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IRWIN GOLDMAN

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Edited by
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# 1

# Dani Zamir: Pioneer in Tomato Genetics and Quantitative Trait Dissection

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## ABSTRACT

The dedicatory chapters for PBR have traditionally not had abstracts; but if there is a strong sense that there should be one I can write it- however this hasn't always been done.

**KEYWORDS:** Tomato, quantitative trait loci, introgression lines, tomato genome, overdominance, introgression breeding

## OUTLINE

I. INTRODUCTION
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## ABBREVIATIONS

| | |
|---|---|
| ILs | Introgression Lines |
| QTL | Quantitative Trait Locus |
| CWR | Crop Wild Relative |

## I. INTRODUCTION

For more than four decades, Dani Zamir has been among the most influential scientists in plant breeding throughout the world (Figure 1.1). Professor Zamir has spent his career at the Hebrew University of Jerusalem, in Rehovot, Israel, where he and his students have made great strides in improving our understanding of the genetic basis of quantitative traits in crop plants and in developing tools for advancing the science of plant breeding. Zamir was able to combine those efforts with practical plant breeding, leading to the development of highly productive cultivars and the establishment of practical breeding programs in horticultural species. He also mentored many undergraduate and graduate students in plant genetics and taught a popular course. Now Professor Emeritus, Dani Zamir's work on tomato genomics, genetics, and breeding continues into his fifth decade of work on

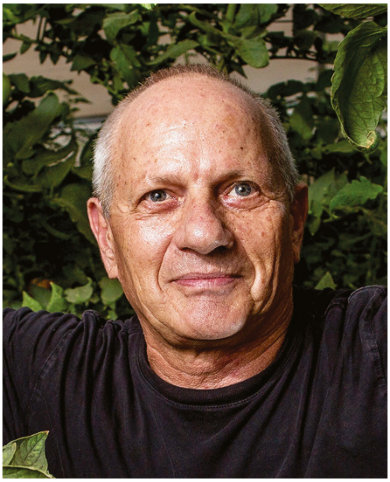

**Fig. 1.1.** Dani Zamir, Professor Emeritus, Hebrew University of Jerusalem, Israel.
*Source:* Photo credit: D. Zamir.

the crop. This dedication focuses on a few of his key accomplishments in the field of plant breeding and plant genetics.

Dani Zamir was born in 1950 in Israel. Following his military service, he received degrees from the Hebrew University of Jerusalem (undergraduate) and the University of California-Davis (graduate), completing his doctorate in 1981. He started his career as a lecturer in genetics at the Hebrew University's Faculty of Agriculture in Rehovot, Israel, in 1982 and was appointed senior lecturer in 1985. In 1992, he became associate professor and in 1996, professor of Genetics. He retired from his formal teaching and research at the University in 2018 and is now Professor Emeritus. Zamir also held adjunct appointments in genetics at Seoul University in South Korea and Cornell University in Ithaca, New York. Throughout his career, Zamir taught a popular course in general genetics to undergraduates at Hebrew University and was a mentor for numerous students.

Zamir has also founded two companies, each of which has achieved substantial success. The first, AB Seeds, initiated approximately 20 years ago, is a breeding and genetics company specializing in crop seeds including tomato. The company was sold to De Ruiter in 2008 and later purchased by Monsanto. More recently, Zamir and his student Yaniv Semel established the company Phenome Networks, which has developed proprietary software for managing complex breeding programs and the phenotypic and genotypic data that they generate. The company, based in Rehovot, Israel, serves a wide variety of public and private customers and helps users track crossing, trialing, phenotyping, and genotyping activities that are core components of breeding programs.

Zamir has served on the advisory boards of a number of institutions, journals, and projects, including Genoplante (France), the Max Planck Institute for Plant Breeding (Germany), the Department of Plant Molecular Biology at the University of Barcelona (Spain), the Grapevine Genome Project (Italy), the International SOL Genome Project, and the journals *G3: Genes, Genomes, Genetics*; *Scientific Data*; *The Plant Journal*; and *Scientific Reports.*

Zamir was also recipient of the Kaye Innovation Prize from the Hebrew University of Jerusalem in 2007, the EMET Prize in Agriculture in 2015, which recognizes excellence in academic and professional achievements that have significant influence on society, and the highly prestigious Israel Prize 2020. The Israel Prize is awarded by the State of Israel and is considered the highest honor the state bestows on an individual. It is highly selective and awarded annually in a formal state ceremony attended by the President, Prime Minister, and other dignitaries. The recipients of the prize are Israeli citizens or organizations who have displayed excellence in their field(s) or have contributed strongly to the culture of Israel. Receipt of this award is a singular achievement and a powerful indicator of the impact of Dani Zamir's work in agricultural science.

## II. UNDERSTANDING QUANTITATIVE GENETIC VARIATION

Dani Zamir has long been a proponent of understanding and utilizing genetic variability, particularly that from crop wild relatives (CWRs), to improve modern crops. Among his most well-known projects was the development of tomato (*Solanum lycopersicon*) introgression lines (ILs) containing small, molecular marker-defined chromosomal segments from the wild species *Solanum pennellii*. His approach, which became known as *Introgression Breeding*, is predicated on the idea that crop domestication may have left behind useful allelic variation. In a publication that has been cited nearly 1,300 times, Eshed and Zamir (1995) argued that some of this variation may be valuable in a modern breeding context and that genetic tools could be developed to identify and introgress that variation into modern cultivars without the disadvantages of using CWRs directly as parents in a breeding program. The approach gained worldwide acclaim and has been attempted in a number of crop species. The resulting progenies from these types of approaches are called *Introgression Lines,* or ILs.

Zamir (2001) later suggested that a genetic infrastructure could be developed based on "exotic libraries" where individual breeding lines or cultivars in the library would contain a marker-defined chromosomal segment from a CWR that had been introgressed through sexual recombination. A full set of lines of this sort would constitute a library of the genome of the CWR, albeit nested inside the genome of cultivated crop accessions. A scientist could obtain lines from the library to screen for traits of interest and potentially identify one or more lines carrying segments with valuable traits. These lines could then be easily introgressed into breeding material or cultivars using the markers flanking the introgression. These ideas were later more fully expanded to consider how this approach could be used to source natural variation for plant breeding programs (Zamir 2008).

Zamir's key insights into the value of allelic variation in CWRs were (1) that there were ways to access their value without using their entire genome as a parent in a breeding program and (2) that the genome of the wild relative could be assembled piece by piece into a library that was based on a cultivated genetic background. Plant breeders have long been aware of the pitfalls of using CWR as parents, including substantial linkage drag with undesirable traits, introduction of sterility and incompatibility, and limited recombination between wild and cultivated chromosomes. Granted, there are numerous examples of introgressions of important alleles from CWRs into cultivated crops; though these almost always involved substantial backcrossing to the cultivated parent to remove the genome of the wild parent and retain only the small segment associated with the trait of interest. In a number of these cases, unwanted segments of wild species chromosomes remain and are difficult to remove because of limited recombination at or near the unwanted genes of interest. The IL approach circumvents this problem by pre-developing a set of marker-defined ILs and allowing for a more custom-designed breeding approach (Figure 1.2).

But of even greater value may be the use of CWRs as a source for valuable quantitative trait locus (QTL) variation. Zamir and his students and colleagues were among the first to propose and demonstrate a practical approach to utilizing the potential of CWRs as sources of important quantitative variation (Zamir 2008). Prior to this time, CWRs were primarily considered as sources of valuable qualitative genetic variants, particularly for traits such as disease resistance. Traits like yield and productivity were considered mainly in the context of cultivated genetic

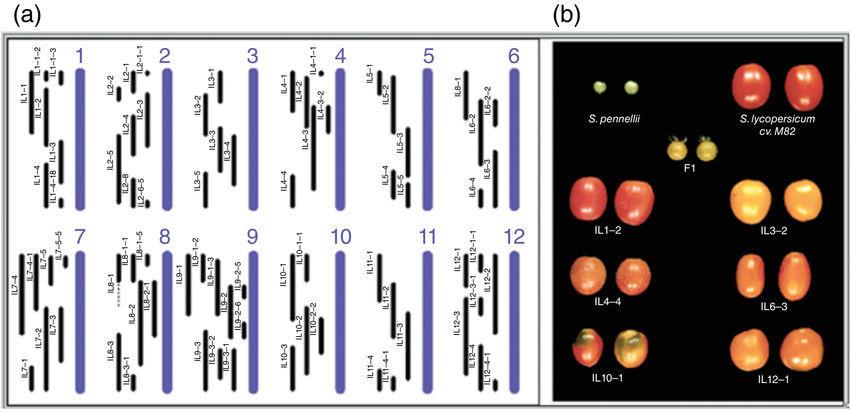

**Fig. 1.2.** The *S. pennellii* Introgression Line (IL) population. (a) Genome introgressions in the 76 *S. pennellii* ILs, which are nearly isogenic to each other and to M82 and differ only for the marked introgressed chromosome segments. (b) Green fruits of the wild species, *S. pennellii*, the lycopene-rich red fruits of *S. lycopersicum*, their $F_1$ hybrid and six ILs. *Source:* D. Zamir.

backgrounds. But an important insight offered by Zamir and colleagues focused on the observation that bottlenecks caused by domestication and modern breeding may have left behind valuable quantitative traits. By going back to CWRs, some of these valuable quantitative traits could be accessed; however, introgressing them carefully into cultivated backgrounds using very precise marker-delineated segments was the key to harnessing their potential. The IL concept provided a framework for how this could be accomplished.

More specifically, Eshed et al. (1996) conducted a series of field trials with ILs and their hybrids in two distinct genetic backgrounds. Seven out of 8 hybrids displayed from 7 to 13% higher yield than their near-isogenic controls (without introgressions). This finding demonstrated a significant interaction between the introgression and genetic background for yield in tomato. When the two introgressions with the largest yield advantage were combined into a single genetic background, a 20% yield increase compared to the control was realized.

The IL system is used by hundreds of researchers and breeders in academia and industry around the world. It has become the most helpful tool for identifying and introducing beneficial genes into cultivated varieties from their wild relatives. Moreover, the success of the tomato ILs has become a model for the development of similar systems in other agricultural crops (rice, barley, and wheat, for example) in China, Japan, Korea, and other countries.

## III. CLONING OF QUANTITATIVE TRAIT LOCI

Dani Zamir has been among the world pioneers in applying molecular markers for mapping quantitative traits in plants. One of the most important achievements in this area was the first example of cloning and characterization of a QTL, performed by Zamir and his student Eyal Fridman, currently a researcher in Israel's Volcani Institute. This was the first example of a cloned QTL from any organism. Their efforts identified a QTL for levels of soluble solids, primarily sugars, in tomato fruit that was determined by a variant of the enzyme invertase. The milestone article, published in April 2000 (Fridman et al. 2000), has been one of the most notable achievements of Israeli science in genetics and agriculture. In parallel with Zamir's work, a QTL gene for fruit size in tomato that segregated in one of the ILs was identified by Steven Tanksley from Cornell University, one of Zamir's research partners for many years, and this article was published in July 2000 (Frary et al. 2000).

To clone this QTL, Fridman et al. (2000) first identified a moderate QTL known as Brix-9-2-5, which increases sugar yield of tomatoes without compromising yield. This QTL was mapped to a single-nucleotide polymorphism (SNP)-defined region of 484 base pairs within a flower- and fruit-specific cell wall invertase gene (*LIN5*). *LIN5* is considered a "sink gene" that is involved with the unloading of sugars into the fruit. Further QTL analysis with segregating populations from five tomato species localized the functional polymorphism of Brix-9-2-5 to an amino acid near the catalytic site of the invertase crystal, which affects enzyme kinetics and fruit sink strength (Fridman et al. 2004). The work helped demonstrate the relationship between genetic variation at the sequence level and the manifestation of a QTL. This first cloning of an important crop QTL highlighted the value of the IL approach, and the enormous collection of characterized lines, advanced by Zamir and colleagues over many years.

## IV. CHARACTERIZATION OF GENETIC PHENOMENA

Dani Zamir's commitment to working with tomato extends through five decades, and he is therefore in an enviable position to study and describe the history of tomato genetics and breeding. Working with a large multinational team, Zamir and colleagues examined the modern history of tomato domestication and breeding through the lens of the cumulative genetic information collected by researchers throughout the years (Lin et al.2014). Their work revealed that modern tomato can be partially described by two independent sets of QTLs that conferred important changes to tomato fruit. These QTL, particularly fruit mass QTLs known as fw1.1, fw5.2, fw7.2, fw12.1, and len12.1, are responsible for the large size of modern tomato fruit, which is more than 100× larger than its wild progenitor. They also proposed a two-step evolution of tomato fruit mass through domestication sweeps associated with these QTL. In addition to changes in fruit mass, they reported several QTL on chromosome 5 that confer greater fruit firmness (fir5.1) and higher soluble solids (ssc5.1, ssc5.2, and ssc5.3) were likely selected during the development of processing tomatoes. Processing tomatoes are largely used for the production of tomato paste, which is a staple of processed foods such as ketchup. This genetic signature of processing tomato was facilitated by the presence of a very large centromere on chromosome 5, which likely reduced the amount of recombination present in the region where these QTL reside (Lin et al. 2014) (Figure 1.3).

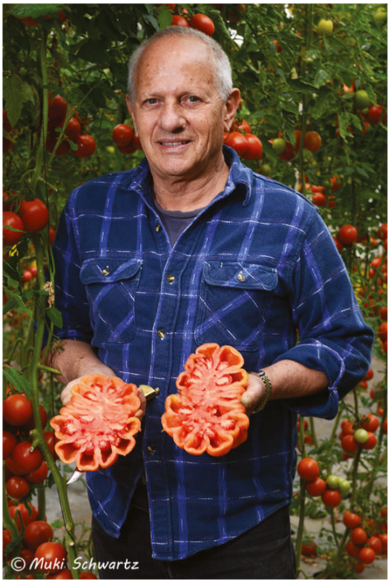

**Fig. 1.3.** Dani Zamir with multi-loculed tomato germplasm. *Source:* Photo credit: M. Schwartz.

Among Zamir's important contributions to agricultural research are his insights into understanding the genetic basis of overdominance (Semel et al. 2006), epistasis (Eshed and Zamir 1995), and heterosis itself (Lippman and Zamir 2007; Lippman et al. 2007; Krieger et al. 2010). For as long as humans have bred plants and animals, they have recognized the phenomenon of hybrid vigor, or heterosis, in which the $F_1$ progeny of a cross exceeds the value of the parents in terms of productivity. Despite the obvious importance of heterosis to global food production, its genetic basis has remained poorly understood; perhaps in part because many loci contribute to yield and productivity traits, and these loci behave in a variety of different ways.

In a collaboration with Uri Krieger and Zachary Lippman, Zamir worked out genetic effects at the locus known as *SINGLE FLOWER TRUSS* (*SFT*), which codes for a protein that produces the flowering hormone florigen (Lifschitz et al. 2006). Heterosis has been associated with several potential explanations, including the dominance hypothesis, the overdominance hypothesis, and epistasis. The overdominance hypothesis suggests that interaction between alleles at a locus is the cause of hybrid vigor. Identification of a number of examples of putative overdominance have revealed the phenomenon of pseudo-overdominance, where dominant loci are linked and appear as an overdominant locus. Krieger et al. (2010) examined a tomato mutant, sft-e4537, which displayed overdominant-type heterosis and possessed a missense mutation in the gene *SFT*. Plants carrying this mutation in the homozygous recessive condition flower very late and their flowering branches quickly revert to vegetative branches. Heterozygotes display substantial heterosis, derived from a suppression of growth termination mediated by the *SELF PRUNING* (*SP*) gene, an antagonist of *SFT*. This elegant example of a mechanism for overdominance illustrates how this elusive genetic phenomenon is a plausible explanation for heterosis in tomato. That is not to say that all loci behave in this manner, but the confirmation of a truly overdominant locus goes a long way to confirming the truth of one of the most widely held hypotheses of heterosis. Interestingly, this example also confirms the importance of epistasis, one of the three primary hypotheses for heterosis, given that the *SFT* and *SP* loci interact in this example.

## V. SEQUENCING THE TOMATO GENOME

Zamir was the leader of the SOL Genome Project, in which the complete DNA sequence of the tomato was deciphered (Tomato Genome Consortium 2012). To this end, Prof. Zamir organized research groups from the United States, the United Kingdom, the Netherlands, Italy, France, India, Korea, and Japan into a group known as the International Tomato Genome Sequencing Project, who worked together to sequence the tomato genome. Zamir was one of the two corresponding authors of the article on the tomato genome published in 2012 in *Nature* that garnered the issue's cover and a special feature (Tomato Genome Consortium 2012). This paper has now been cited more than 2,000 times and represents a tremendous multinational effort to sequence the genome of one of our most important crops.

The International Tomato Genome Sequencing Project was begun in 2004 by an international consortium of scientists from Korea, China, the United Kingdom, India, the Netherlands, France, Japan, Spain, Italy, and the United States. The group found that tomato genome was highly syntenic with other sequenced solanaceae crops and comprised more low-copy sequences than other crop genomes. They compared the cultivated genome to the related wild species *Solanum pimpinellifolium*, and the two genomes were divergent for only 0.6% of their nucleotides. However, the cultivated genome was 8% divergent from potato with a number of chromosomal inversions differing between the two. The researchers found two genome triplications in the history of tomato, one of which is approximately 130 million years ago and the other about 60 million years ago. These large-scale events were key to the diversification of genes for fruit fleshiness and color, particularly the more recent triplication event.

As critically important as this international effort was, Zamir's involvement in the ultimate success of the tomato genome project goes far deeper. Over many decades, Zamir collaborated with Cornell University scientist Steve Tanskley, who played a key role in building the molecular marker linkage map that was used to piece together much of the early information about the tomato genome and the location of traits of interest. Zamir's career spans the critical period from the early 1980s through the early 2000s which saw the development of molecular markers for plant breeding applications. Beginning with allozyme markers in the 1980s, then restriction fragment length polymorphisms (RFLPs) in the late 1980s and early 1990s, polymerase chain reaction (PCR)-based markers in the 1990s, and finally sequence-based markers in the 2000s, the possibility of associating chromosome segments with some type of molecular marker improved dramatically during this period. High-density molecular marker linkage maps became common by the 1990s and expanded dramatically in the 2000s with sequence-based markers. These developments were greatly facilitated by improvements in genome sequencing, particularly next-generation technologies that became available more recently. In addition, tomato, along with maize and rice, was always among the most well-developed models for marker systems in crops. Zamir was instrumental in the iterative development of marker-based information in tomato, contributing to virtually all of these developments over a period of decades. Marker-based regions were critical to the sequencing effort. Thus, the sequencing of the tomato genome represents one of the more recent successes of Zamir's collaborations, built piece by piece on a foundation of tomato breeding and genetics knowledge.

## VI. PRACTICAL PLANT BREEDING

Dani Zamir lives up to his principles by being involved in practical breeding. Based on the new methods he had developed, he has bred, together with a seed company he founded, AB Seeds, a processed tomato variety, 'AB2', which was a leading variety in California for a number of years. In many ways, this hybrid variety served as practical proof of the principles described by Zamir's scholarly work. The QTL