12S | NY | CT217-CT240-CT20 | 0.0002 | 29 | 0.5 |
| | | 10 | 10L–5S–12S | FR | CT99-CT240-TG285 | <0.0001 | 60 | 0.4 |

(*continued*)

mined only in FR. For the traits scored in each location, 32 QTL were identified in NY and 30 QTL were detected in FR. These 62 loci were distributed on all 12 linkage groups with 47% of the QTL found on linkage groups 6 (14 QTL) and 10 (15 QTL). For the characteristics that were measured in both locations, 15 QTL were detected in both NY and FR. These 15 loci represented 44% of the total number of different QTL identified for these traits. The correspondence between the QTL identified in the two locations may have been lower than expected because different growth conditions were used in the different environments: greenhouse in NY and field in FR. In general, values for the percentage of phenotypic variation explained by each marker were high. This is probably a reflection of the relatively small population size used for this study.

**QTL detected for each trait:** Because the significance levels and magnitudes of effect for QTL detected by both single-point linear regression and interval analysis were very similar, only the values obtained from linear regression are presented (Table 1).

*fw:* Only one fruit weight QTL was detected in NY on linkage group 9; however, two QTL were found in FR on linkage groups 2 and 11. The QTL on linkage group 9, *fw9.1*, accounted for 44% of the phenotypic variation for fruit weight in NY. Although this locus was detected in FR by single-point regression, this result was not confirmed by interval mapping. The QTL on linkage group 2 in FR, *fw2.1*, was more significant than the one on linkage group 11, *fw11.1* ($P = 0.002$ *vs.* 0.009, respectively), and explained 23% of the fruit weight variation in FR. Simultaneous fit of the two QTL identified in FR accounted for only 17% of variation for the trait. For all of the *fw* loci, as expected, the *S. melongena* alleles

**TABLE 1**

**(Continued)**

| Trait | QTL | Eggplant linkage group | Tomato chromosome | Location | Significant marker(s) | *P* value | % PVE | *d/a* |
|---|---|---|---|---|---|---|---|---|
| Leaf rib anthocyanin (lra) | *lra10.1* | 10 | 10L–5S–12S | FR | CT99-CT240-TG285 | <0.0001 | 76 | 0.8 |
| Stem anthocyanin (sa) | *sa6.1* (−) | 6 | 6 | NY | TG178-TG240-CT204 | 0.0001 | 33 | −0.2 |
| | | 6 | 6 | FR | TG178-TG240-GP89 | 0.01 | 20 | −0.5 |
| | *sa6.2* | 6 | 6 | NY | CT193-CT109 | 0.007 | 19 | 0.2 |
| | *sa10.1* | 10 | 10L–5S–12S | NY | CT217-CT240-TG285 | 0.0002 | 29 | 0.8 |
| | | 10 | 10L–5S–12S | FR | CT217-CT240-TG241 | <0.0001 | 39 | 0.9 |
| | *sa12.1* (−) | 12 | 11L–12S | NY | CT79-CT211-cLET8K4 | 0.01 | 24 | 3.0 |
| Prickle anthocyanin (pa) | *pa10.1* | 10 | 10L–5S–12S | NY | CT100-CT240-TG285 | <0.0001 | 93 | 0.8 |
| | | 10 | 10L–5S–12S | FR | CT99-CT240-CD72A | <0.0001 | 90 | 0.9 |
| Corolla anthocyanin (ca) | *ca3.1* | 3 | 3 | FR | CT115 | 0.0007 | 26 | 2.0 |
| | *ca5.1* (−) | 5 | 5L–12L | FR | TG351-TG565-T801 | 0.0003 | 31 | −5.5 |
| | *ca6.1* (−) | 6 | 6 | FR | TG240-GP89-CT109 | 0.0002 | 30 | −0.7 |
| | *ca10.1* | 10 | 10L–5S–12S | FR | CT240-CD72A-TG285 | 0.0009 | 26 | 0.3 |
| Fruit stripe (fst) | *fst4.1* | 4 | 4L–10S | NY | TG230-TG303-TG62 | <0.0001 | 67 | −0.9 |
| | | 4 | 4L–10S | FR | TG230-TG303-T877 | <0.0001 | 49 | −1.0 |
| | *fst10.1* (−) | 10 | 10L–5S–12S | FR | CD19-CT99-CT242 | 0.002 | 25 | 1.3 |
| Leaf prickle (lp) | *lp6.1* | 6 | 6 | NY | TG365-CT109-TG482 | <0.0001 | 62 | −0.6 |
| | | 6 | 6 | FR | TG240-CT109-TG482 | <0.0001 | 79 | −0.7 |
| | *lp10.1* (−) | 10 | 10L–5S–12S | FR | CT20-TG285 | 0.006 | 23 | 1.8 |
| Stem prickle (sp) | *sp6.1* | 6 | 6 | NY | TG365-TG162-TG642 | <0.0001 | 37 | −0.5 |
| | | 6 | 6 | FR | TG365-CT109-TG482 | <0.0001 | 64 | −0.5 |
| Flower calyx prickle (flcp) | *flcp6.1* | 6 | 6 | FR | TG240-CT193-TG642 | <0.0001 | 64 | −0.8 |
| Fruit calyx prickle (ftcp) | *ftcp6.1* | 6 | 6 | NY | TG292-CT109-TG482 | <0.0001 | 51 | −0.3 |
| | | 6 | 6 | FR | TG240-TG162-TG642 | <0.0001 | 65 | −0.7 |
| | *ftcp9.1* | 9 | 9 | NY | TG328 | 0.006 | 29 | 1.0 |
| | *ftcp11.1* (−) | 11 | 4S–11S | FR | T408-TG194 | 0.008 | 19 | 9.0 |
| | *ftcp11.2* (−) | 11 | 4S–11S | NY | CT175-TG339 | 0.003 | 34 | −10.0 |
| Petiole prickle (pp) | *pp6.1* | 6 | 6 | FR | TG240-CT109-TG482 | <0.0001 | 71 | −0.4 |

Traits that were measured in both locations are underlined. QTL are named according to trait abbreviations. The first number following each abbreviation indicates the linkage group and the second number distinguishes QTL that mapped to the same linkage group and affected the same trait. QTL that were identified in the same genomic region in both locations are underlined. A (−) after a QTL indicates that the parental alleles had effects opposite to those predicted by the parental phenotypes. The homeologous tomato chromosomes for each eggplant linkage group are included for reference purposes. Location is coded: NY, New York; FR, France. Significant marker(s) column includes the most significant marker ($P \leq 0.01$) linked to the trait (underlined) as well as flanking markers that were significant at $P \leq 0.05$ as determined by single-point linear regression. Statistics in the remaining columns pertain to the most significant marker and were obtained from simple linear regression analysis. % PVE is percentage of phenotypic variation explained. *d/a* is the gene action for each QTL.

were associated with an increase in fruit weight. For *fw2.1*, the *S. linnaeanum* allele was nearly dominant while *fw9.1* was additive.

*fl:* Two fruit length QTL were identified on linkage groups 2 and 9 in both NY and FR. These two QTL, *fl2.1* and *fl9.1*, were localized to the same intervals for both locations and accounted for 23–29% of the variation for fruit length. An additional locus was detected in FR on linkage group 11, *fl11.1*. When simultaneously fit, the combined effects of the loci explained ~47% of the total phenotypic variation for fruit length in each location. All of the QTL showed the expected effects of the parental alleles.

*fd:* No fruit diameter QTL were identified in NY; however, two QTL were identified in FR on linkage groups 1 and 11. The more significant QTL in FR was *fd1.1* ($P = 0.002$), which explained 23% of the phenotypic variation for the trait. Together, the two loci explained 17% of the total variation for fruit diameter. For both loci, the *S. melongena* alleles were associated with an increase in fruit diameter.

*fs:* Loci for fruit shape were detected on linkage groups 2 and 7 in both NY and FR. The QTL on linkage group 7, *fs7.1*, was the more significant in both locations and had a magnitude of effect slightly higher than that of the QTL on linkage group 2, *fs2.1*. Collectively, these QTL explained 34 and 36% of the variation for fruit shape in NY and FR, respectively. For both *fs2.1* and *fs7.1*, the *S. linnaeanum* alleles were associated with slightly more oblate fruit. This was expected as the fruits of the wild parent are rounder and more oblate than those of *S. melongena*.

*ovl:* Ovary length was measured only in NY. One QTL was identified on linkage group 1, which explained 35% of the variation for the trait. Interestingly, for this QTL, the *S. melongena* allele had an effect opposite to that predicted on the basis of the phenotypes of the mature fruit as it was associated with a decrease in ovary length.

*ovd:* Ovary diameter was measured only in NY. Three QTL were detected for the trait on linkage groups 4 and 9. The most significant locus was *ovd9.2* ($P$ = 0.0008), which accounted for 35% of the phenotypic variation. When simultaneously fit, the three QTL explained 24% of the variation in ovary diameter. For all loci, the *S. linnaeanum* alleles increased ovary diameter, an effect that was not expected because *S. melongena* bears fruit much larger than that of *S. linnaeanum.*

*ovs:* Ovary shape was measured only in NY. Only one QTL was identified, *ovs4.1*, which explained 36% of the phenotypic variation for the trait. The *S. melongena* allele of this locus had the expected effect and was associated with more elongated ovaries.

*oln:* Ovary locule number was determined only in NY. One QTL was identified on linkage group 5. This QTL, *oln5.1*, accounted for 29% of the variation in locule number. The effect of the *S. melongena* allele for this locus was consistent with the parental phenotypes and was associated with an increase in locule number.

*fap:* One QTL was identified for fruit anthocyanin presence on linkage group 10 in both NY and FR. This locus, *fap10.1*, explained 86–93% of the phenotypic variation for anthocyanin presence and had a dominant gene action. The *S. melongena* allele for *fap10.1* had the expected effect and was associated with increased anthocyanin.

*fai:* Three QTL for fruit anthocyanin intensity were identified in NY on linkage groups 1, 10, and 12. No QTL were detected in FR. The most significant *fai* locus in NY was *fai12.1* ($P$ = 0.001, 48% PVE). Together, the three QTL explained 57% of the phenotypic variation for anthocyanin intensity. Except for *fai1.1*, the *S. melongena* alleles for the *fai* QTL were associated with an increase in anthocyanin intensity.

*fc:* The fruit color trait took into account both hue (green or purple) and intensity (light to dark). Two *fc* QTL were found in NY on linkage groups 8 and 10; however, only the QTL on linkage group 10 was identified in FR. This QTL, *fc10.1*, was highly significant and accounted for 76–81% of the phenotypic variation for fruit color. When fit simultaneously, the two loci identified in NY explained 76% of variation for the trait. The *S. melongena* allele for *fc10.1* behaved in a partially dominant manner and had an effect in increasing color that was consistent with the parental phenotype. The other locus, *fc8.1*, had an effect opposite to that predicted by the parental phenotypes as the *S. linnaeanum* allele was associated with increased fruit color.

*lla:* Four QTL were detected for leaf lamina anthocyanin in NY on linkage groups 2, 6, 9, and 10, whereas only two QTL were detected in FR on linkage groups 6 and 10. These two loci colocalized with the two most significant QTL identified in NY, *lla6.1* and *lla10.1* ($P$ = 0.0003 and 0.0002, respectively). In NY, these QTL individually explained 27–29% of the phenotypic variation for leaf lamina anthocyanin, whereas, in FR, they explained 22–60% of the variation. When simultaneously fit, the loci accounted for 42 and 63% of the variation for the trait in NY and FR, respectively. Both *lla6.1* and *lla10.1* showed additive gene action. For all but *lla6.1*, the *S. melongena* alleles had the expected effect of increasing anthocyanin.

*lra:* Leaf rib anthocyanin was measured only in FR, where one QTL was detected. This locus was located on linkage group 10 and explained 76% of the phenotypic variation for the trait. Alleles for this QTL had effects that were consistent with the difference between the parents.

*sa:* Four QTL for stem anthocyanin were identified in NY on linkage groups 6 (two QTL), 10, and 12 and two QTL were found in FR on linkage groups 6 and 10. These two loci, *sa6.1* and *sa10.1*, were identified in both locations and were the most significant QTL in NY ($P$ = 0.0001 and $P$ = 0.0002, respectively). Individually these two QTL explained 20–39% of the variation in stem anthocyanin observed in NY and FR. When simultaneously fit, the four QTL identified in NY and the two QTL detected in FR accounted for 49 and 31%, respectively, of the phenotypic variation for the trait. For *sa6.1*, the *S. linnaeanum* allele behaved in an additive manner and had the unexpected effect of increasing anthocyanin. In contrast, for *sa10.1* the *S. melongena* allele was partially dominant and was associated with an increase in anthocyanin.

*pa:* One prickle anthocyanin QTL was detected in both NY and FR on linkage group 10. This QTL was highly significant and had a very strong effect on the phenotype in both locations (90 and 93% PVE for FR and NY, respectively). This locus was partially dominant and its parental alleles had effects consistent with the parental phenotypes.

*ca:* Corolla anthocyanin was measured only in FR, where four different QTL were identified on linkage groups 3, 5, 6, and 10. The most significant QTL, *ca5.1* and *ca6.1* ($P$ = 0.0003 and 0.0002, respectively), also accounted for the greatest percentage of the phenotypic variation for the trait (31 and 30%, respectively). The combined effects of all four loci explained 47% of the variation in corolla anthocyanin. Unlike the other two loci, the *S. linnaeanum* alleles for both *ca5.1* and *ca6.1* had the unexpected effect of increasing corolla anthocyanin. For *ca5.1*, this effect of the wild alleles was overdominant ($d/a = -5.5$) as reflected by the more intense purple color of flowers from individuals that were heterozygous at this locus.

*fst:* One fruit stripe QTL was identified in NY on linkage group 4 and two QTL were identified in FR on

linkage groups 4 and 10. The QTL detected on linkage group 4 in both NY and FR localized to the same interval. This shared locus, *fst4.1*, was the more significant fruit stripe QTL in FR and accounted for 67 and 49% of the phenotypic variation for the trait in NY and FR, respectively. Together, the two QTL identified in FR explained 39% of variation in fruit stripe. The *S. linnaeanum* allele for *fst4.1* had the expected effect of increasing fruit stripes. For this QTL, the *S. linnaeanum* allele was dominant. In contrast, for *fst10.1*, the *S. melongena* allele was associated with an increase in stripes and had dominant gene action.

*lp:* A single QTL for leaf prickles was identified in NY on linkage group 6. This QTL (*lp6.1*) was also detected in FR and was more significant ($P < 0.0001$ *vs.* $P = 0.006$) than the only other QTL identified at that location, which mapped to linkage group 10 (*lp10.1*). In both locations *lp6.1* had a very high magnitude of effect and explained 62–79% of the variation for leaf prickles in NY and FR, respectively. The combined effects of the two loci detected in FR accounted for 73% of the total variation for leaf prickles. The *S. melongena* allele for *lp6.1* had the expected effect and was associated with fewer prickles. In contrast, the *S. melongena* allele of *lp10.1* showed the opposite effect.

*sp:* Only one QTL was detected for stem prickle in both NY and FR on linkage group 6. This QTL mapped to the same interval in both locations, was highly significant, and explained 37 (NY) to 64% (FR) of the variation in stem prickliness. As expected, the *S. linnaeanum* allele for this locus was associated with increased prickliness.

*flcp:* Prickles on the flower calyx were evaluated only in FR, where one QTL was detected. This QTL was found on linkage group 6 and accounted for 64% of the phenotypic variation in the trait. For this QTL, the *S. melongena* allele had the predicted effect and decreased flower calyx prickliness.

*ftcp:* Three fruit calyx prickle QTL were found in NY on linkage groups 6, 9, and 11. Two QTL were also identified on linkage groups 6 and 11 in FR; however, only *ftcp6.1* was localized to the same interval in both locations. In both NY and FR, *ftcp6.1* was the most significant QTL and had the greatest magnitude of effect (51 and 65% for NY and FR, respectively). When fit simultaneously, the three NY and two FR loci explained 60 and 58%, respectively, of the total variation for fruit calyx prickle. Only the QTL on linkage group 11 showed allelic effects that were not expected on the basis of the parental phenotypes.

*pp:* Petiole prickle was measured only in FR, where one QTL was identified on linkage group 6. This locus, *pp6.1*, was highly significant and affected 71% of the phenotypic variation for petiole prickle. For this QTL, the *S. linnaeanum* allele had the expected effect of increasing prickliness.

## DISCUSSION

**Domestication of eggplant involved a limited number of major loci:** The domestication of crop plants is often attributed to a relatively limited number of genetic factors with major effects (*e.g.*, Paterson *et al.* 1995; Doebley *et al.* 1997). An examination of the genetic control of domestication-related traits in eggplant supports these previous studies. Increases in fruit size and weight accompanied the domestication of all fruit crops. In eggplant, this trait was found to be controlled primarily by only two loci, which mapped to linkage groups 2 and 9. Eggplant domestication also involved diversification in fruit shape from the round fruit that is typical of many wild species to the elongated fruit that is characteristic of cultivated *S. melongena*. In this study, fruit shape was controlled by only two loci with major effects. These results are consistent with studies in the related crop, tomato, which showed that fruit weight and shape are determined by <10 major QTL plus several minor loci (Grandillo *et al.* 1999).

Fruit and plant color is another appearance trait that was affected during eggplant domestication. Most wild relatives of *S. melongena* have green fruits when half ripe, while cultivars display a diversity of colors due to the presence or absence of anthocyanin and chlorophyll in fruit tissue and the light sensitivity of pigment synthesis. The purple fruit color of many eggplant cultivars is the result of anthocyanin accumulation. Anthocyanin accumulation was found to be determined by a major locus on linkage group 10, which explained as much as 93% (*fap10.1* and *pa10.1*) of the phenotypic variation for the trait in fruit and other plant tissues. Additional loci for anthocyanin content were found throughout the genome; however, in comparison to the QTL on linkage group 10, these loci were of minor effects.

During domestication, crop plants were often modified for the convenience of the humans that sow, tend, and harvest them. The prickliness of eggplant is an example of this type of modification. Cultivated eggplant has few or no prickles while its wild relatives are well protected from herbivores by numerous prickles. This trait was determined primarily by a single QTL located on linkage group 6 that accounted for as much as 79% (*lp6.1*) of the phenotypic variation for prickliness. Overall, the four categories of domestication traits examined in this work (fruit weight, fruit shape, fruit and plant color, and prickliness) were controlled by only six loci with large magnitudes of effect.

These results, which indicate that only a few major loci are responsible for the phenotypic differences that differentiate cultivars from their wild relatives, are consistent with previous work in maize, other cereals, and bean. In maize, Doebley *et al.* (1997) found that a single locus *tb1* (*teosinte branched 1*) conditioned the dramatic alteration in plant architecture seen in maize and its progenitor, teosinte. Seed shattering is controlled by single

major genes in sorghum (Paterson *et al.* 1995) and pearl millet (Poncet *et al.* 2000). Similarly, in common bean, seed dispersal, seed dormancy, and photoperiod sensitivity are all determined by a few loci with large magnitudes of effect (Koinange *et al.* 1996). Thus, it appears that the domestication process in diverse crop species was driven by mutations in a relatively limited number of genes with major morphological consequences.

**Colocalization of QTL for related traits:** As expected, QTL for related traits were frequently localized to common genomic regions. The three fruit weight QTL identified in this study always mapped to the vicinity of loci controlling fruit shape or its components (*fl* and *fd*). This is not surprising given the related nature of these traits. However, careful examination of the data for linkage group 2 indicates that *orfx* is the most significant marker for *fw2.1* while CT9 is the most significant marker for *fs2.1*. This result suggests that the two traits may, indeed, be controlled by separate loci on linkage group 2. Additional support for this hypothesis is provided by the orthologous region in tomato, which is known to contain distinct loci for fruit weight (*fw2.2*; Alpert and Tanksley 1996) and shape (*ovate*; Ku *et al.* 1999).

Some of the QTL for fruit shape, length, and diameter mapped to common regions of the genome. However, the position of *fs7.1* could not be predicted on the basis of the *fl* and *fd* QTL. Of the five QTL identified for *ovl*, *ovd*, and *ovs*, only one (*ovl1.1*) overlapped with *fl*, *fd*, and *fs* loci. Moreover, no ovary shape QTL coincided with the major *fs* QTL, *fs2.1* and *fs7.1*. These results suggest that, in general, the size and shape of eggplant ovaries at flower anthesis are controlled by loci that are not directly involved in determining the final size and shape of mature fruit. This is contrary to what has been reported in tomato. In tomato, it was found that major fruit shape QTL determine fruit shape before (*fs8.1*; Ku *et al.* 2000) and during anthesis (*ovate*; Ku *et al.* 2001). This difference between eggplant and tomato may be a result of the differences in the development and anatomy of their fruit. Both eggplant and tomato fruits are classified as berries and the fleshy or juicy parts of their fruit consist of pericarp and placental tissues (Fahn 1990). After the initial stage of cell division during eggplant fruit development, cells of the innermost layer of the pericarp (the endocarp) expand and grow inward to meet the expanding placenta cells, thereby enclosing the seed (Dave *et al.* 1979). However, during tomato fruit development, the cell division stage lasts longer in the pericarp than in the placenta and most of the cellular expansion following this stage occurs in the placental tissues (Hayward 1938; Dave *et al.* 1982; Joubes *et al.* 1999). As a result, the interior of a mature eggplant fruit contains large proportions of both endocarp and placental tissue, whereas the interior of a mature tomato fruit is primarily placental. This difference in anatomy may explain why eggplant and tomato have different mechanisms for the genetic control of ovary and fruit shape.

For this study, fruit color was dissected into two components: fap and fai. The fc trait took into account both color (green or purple) and intensity. Only 1 common QTL was identified for fap and fai. This was the major color locus on linkage group 10. The fact that only 1 of the 4 QTL detected for these two traits was shared indicates that anthocyanin presence and accumulation may be controlled by different genetic factors in eggplant. This agrees with classical studies, which hypothesized that eggplant fruit color is determined by a few basic color genes that are required for anthocyanin production plus several modifier genes that control the qualitative and quantitative expression of the trait including the type of anthocyanin produced, the location of expression, and intensity of color (Tigchelaar *et al.* 1968). Traits related to anthocyanin accumulation in different plant tissues tended to map to the same regions of the genome. A cluster of color QTL was found on linkage group 6, which contained 6 such QTL centered around TG240. In addition, a larger grouping was identified on linkage group 10, which consisted of 13 QTL centered around CT240. This clustering undoubtedly reflects the pleiotropic effects of one or more anthocyanin pathway-related loci at these locations.

Traits related to plant prickliness also mapped to common regions of the genome. Most notably, eight prickle QTL centered around CT109 on linkage group 6. Moreover, at least one QTL for each of the five prickle traits measured in this study was localized to this region of linkage group 6. Similar to the anthocyanin loci, this clustering most likely reflects the pleiotropic effects of a single locus controlling prickles.

**Colocalization of QTL for unrelated traits:** Previous research examining the genetic control of domestication-related traits in crop plants has revealed that the loci for such traits are frequently concentrated in a few chromosomal regions (Koinange *et al.* 1996; Xiong *et al.* 1999; Poncet *et al.* 2000). The coincidence of these otherwise unrelated genes has been proposed as an explanation for the domestication syndrome, the set of phenotypic differences that distinguishes cultivated species from their wild progenitors. The domestication syndrome of eggplant is characterized primarily by differences in fruit size, shape, and color and plant prickliness. As already mentioned, fruit size and shape are related traits; therefore, their colocalization was discussed in the previous section. In this study, only one linkage group showed linkage of major loci for unrelated domestication traits. Linkage group 6 contained several important QTL for both plant anthocyanin content and prickliness. All of the cultivated alleles for the prickliness QTL on linkage group 6 had the favorable effect of decreasing the number of prickles whereas the *S. melongena* alleles for the color QTL were associated

**TABLE 2**

**Domestication-related loci with putative conservation in the Solanaceae**

| | Eggplant | | Putative ortholog | | | | | |
|---|---|---|---|---|---|---|---|---|
| Trait | Locus name | Linkage group | Locus name | Chromosome | Crop | Locus type | Mapping accuracy | Reference |
| Fruit weight | *fw2.1* | 2 | *fw2.2* | 2 | Tomato | QTL | **** | Frary *et al.* (2000) |
| | | | *fw2.1* | 2 | Pepper | QTL | *** | Ben Chaim *et al.* (2001) |
| | *fw9.1* | 9 | *fw9.2* | 9 | Tomato | QTL | *** | Grandillo *et al.* (1999) |
| | *fw11.1* | 11 | *fw11.1* | 11 | Tomato | QTL | *** | Grandillo *et al.* (1999) |
| Fruit shape | *fl2.1* | 2 | *ovate* | 2 | Tomato | Morphological | **** | Ku *et al.* (1999) |
| | *fs7.1* | 7 | *fs7.b* | 7 | Tomato | QTL | *** | Grandillo *et al.* (1999) |
| | *ovs4.1* | 4 | *fs10.1* | 10 | Tomato | QTL | *** | Grandillo *et al.* (1999) |
| | | | *fs10.1* | 10 | Pepper | QTL | *** | Ben Chaim *et al.* (2001) |
| Anthocyanins | *fap10.1*[a] | 10 | *af* | 5 | Tomato | Morphological | ** | Tanksley *et al.* (1992) |
| | | | *ag* | 10 | Tomato | Morphological | ** | Tanksley *et al.* (1992) |
| | | | *F* | 10 | Potato | Morphological | ** | van Eck *et al.* (1993) |
| | | | $I_{ep}$, $I_{co}$ | 10 | Potato | Morphological | ** | van Eck *et al.* (1994) |
| Fruit stripe | *fst4.1* | 4 | *Fs* | 10 | Tomato | Morphological | * | Tanksley *et al.* (1992) |
| | | | *u* | 10 | Tomato | Morphological | *** | Grandillo and Tanksley (1996) |

Eggplant QTL are named as in Table 1 and putative orthologous loci are named according to the references listed. Mapping accuracy is coded: *, locus position deduced by comparison of classical and molecular maps; **, locus mapped but position on high density molecular map is approximate; ***, locus mapped relative to markers on high density map; ****, locus cloned.

[a] Several anthocyanin QTL cosegregated with *fap10.1*: *fai10.1*, *fc10.1*, *lla10.1*, *lra10.1*, *sa10.1*, *pa10.1*, and *ca10.1*.

with reduced anthocyanin content. However, because no fruit color loci were identified on linkage group 6, the presence of cultivated alleles at these loci was not reflected in poor fruit color. Thus, it is probable that the selection pressure exerted by the early domesticators of eggplant was targeted at the prickle locus/loci on linkage group 6 and that the color loci were unintentionally included during this selection process. Given these results, eggplant does not provide strong evidence for the colocalization of domestication syndrome traits. Eggplant may not show linkage of such traits because it is a predominantly self-pollinated crop and it has been hypothesized that linkage blocks of domestication-related characters would have only an adaptive advantage in outcrossing species (Koinange *et al.* 1996).

**Domestication traits are conserved in the Solanaceae:** Many of the major domestication-related characters in eggplant appear to have been conserved during the evolution and domestication of other Solanaceae. This is evident as several eggplant loci have putative orthologs involved in the domestication of tomato, pepper, and/or potato. In this study, a locus was considered to be potentially orthologous to an eggplant QTL if it mapped to a syntenic region in both species. Table 2 summarizes these conserved QTL and indicates the relative confidence for the accuracy of each match.

All three QTL for fruit weight, *fw2.1*, *fw9.1*, and *fw11.1*, have counterparts in the other solanaceaous crops. *fw2.1* was identified only in FR; however, if the significance threshold for declaration of a QTL was lowered to $P \leq 0.05$, *fw2.1* was also detected in NY. The positioning of this locus and the fact that the most significant marker was *orfx*, the gene corresponding to the major tomato fruit weight QTL *fw2.2* (Frary *et al.* 2000), indicate that these two loci are probably orthologous. Similar to *fw2.2*, the wild, small-fruited allele of *fw2.1* is partially dominant to the cultivated, large-fruited allele. The identification of a pepper QTL, *fw2.1* (Ben Chaim *et al.* 2001), in the same genomic region provides additional evidence that this locus had an important role in the significant fruit weight changes that accompanied domestication in the Solanaceae. The other two eggplant *fw* QTL, *fw9.1* and *fw11.1*, appear to have orthologous counterparts in tomato, *fw9.2* and *fw11.1*, respectively (Grandillo *et al.* 1999). Although these QTL have not been as extensively studied as *fw2.2* in tomato, they were identified in two or more different wild species studies, suggesting that they are conserved within the genus Lycopersicon (Grandillo *et al.* 1999). Inclusion of the eggplant results extends this putative conservation to the Solanaceae family.

Three different fruit/ovary shape-related QTL appear to have been conserved during domestication. Two of these loci, *fs7.1* and *ovs4.1*, correspond to fruit shape QTL that have been mapped in wide crosses of tomato and/or pepper using some of the same markers that were used to construct the eggplant linkage map. The locus *fs7.1* seems to correspond to *fs7.b* in tomato

(Grandillo *et al.* 1999) while *ovs4.1* seems to correspond to *fs10.1* in tomato (Grandillo *et al.* 1999) and pepper (Ben Chaim *et al.* 2001). Although *fs7.1* and *ovs4.1* are major fruit/ovary shape QTL in eggplant, their putative orthologs have relatively minor effects in tomato and pepper. This disparity might be explained by the fact that the three species were domesticated independently. The farmers that domesticated eggplant may have fortuitously found mutations in the genes on linkage groups 4 and 7, which had major effects on fruit shape. In contrast, mutations with major phenotypic effects may not have occurred at these two loci in the tomato and pepper lineages. Such serendipity during domestication has been postulated as an explanation for incongruities in the genetic control of shattering in sorghum and maize (Paterson *et al.* 1995). The third fruit shape-related locus in eggplant that has a putative ortholog in tomato is *fl2.1*, the most significant *fl* QTL identified in this study. This QTL seems to correspond to *ovate*, one of the two major fruit shape loci in tomato (Grandillo *et al.* 1999). *Ovate* determines the transition from round to pear-shaped tomato fruit with specific effects on fruit length and neck constriction (Ku *et al.* 1999). For both *ovate* and *fl2.1*, the cultivated alleles are associated with fruit elongation; however, the elongated allele of *ovate* is recessive (Ku *et al.* 1999), whereas that of *fl2.1* is additive.

The major anthocyanin QTL on linkage group 10 appear to have two potential counterparts in tomato, *af* (anthocyanin free) and *ag* (anthocyanin gainer). In tomato, *af* has been mapped to the short arm of chromosome 5 (Tanksley *et al.* 1992); molecular markers from this region are found on eggplant linkage group 10. This linkage group also contains markers from the long arm of tomato chromosome 10, the location of *ag* (Tanksley *et al.* 1992; Figure 2). Thus, in eggplant these two regions containing *af* and *ag* are found together and correspond to the most important anthocyanin locus. The *af* mutant of tomato is marked by a complete absence of anthocyanin in the plant; therefore, the action of this gene determines the presence/absence of anthocyanin. In contrast, the *ag* mutant of tomato is characterized by delayed expression of anthocyanin during plant development and also affects anthocyanin distribution in the plant. Thus, *ag* is a regulator of anthocyanin accumulation in tomato. Although anthocyanin presence, intensity, and distribution traits were measured in eggplant, the results did not provide sufficient evidence for the declaration of distinct loci for these different characters on linkage group 10. Although the current data do not reveal whether the individual eggplant anthocyanin QTL correspond to *af*, *ag*, or both, parsimony and the phenotypic similarity of *ag* and the eggplant QTL suggest that *ag* is the more likely ortholog. This hypothesis could be tested by fine mapping of the anthocyanin QTL cluster on linkage group 10. Counterparts to the eggplant anthocyanin loci are also found in potato. Both potato flower (*F*; van Eck *et al.* 1993) and tuber skin color ($I_{ep}$, $I_{co}$; van Eck *et al.* 1994) loci have been mapped to the relevant region of chromosome 10. Thus, the conservation of these anthocyanin loci appears to span three different species in the Solanaceae.

The diverse phenotypic expression of the conserved anthocyanin-related regions in eggplant, tomato, and potato suggests that, during domestication of these three species, the same gene targets experienced different mutations affecting gene regulation. For example, during tomato domestication, the linkage group 10 locus may have experienced mutation(s) that downregulated expression such that normal tomato plants express only low levels of anthocyanin. In certain circumstances, however, anthocyanin production is increased in tomato (and eggplant). For example, cold-stressed plants often exhibit abnormally high anthocyanin expression. In eggplant, perhaps the most striking expression of the linkage group 10 anthocyanin QTL is purple fruit color. Obviously, such a phenotype is not normally seen in tomato; however, a monosomic alien addition line of tomato that contains an extra copy of chromosome 10 from *S. lycopersicoides* in a *L. esculentum* background does have purple fruit (Chetelat *et al.* 1998). This observation also supports the hypothesis that *ag*, and not *af*, is the ortholog of the anthocyanin QTL on eggplant linkage group 10. The differing expression of anthocyanins in the Solanaceae also suggests that each species has unique genetic controls for this trait. In eggplant, these controls may be represented by the QTL for which there were no putative orthologs in tomato, potato, or pepper.

The major fruit stripe locus, *fst4.1*, also shows conservation in the Solanaceae and has two potential counterparts in tomato: *Fs* (fruit stripe) and *u* (uniform ripening; Figure 3). *Fs* is characterized by dark green stripes that begin at the blossom end and extend toward the stem end; these stripes disappear when the fruit is ripe (Clayberg 1962). Similarly, the *u* mutant is apparent only in unripe tomato fruit and is characterized by uniformly green shoulders whereas normal fruit have a darker green shoulder (MacArthur 1934). Genetic analysis of *Fs* and *u* indicates that these two mutants on chromosome 10 are tightly linked but not allelic (Clayberg 1962). Because only *u* has been mapped precisely in tomato (Grandillo and Tanksley 1996), it is impossible to determine whether *fst4.1* corresponds to *Fs*, *u*, or both. Although the phenotype of *fst4.1* seems to resemble more closely that of *Fs*, a *L. hirsutum* variant of the wild-type *U* allele has pigmentation extending from the shoulder to the blossom end in stripes (S. D. Tanksley, personal communication). Therefore, either or both loci may be the tomato counterparts to the gene(s) that condition fruit striping in eggplant.

Overall, 8 different loci identified in eggplant were found to have putative orthologs in other solanaceous crops (for purposes of this discussion, QTL for similar

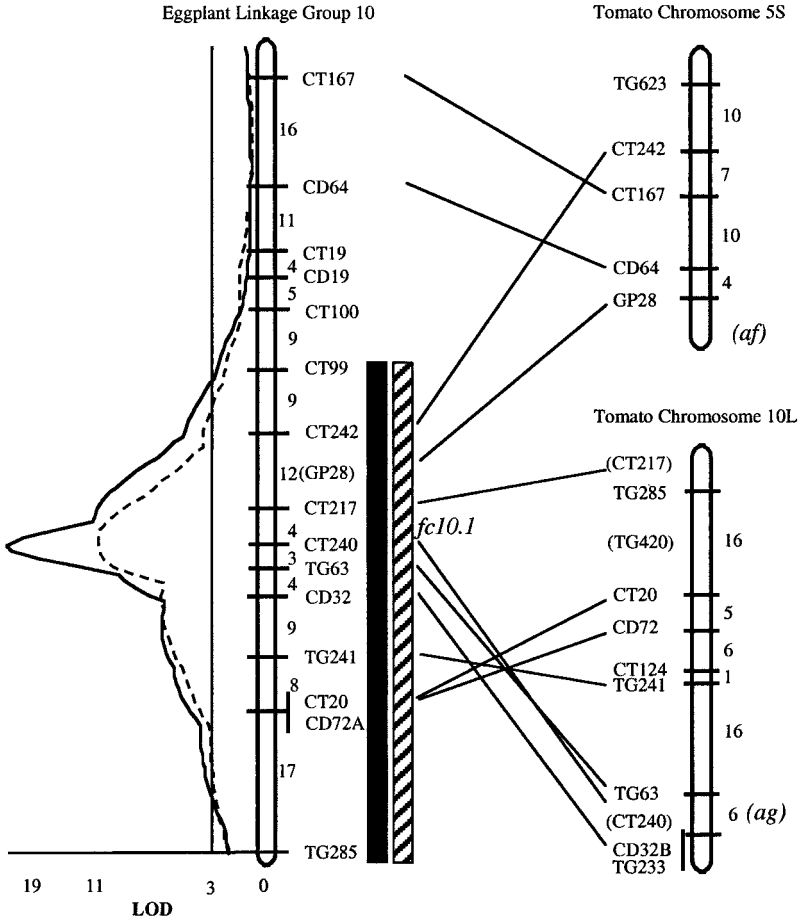


FIGURE 2.—Comparative mapping of the anthocyanin QTL on eggplant linkage group 10. Simple interval analysis for *fc10.1* is shown to the left of the molecular map of eggplant linkage group 10 (solid line for NY data, dashed line for FR data). Bars to the right of the linkage group represent the position of the QTL as determined by single-point regression analysis ($P \leq 0.05$; see Table 1 for details; solid bar for NY data, hatched bar for FR data). Molecular maps for tomato chromosome arms are from TANKSLEY *et al.* (1992). Eggplant linkage group 10 also contains a homeologous segment of the short arm of tomato chromosome 12, which is not shown.

traits that mapped to overlapping regions were not considered as different loci). These 8 QTL represented 40% (8/20) of the different fruit weight, shape, stripe, and plant color loci detected in this study. Together, the 3 conserved fruit weight loci accounted for as much as 54% (NY data) of the variation for this trait as determined by multiple regression analysis using the most significant markers for each QTL. Similarly, the combined action of *fl2.1*, *fs7.1*, and *ovs4.1* explained 31% of fruit shape variation in NY. Thus, a significant proportion of the phenotypic variation for these two traits was explained by loci that have been conserved during the evolution and domestication of the Solanaceae.

Some of the traits that did not show conservation of function across species were not expected to have orthologs as the traits were unique to eggplant. For example, none of the prickle QTL had counterparts in tomato, potato, or pepper. Explanations for the lack of conservation of other traits are not as simple. For example, QTL for locule number in eggplant did not correspond to any of the major locule number QTL identified in tomato (LIPPMAN and TANKSLEY 2001). There may be several reasons for this. In this study, locule number was measured at the ovary stage because it is impossible to distinguish individual locules in mature eggplant fruit. However, even at the ovary stage, locule number is difficult to determine in eggplant because there are no clear divisions between locules. Compounding this problem is the fact that only a few transverse sections were examined for each individual plant. It is also possible that locule number is controlled by distinct loci in the two species. This explanation is tenable because of the previously mentioned differences in eggplant and tomato fruit anatomy.

**Implications of conservation of gene function:** The finding that a significant proportion of the major QTL for domestication traits in eggplant are conserved in tomato, potato, and pepper supports the hypothesis that a limited number of major loci were involved in the dramatic phenotypic changes that occurred during domestication. Moreover, the fact that eggplant and the other solanaceous crops share so many common QTL despite their independent domestication on different continents further reinforces the idea that only a minute fraction of the ~35,000 genes contained in the tomato genome (VAN DER HOEVEN *et al.* 2002) govern traits related to domestication. The finding that only a few conserved major loci are responsible for the dramatic phenotypic changes that accompanied domestication in the Solanaceae may also explain why this family has been the source of so many different domesticated species.

Although only a limited number of targets for muta-

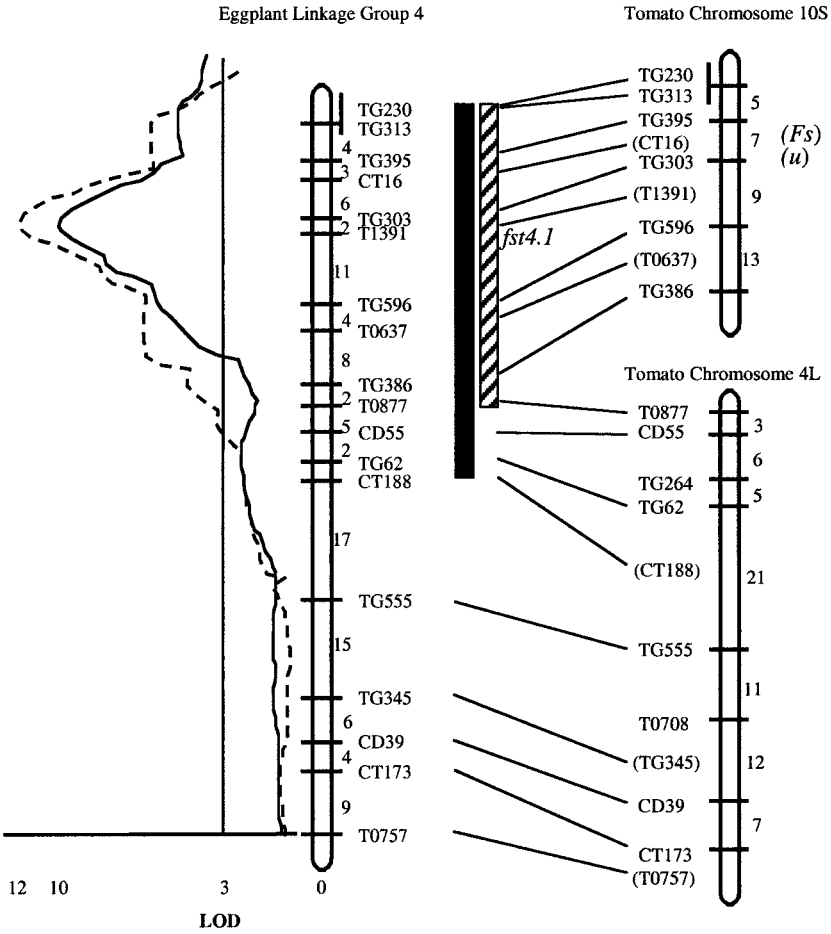


FIGURE 3.—Comparative mapping of fruit stripe locus on eggplant linkage group 4. Simple interval analysis for *fst4.1* is shown to the left of the molecular map of eggplant linkage group 4 (solid line for NY data, dashed line for FR data). Bars to the right of the linkage group represent the position of the QTL as determined by single-point regression analysis ($P \leq 0.05$; see Table 1 for details; solid bar for NY data, hatched bar for FR data). Molecular maps for tomato chromosome arms are from TANKSLEY *et al.* (1992).

tions have large effects on the phenotypic expression of domestication traits, independent and random mutation events were capable of giving rise to the tremendous diversity seen in the Solanaceae. This indicates that a single locus may have very different phenotypic expression in eggplant, tomato, potato, and pepper. The diverse phenotypic expression of a locus is determined primarily by the type of mutation that occurred during evolution and subsequent domestication of the species. Mutations can occasion changes in or the loss or gain of gene function or can alter gene regulation. Altered gene regulation has been invoked as the explanation for the phenotypes of several domestication-related traits in crops including maize (*tb1*, DOEBLEY *et al.* 1997), tomato (*fw2.2*, FRARY *et al.* 2000), and curd appearance in cauliflower (*BoCAL*, PURUGGANAN *et al.* 2000). Several of the changes in plant phenotype that were selected during eggplant domestication including increased fruit weight (*fw2.1*), increased locule number (*oln5.1*), and reduced prickliness (*lp6.1* and others) are specified by recessive alleles. Recessive mutations, which generally result in loss of gene function or genetic control, have also been reported to have important roles in the domestication of the scarlet eggplant, *S. aethiopicum* (LESTER and THITAI 1989), and many other plant species (LESTER 1989).

Despite the vast diversity of the plant kingdom, which includes >200,000 different species of flowering plants, humans are dependent on only a few domesticated crop species. This dependence makes us vulnerable to any factors that threaten those few species: disease epidemics, climate changes, and environmental degradation, for example. However, given the likelihood that only a few major genes encode the evolutionary changes that accompany the domestication process, it is conceivable that we can ascertain this repertoire of triggers and use this knowledge to develop new crops. Thus, in the future it may be possible to select an inedible plant that grows in a specific habitat (*e.g.*, in saline conditions) and to domesticate it by nonrandom mutations at target loci. Rapid, tailored domestication of such species could provide crops suitable for marginal or nonagricultural lands and could help to feed the people living in those areas.

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