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The genetic basis of seed-weight variation: tomato as a model system

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Abstract The seeds of domesticated plants are normally much larger than those of their wild counterparts. This change in seed weight was most likely in response to the selection pressure for yield, uniform germination and seedling vigor which was exerted by humans during domestication. However, despite the evolutionary and agronomic significance of seed weight, very little is know about the genetic and developmental controls of this trait; and, thus far, none of the genes in this pathway have been isolated from any plant species. QTL mapping experiments conducted in tomato during the past decade have allowed the identification of many seed-weight QTLs and have also revealed that only a few loci are responsible for the majority of the seed-weight changes that accompanied the domestication of tomato. This review presents a consensus map for seed weight QTL identified in previously published reports and in unpublished results from our laboratory. This summary of seed-weight QTL data allows for the identification of the major loci controlling this trait in the genus *Lycopersicon*. It is hoped that this work will allow the elucidation of this important phenotypic transition that occurred during crop-plant domestication and will also provide the starting point for the cloning of a gene responsible for seed-weight variation.

Keywords Domestication · Evolution · QTL · Map-based cloning · *Lycopersicon esculentum*

Introduction

Seeds are a major constituent of the human and animal diet. For much of the world's population seeds are an essential source of energy and nutrients in the form of proteins, carbohydrates and fats. Many of the most important crops, including rice, wheat, maize and beans, are seed crops. Obviously, for these species, seed weight is a primary component of yield and the ability to modify seed weight through breeding or other genetic manipulations would have tremendous benefits for agriculture and for the rapidly growing world population. In order to accomplish this, it is essential that the genetic factors determining seed weight are identified.

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Control of seed weight

Seeds are composed of the embryo, the endosperm and the seed coat. Each of these three structures is genetically distinct. The embryo develops from the fertilized ovule, contains an equal representation of the maternal and paternal genes and, upon germination of the seed, will develop further to become the mature progeny plant. The endosperm is usually formed by the fusion of two polar nuclei and one sperm nucleus; therefore, it contains two doses of the maternal parent's genes and one dose of the paternal parent's genes. The endosperm serves as a source of food for the embryo during development and germination. The seed coat protects the embryo and endosperm and is derived from the integuments of the ovule; thus, it contains only maternal genes. Therefore, in total the seed represents a complex genetic structure.

Seed development consists of three stages: cell division, cell differentiation and seed maturation. Each of these processes requires the coordinate regulation of genes in the embryo, the endosperm and the seed coat. Although seed development has been extensively studied in some species (reviewed in Cuming 1993; Meinke 1994), much of this work has focused on the characterization of mutants with defects in pattern formation (morphogenesis), pigmentation, and seed maturation. Very little work has examined the developmental biology of seed weight/size. One reason for this may be

that *Arabidopsis*, one of the best studied model systems, has seeds which show little variation in size even when different genetic backgrounds are compared (Meinke 1994). Therefore, most studies examining the developmental and genetic factors controlling seed weight/size have been done with less well-characterized species, (e.g., bean, soybean, and pea). It must be added, however, that the species chosen have been more practical in terms of their larger seed size and agricultural importance. Some of the work has shed new light on the determinants of seed size. For example, in *Vicia faba* the activity of cell wall-bound invertase in the seed coat provides a high hexose environment in the endosperm cavity which has been associated with cell division in the embryo. More specifically, it has been found that the seed coat of larger seeded genotypes of *V. faba* produced more cells and displayed a prolonged activity of invertase which, in turn, was correlated with a longer cell-division phase for the embryo (Weber et al. 1996). Correlations between embryo cell number and seed dry weight have also been reported for pea (Davies 1975), soybean (Egli et al. 1981), maize (Reddy and Daynard 1983) and wheat (Jenner et al. 1991).

Seed weight and evolution

Seed weight varies tremendously among plant species ranging from the enormous seed of the double coconut (10 kg) to the dust-like seeds of orchid (1 µg) (Boesewinkel and Bouman 1995). Most domesticated plant species produce seeds that are larger than (as much as ten-fold) those of their wild counterpart (Evans 1993). For wild plants, which must self-propagate, a good reproductive strategy is to produce large numbers of small seeds that can be easily disseminated, thus increasing the probability of finding a suitable environment for germination and survival. The needs of plants for survival in the wild are at odds with the requirements of human agriculture. During domestication and subsequent plant breeding, humans have selected for plants that produce larger seeds which give uniform germination and high vigor under direct field seeding and which do not depend upon natural vectors (e.g., winds, birds, rodents) for dispersal. Small seeds, while ideal for high fecundity and distribution in the wild, do poorly under the direct-seeded, monocultural conditions of modern agriculture. A second, more obvious, reason for the increase in seed weight during domestication is that humans have selected for larger seeds as a means of increasing yield. Of course, this latter point applies only to those species for which the seed is the consumed product (e.g., wheat, soybean, sunflower). In contrast, selection of large seeds for improved germination and vigor applies to most crops, even those in which the seed is not the primary agricultural product.

Although the human population depends upon seeds for its survival and a major feature of crop-plant domestication has been the increase in seed weight, the genes involved in this important change are not widely known. A notable exception is maize for which numerous defective kernel (*dek*) mutants have been identified and studied (Kowles et al. 1992). If we are to understand the pathway(s) of plant domestication and to begin engineering plants for modifications in seed-weight and composition, we must identify the key loci underlying this variation. In the past, it has been difficult to unravel the genetic and molecular basis of seed weight variation. In domesticated plants, the differences in seed weight are often polygenic, rendering classical approaches of gene identification impractical. However, the advent of quantitative trait locus (QTL) analysis (reviewed in Tanksley 1993) now allows for the identification of the genes responsible for the changes in seed weight that accompanied domestication. For example, research in various legume species including mungbean (Fatokun et al. 1992), cowpea (Fatokun et al. 1992), pea (Timmerman-Vaughan et al. 1996) and soybean (Maughan et al. 1996) has identifed several QTLs for seed weight. In addition, recent work in *Arabidopsis thaliana* identified several loci responsible for the natural genetic variation in seed size (Alonso-Blanco et al. 1999).

Tomato as a model for understanding the basis of seed-weight variation

Although seeds are not the primary food product of the crop, the seeds of cultivated tomato have become several-fold larger than their wild counterparts as a result of domestication and breeding. Thus, cultivated varieties of *Lycopersicon esculentum* produce seeds weighing more than 3 mg whereas seeds of wild relatives such as *Lycopersicon pennellii* weigh less than 1 mg (Fig. 1). Because of the ease of interspecific crosses and genomic tools, such as high-density linkage maps (Pillen et al. 1996) and yeast artificial chromosomes (YACs) (Martin et al. 1992), as well as bacterial artificial chromosomes (BACs) (Giovannoni and Wing, personal communication) and binary BAC (BIBAC) (Hamilton et al. 1999) libraries that are now in place for map-based cloning, tomato is ideally suited for identifying and isolating the genes responsible for seed-weight changes during domestication.

The genetics of seed weight variation in tomato

Like most other plant species, the seeds of tomato are composed of the embryo, the endosperm and the seed coat. Each of these three structures is genetically distinct and could potentially contribute to seed-weight variation. The seed weight of tomato is quantitatively inherited and determined mainly by additive gene action (Nieuwhof et al. 1989). Maternal effects which encom-

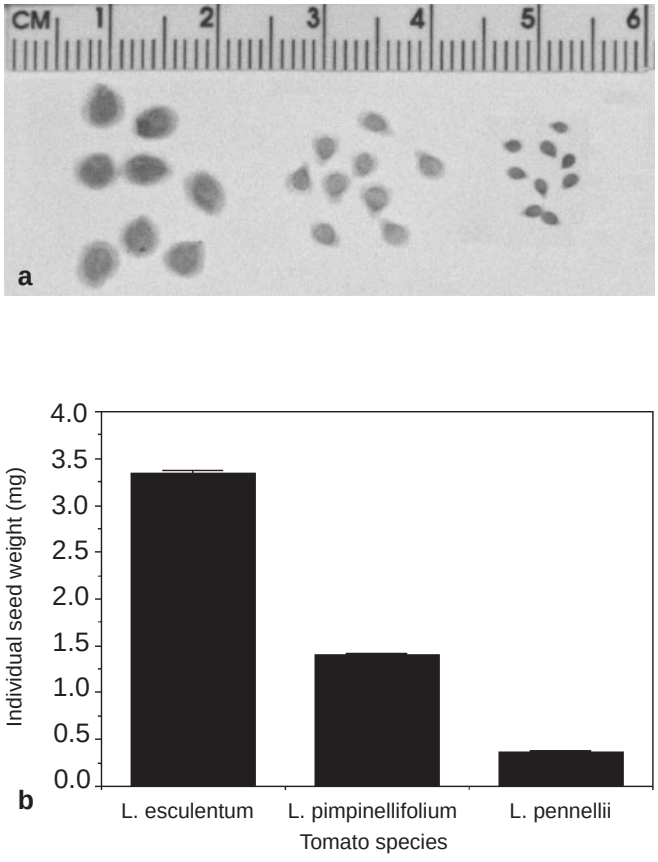


Fig. 1 Comparison of seed sizes (**a**) and weights (**b**) of three tomato species. From left to right, *L. esculentum*, *L. pimpinellifolium*, and *L. pennellii*

pass the maternal environment as well as the maternal genotype also play a critical role in determining seed weight (Pet and Garretsen 1983; Nieuwhof et al. 1989). This review summarizes what has been discovered about the genetic control of seed-weight variation in tomato during the past 20 years.

The identification of loci controlling seed-weight variation

Number of QTLs

A number of QTL studies using seven different populations involving interspecific crosses between cultivated tomato and five wild relatives (Table 1) have been conducted in tomato and have allowed most of the loci controlling seed-weight changes to be identified (Tanksley et al. 1982; Weller et al. 1988; Goldman et al. 1995; Grandillo and Tanksley 1996; Doganlar and Tanskley, unpublished). The number of QTLs detected by each study varied from 3 (Doganlar and Tanksley, unpublished) to 14 (Goldman et al. 1995) depending on the analytical approach used to analyze data, the statistical threshold chosen to declare a significant QTL, and the number and types of markers and populations used for each study (Table 1). For example, Goldman et al. (1995) identified 14 QTLs dispersed on nine chromosomes in a recombinant inbred population. The genome coverage of the recombinant inbred lines was greater than that of the other populations (F_2 and BC) and resulted in an ability to detect numerous QTLs. Table 2 presents a list of significant seed-weight QTLs detected in the seven interspecific populations. Overall, a total of 24 seed-weight QTLs were identified in these studies. Based on their map positions, 12 seed-weight QTLs were detected in only one species, while eleven seed-weight QTLs were detected in two or more different species. Interestingly, one seed-weight QTL (*sw4.1*) was detected in all five wild species.

Magnitude of effect and gene action of seed-weight QTLs

The magnitude of effect of seed-weight QTLs was determined in only three studies (Goldman et al. 1995; Grandillo and Tanksley 1996; Doganlar and Tanksley, unpublished).

Table 1 Number of significant QTLs for seed weight detected in seven populations derived from crosses between cultivated tomato and five wild tomato species. MO=morphological markers; RF=RFLP; RA=RAPD; I=isozymes

Wild species accession number	References	Population structure	Number of plants/families	Number and class of markers	Genome coverage (%)	Number of QTLs detected
L. cheesmanii (LA483)	Goldman et al. 1995	F_8RIL	97	129 RF, 2 MO, 1 IS	96	14
L. hirsutum (LA1777)	Doganlar (unpublished)	BC_2/BC_3	315	122 RF	99	6
L. parviflorum (LA2133)	Doganlar (unpublished)	BC_2/BC_3	170	128 RF	99	3
L. pimpinellifolium (LA1589)	Grandillo and Tanksley 1996	BC_1	257	114 RF, 4 RA, 2 IS	94	4
L. pimpinellifolium (CIAS27)	Weller et al. 1988	F_2	1200	10 IS	18	4
L. pimpinellifolium (LA1589)	Doganlar et al. (unpublished)	BC_2F_6RIL	206	140 RF	94	4
L. pennellii (LA716)	Tanksley et al. 1982	BC_1	400	12 IS	25	5

Table 2 List of significant seed-weight QTLs detected in seven interspecific populations derived from crosses between cultivated tomato and five wild tomato species. For loci identified in multiple studies, the largest values for additivity, magnitude of effect and % phenotypic change are listed. (?) not determined

Proposed QTL symbol	Chr.	Significant marker(s)	Additive effect[a]	(R^2) or PVE (%)[b]	Δ%[c]	Wild species[d]	Reference[e]
sw1.1	1	TG255-TG389	0.08	22.8	+ 7	A, E	3, 5
sw1.2	1	*Prx1-y*	?	?	–11	A, B	1, 2
sw1.3	1	TG71	0.05	7.9	?	E	3
sw1.4	1	*Skdh1*	?	?	–22	A	1
sw2.1	2	*Est-1*-TG48	0.05	15.2	–10	A, B, E	1, 3, 5
sw2.2	2	*d*	?	?	?	B	2
sw2.3	2	TG165	0.007	5	+29	B	5
sw3.1	3	CT263-TG74	0.05	10.7	+14	D, E	3, 5
sw4.1	4	CT175-*Adh*1	0.07	24.5	–32	A, B, C, D, E	1, 3, 4, 5
sw4.2	4	GP180-TG123	?	9	–32	B, C, D	4, 5
sw4.3	4	CT50-CD32	0.05	16.1	?	B, E	3, 4, 5
sw5.1	5	TG623-TG432	?	8	–15	C	5
sw6.1	6	TG54-TG552	0.05	16.7	–13	C, E	3, 5
sw6.2	6	TG279-TG99	0.05	16.7	?	E	3
sw7.1	7	*Got2*-CT150	?	7	–17	A, B, D	1, 5
sw7.2	7	TG156	0.05	14.1	?	E	3
sw8.1	8	*l-Aps2*	?	?	?	A, B	1, 2
sw8.2	8	TG553-CT68	?	5	+12	D	5
sw9.1	9	CD32A-TG291	0.04	15.7	?	E	3
sw10.1	10	CT16-CD45	?	7	+15	B	4, 5
sw10.2	10	CT112B-CT20	?	4	?	D	5
sw11.1	11	*a* (TG36)	0.06	11.1	?	B, E	2, 3
sw12.1	12	CT211A-CT99	?	3	+13	B, D	4, 5
sw12.2	12	TG296	0.04	11.3	?	E	3

[a] a=Additive effect of a single allele (WW-EE/2

[b] Percent variation explained (PVE%) is calculated as partial R^2. R^2 estimates the percentage of total phenotypic variation explained by locus

[c] Percent phenotypic change (Δ%) associated with the presence of the wild species alleles at a given marker locus was estimated as [(EW-EE)/EE]*100, where EW is the phenotypic mean of individuals heterozygous for the marker locus and EE is the phenotypic mean of individuals homozygous for the given marker locus

[d] A *L. pennellii*, B *L. pimpinellifolium*; C *L. parviflorum*; D *L. hirsutum*; E *L. cheesmanii*

[e] 1 Tanksley et al. (1982); 2 Weller et al. (1988); 3 Goldman et al. (1995); 4 Grandillo and Tanksley (1996); 5 Doganlar and Tanksley (unpublished)

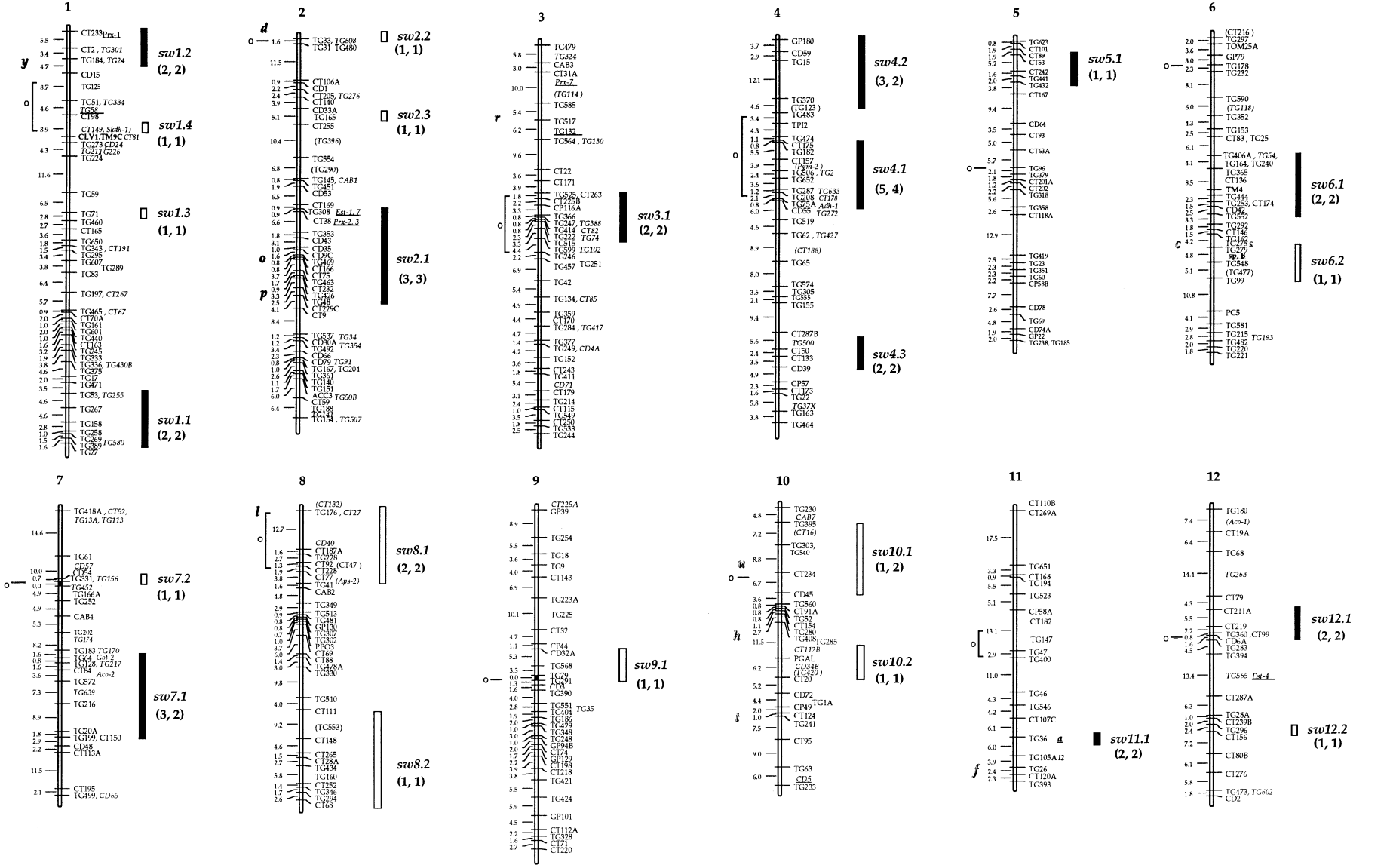
In these studies, an R^2 value was calculated to determine the percent of phenotypic variation explained by each significant marker class. The magnitude of the effect accounted for by each QTL varied from 3 to 24.5% (Table 2). Among the QTLs, *sw4.1* located between CT175 and *Adh-1* had the largest effect on the trait and accounted for as much as 24.5% (*Lycopersicon pimpinellifolium*; Grandillo and Tanksley 1996) of the total phenotypic variation for seed weight. The actual effect of a single dose of a wild-relative allele on seed weight was calculated as the percent phenotypic change (Δ%). The percent phenotypic change associated with the presence of a wild-species allele at a given marker locus was estimated as [(EW-EE)/EE]*100, where EW is the phenotypic mean of individuals heterozygous for the marker locus and EE is the phenotypic mean of individuals homozygous for the given marker locus. The greatest percent change for *sw4.1* was seen in the *Lycopersicon parviflorum* population (Doganlar and Tanksley, unpublished) in which individuals with a single dose of the wild allele at the QTL (i.e., heterozygous plants) had seeds which were 32% lighter than seeds from individuals that were homozygous for the *L. esculentum* allele. The smallest percent change in weight (an 8.4% decrease) for *sw4.1* was detected in the *L. pennellii* population (Tanksley et al. 1982) (Table 2).

As most of the studies used backcross populations, the gene action of the alleles at the seed weight QTLs could only be determined in two cases (Goldman et al 1995; Doganlar and Tanksley, unpublished). The additive effect of a single allele is estimated as (WW-EE)/2, where WW is the phenotypic mean of individuals homozygous for the wild allele at the marker locus and EE is the phenotypic mean of individuals homozygous for the esculentum allele at the locus. Based on these calculations, the seed-weight QTLs were behaving in an additive manner (Table 2).

Conservation of seed weight QTLs across species

Figure 2 presents a consensus map depicting the seed-weight QTLs identified to date in the five studies presented in Table 1. An examination of this consensus

Fig. 2 Consensus map showing the locations of seed-weight QTLs in tomato. Data taken from seven different populations-generated by crosses between *L. esculentum* and five different wild species. *Black bars* represent the map locations of QTL detected in at least two different wild species. White bars represent the map locations of QTLs identified in only one wild species. (m, n) m=number of different species; n=number of studies


1
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11
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sw1.2 (2, 2)
sw1.4 (1, 1)
sw1.3 (1, 1)
sw1.1 (2, 2)
sw2.2 (1, 1)
sw2.3 (1, 1)
sw2.1 (3, 3)
sw3.1 (2, 2)
sw4.2 (3, 2)
sw4.1 (5, 4)
sw4.3 (2, 2)
sw5.1 (1, 1)
sw6.1 (2, 2)
sw6.2 (1, 1)
sw7.2 (1, 1)
sw7.1 (3, 2)
sw8.1 (2, 2)
sw8.2 (1, 1)
sw9.1 (1, 1)
sw10.1 (1, 2)
sw10.2 (1, 1)
sw11.1 (2, 2)
sw12.1 (2, 2)
sw12.2 (1, 1)

map reveals that several regions on chromosomes 2, 4 and 7 have QTLs that were identified in populations derived from crosses with three or more different wild species. A list of significant seed-weight QTLs based on their conservation in wild species and their magnitude of effect on the seed-weight trait is shown in Table 2. While seed weight is obviously controlled by several loci, *sw4.1* appears to be responsible for the major transition in seed weight in tomato. No other seed-weight QTL in tomato shows such strong conservation across related species, suggesting that *sw4.1* is an orthologous seed-weight gene that has been conserved throughout the evolution of the different species of tomato from a common ancestor and may be the site of a key allelic change that occurred during the evolution and/or domestication of cultivated tomato.

Similar results have been found in research that was conducted with mung bean and cowpea by Fatokun et al. (1992). These researchers found that a genomic region that had the greatest effect on seed weight spanned the same RFLP markers in the same linkage order in both species. They concluded that this genomic region had been conserved during the evolution of mungbean and cowpea. Later work (Timmermann-Vaughan et al. 1996) showed that pea also contained this conserved genomic region. In addition, Maughan et al. (1996) studied the seed-weight of soybean to determine whether soybean shares orthologous seed-weight genes with cowpea or mungbean. They found that soybean and cowpea share an orthologous seed-weight gene, but that this gene is not found in mungbean. Additionally, Hulbert et al. (1990) reported clusters of seed-weight genes with a similar linear order in maize and sorghum.

Associations between seed weight QTLs and other traits

QTLs for seed weight are often in close proximity to loci for fruit weight and soluble-solids content (Goldman et al. 1995; Grandillo and Tanksley 1996). That is, the confidence intervals for the QTLs overlap in the same marker intervals. The major cluster of seed-weight QTLs on chromosome 4 is also the site of a cluster of fruit-weight QTLs that are shared by several different populations (Grandillo and Tanksley 1999). In addition, a region at the base of chromosome 4 is shared by QTLs for seed weight, fruit weight and soluble-solids content. A similar region is found on the long arm of chromosome 6 where seed-weight QTLs from two different populations are in the same span as QTLs for fruit weight and soluble solids. The short arm of chromosome 9 has several QTLs for soluble solids which coincide with seed-weight QTL from *Lycopersicon cheesmanii, L. pennellii* and *L. parviflorum*. It has been reported that seed weight and fruit weight are positively correlated but that seed weight and soluble-solids content are negatively correlated (Goldman et al.; 1995; Grandillo and Tanksley 1996). Whether these relationships are due to linkage or pleiotropy has not yet been determined. However, in the case of *sw4.1*, high-resolution mapping indicates that this particular seed-weight locus does not coincide with any known fruit-weight QTL (Doganlar and Tanksley, unpublished).

Associations between seed-weight QTLs and other traits were also detected by Alonso-Blanco et al. (1999) in *Arabidopsis*. Five of the 11 seed-weight QTLs identified in their study were mapped to the same regions as QTLs for ovule/seed numbers, ovary length, seed length and fruit length. Based on these findings, the authors suggested that maternal factors affecting carpel and ovule development and numbers were controlling seed size at those loci.

Candidate seed-weight QTLs for cloning

The conservation of *sw4.1* across *Lycopersicon* species, its potential role in the evolution and domestication of cultivated tomato, its significant contribution to seed-weight variation, and its independence from fruit-weight QTLs make *sw4.1* a prime candidate for map-based cloning. *sw4.1* accounts for 8.4–24.5% of the total phenotypic variation in segregating populations or up to 54% of the seed-weight variation in a nearly isogenic line (NIL) F_2 population (Doganlar and Tanksley, unpublished). Moreover, *sw4.1* is apparently the site of a key allelic change that differentiates large-seeded cultivated tomato and its small-seeded wild relatives.

At present, no locus controlling natural variation in seed weight has been cloned in any plant species. The cloning of such a locus in tomato would provide insight into the developmental processes that determine seed weight. The discovery of a major orthologous QTL for seed weight within one taxonomic group (i.e., *Lycopersicon*) may lead to the identification of the same orthologous QTL in additional species outside the genus. Therefore, a cloned locus might facilitate the identification of seed-weight QTLs in other crop-species such as bean, pea, and soybean in which the ability to manipulate seed-weight would be invaluable.

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