

The 21st century tomato

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When tomatoes ripen in our gardens, we watch them turn gradually from hard, green globules to brightly colored, aromatic, and tasty fruits. This familiar and seemingly commonplace transformation masks a seething mass of components interacting in a well-regulated albeit highly complex manner. For generations, agriculturalists and scientists have bred tomatoes for size, shape, texture, flavor, shelf-life, and nutrient composition, more or less, one trait at a time. With the advent of molecular biology, mutagenesis and genetic transformation could produce tomatoes that were more easily harvested or transported or turned into tomato paste. Frequently, however, optimizing for one trait led to deterioration in another. For example, improving flavor could have a negative effect on yield.

The revolution in genomics, with a wealth of data emerging from sequencing and simultaneous expression analysis of thousands of genes, has made it possible to study the numerous pathways and regulatory networks—systems--that operate to produce a desirable fruit. This systems approach in the new fields of metabolic and functional genomics is producing the tools, information, and biological materials needed for screening and breeding efforts in tomato and other members of the Solanaceae.

Dr. Fernando Carrari and his colleagues, Laura Kamenetzky, Ramon Asis, Luisa Bermudez, Ariel Bazzini, Sebastian Asurmendi, Marie-Anne Van Sluys, Jim Giovannoni, Alisdair Fernie, and Magdalena Rossi use a systems approach that integrates genomic, genetic, and biochemical tools to model the metabolic networks that interact in the process of tomato

fruit development.

Tomato (*Solanum lycopersicum*) is a member of the Solanaceae or nightshade family, which also includes potato, eggplant, tobacco, and chili peppers. The center of origin and diversity of tomato species is in the northern Andes, where endemic populations of wild tomato species still grow. These wild populations represent considerable genetic diversity, whereas cultivated tomatoes are genetically very narrow. The Tomato Genome Consortium is an international collaboration that is sequencing, mapping and analyzing the genomes of both wild and cultivated varieties. Carrari and his co-workers, as well as other scientists, have begun to make use of this wealth of sequence data in functional and metabolic analyses of tomato and other crops.

Plants produce an immense variety of chemical compounds for growth, metabolism, signaling, defense, and reproduction. These metabolites function in complex networks and pathways in which they regulate and are regulated by parallel networks of genes. It is not possible to realistically model these metabolic systems one compound or gene at a time. Moreover, many, if not most traits in tomato, are not the result of one gene, but of many genes located together in chromosomal regions called quantitative trait loci (QTLs), because they produce a range of values in fruit or plant size or color, rather than just two extremes. Thus metabolites, enzymes, and genes must be analyzed simultaneously and in parallel in order to capture their dynamic relationships. To accomplish this, Carrari and his colleagues made use of the high genetic diversity of an ancestral tomato species, *Solanum pennellii*.

Through crosses, chromosomal segments of *S. pennellii* were introgressed into the genome of the cultivar *Solanum lycopersicum* var. Roma. Different lines of the cultivar were then created that differed only in the chromosomal segment received from the wild species. In this way, over 1200 metabolic QTLs or quantitative metabolic loci (QMLs) were

identified and analyzed. Almost 900 of these QMLs were found to be associated with fruit metabolism.

The scientists then sampled a number of metabolites such as carbohydrates, pigments, and hormones, among others, throughout flower and fruit development. They also used microarrays to determine which genes were expressed at those same times. Pairwise comparisons and network analyses were then made to determine which of those genes and metabolites are associated in possible functional networks. These associations do not establish causality or regulatory direction, because they are only correlational. Expression of certain genes may regulate metabolite activity, but metabolites may also have a regulatory effect on gene expression. To begin to define causal direction, Carrari and his colleagues perturbed these systems by treatment with external metabolites and followed the transmission of information from metabolite to gene. In continuing research, Carrari and co-workers are using these methods, as well as RNA interference and transgenesis to map QMLs and to identify and utilize candidate genes that function at network nodes.

These systems approaches make it possible to model the whole organism throughout its development. Moreover, an understanding of metabolic networks will make it possible to alter metabolic pathways to produce fruits with different secondary compounds that influence texture, taste, aroma, and nutrition, as well as to improve yield. Metabolite analysis also has possible applications in drug discovery, nutrient enhancement and biofuel production. One important goal is the use of ancestral genetic resources in place of simplistic genetic modification to avoid possible deleterious environmental effects as well as resistance by consumers to genetically modified food.

Dr. Carrari, of the Instituto de Biotecnología, (INTA), Argentina, will be presenting this work at a symposium on the Biology of Solanaceous

Species at the annual meeting of the American Society of Plant Biologists in Mérida, Mexico.

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