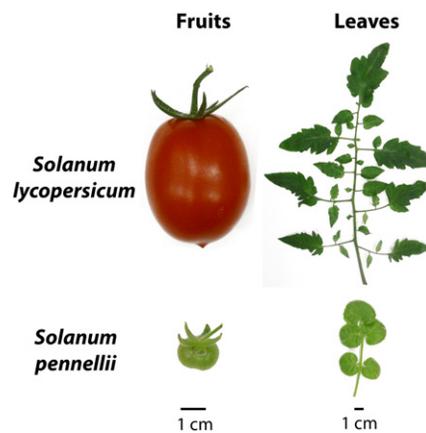


IN BRIEF

A Quantitative Genetic Basis for Leaf Morphology is Revealed in a Set of Precisely Defined Tomato Introggression Lines

What causes the domesticated tomato *Solanum lycopersicum* to have sweet, juicy red fruit and large, compound leaves with narrow-tipped leaflets while its distant wild relative, the Peruvian *Solanum pennellii*, has small, soapy-smelling green fruit with an unpleasant flavor (Matsui et al., 2007) and small compound leaves with thick, rounded leaflets (see figure)? Thoroughly answering this question, which is of interest to breeders and basic biologists alike, requires comprehensive genetic analysis of all of the differences between these species. Much has been learned from examining a set of 76 introgression lines (ILs) generated from crosses between *S. lycopersicum* cv M82 and *S. pennellii* (e.g., see Steinhauser et al., 2011). Each of these lines contains a small introgressed region of the *S. pennellii* genome in a *S. lycopersicum* background, defining unique regions of the genome (termed “bins”) containing, on average, 295 genes. Numerous quantitative trait loci have been mapped using these ILs, including those for morphology, yield, fruit color, metabolites, and others, and such information has been used extensively in tomato breeding. While genotyping these ILs has helped unravel the relationships that underlie domesticated traits at the whole-plant level, such analyses are limited, as only traits with detectable phenotypes can be examined.

By taking advantage of the recently completed tomato genome sequence, **Chitwood et al. (pages 2465–2481)** took studies of the 76 tomato ILs to a new level. First, using RNA-Seq and reduced representation genomic sequencing, the authors genotyped the IL population at ultra-high density, providing the exact gene content harbored by each line. They then used this resource to determine the genetic basis underlying natural variation in leaf form. To describe this variation precisely they performed comprehensive phenotyping of leaf traits, measuring leaf shape, size, complexity, and serration traits, as well



Morphological differences in the fruit and leaves between domesticated tomato (*S. lycopersicum*) and a wild relative (*S. pennellii*). (Reprinted from Chitwood et al. [2013], Figure 1.)

as pavement cell morphology and stomatal density and patterning. The analysis included making dental impressions of leaves to record epidermal characteristics and photographing over 11,000 leaves to assess leaf shape traits. To make sense of the immense natural variation in leaf morphology, each leaf was assigned Elliptical Fourier Descriptors, which express the outlines of objects mathematically, as the sum of ellipses that mimic the shape of the outline. The data were then reduced to a comprehensible form using Principal Component Analysis, which projects as much of the overall variation as possible into a few dimensions. This analysis revealed, among other things, that leaf shape, serration, and complexity can be genetically separated, which contrasts with previous findings from mutagenesis-based studies. The authors then assigned a probability value to each bin in the genome based on its correlation with a trait.

The leaf phenotype data were placed within the context of previously reported metabolic, enzymatic, and whole-plant phe-

notypes. This analysis revealed an interesting association between leaf morphology and sugar accumulation. To further explore this association, the authors performed RNA-Seq analysis of gene expression in the vegetative apices of the ILs, revealing correlations between fruit glucose levels and genes thought to regulate leaf morphology.

Although tomato is bred for improved fruit rather than leaf shape, leaf morphology affects photosynthetic efficiency and is apparently correlated with fruit sweetness. Therefore, leaf size and shape may have been inadvertently bred as much as improved fruit. Understanding the genetic basis of natural variation in the tomato, which is now becoming a reality, will no doubt further enhance tomato breeding.

Jennifer Lockhart
Science Editor
jlockhart@aspb.org

REFERENCES

- Chitwood, D.H., Kumar, R., Headland, L.R., Ranjan, A., Covington, M.F., Ichihashi, Y., Fulop, D., Jiménez-Gómez, J.M., Peng, J., Maloof, J.N., and Sinha, N.R. (2013). A quantitative genetic basis for leaf morphology in a set of precisely defined tomato introgression lines. *Plant Cell* **25**: 2465–2481.
- Matsui, K., Ishii, M., Sasaki, M., Rabinowitch, H.D., and Ben-Oliel, G. (2007). Identification of an allele attributable to formation of cucumber-like flavor in wild tomato species (*Solanum pennellii*) that was inactivated during domestication. *J. Agric. Food Chem.* **55**: 4080–4086.
- Steinhauser, M.C., Steinhauser, D., Gibon, Y., Bolger, M., Arrivault, S., Usadel, B., Zamir, D., Fernie, A.R., and Stitt, M. (2011). Identification of enzyme activity quantitative trait loci in a *Solanum lycopersicum* x *Solanum pennellii* introgression line population. *Plant Physiol.* **157**: 998–1014.

