# Tomato Mutants: Freaks, Anomalies, and Breeders' Resources

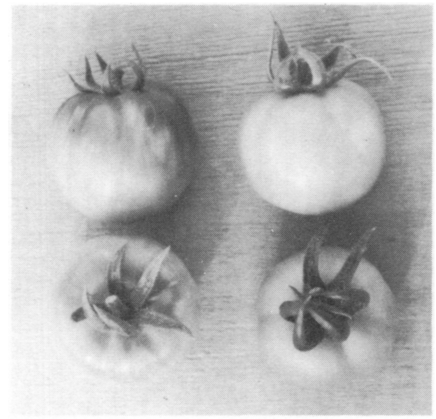

Fig. 2. Immature fruits of normal (left) and uniform ripening (*u*) (right) in lateral view (top) and calyx end (below). Note the absence of green "shoulder" and overall paler color of *u* fruits.

The ghost mutant illustrated on the cover is one of the myriad monogenic variants known in the tomato. Although determined by a single gene (*gh*) of known chromosomal location, the homozygote is remarkably variable. It emerges with normal or slightly bleached cotyledons; the first true leaf is a mosaic of totally white and normal green areas; the subsequently developed leaves may have mostly green tissue, but are generally entirely white or light yellow phase; and either white or yellow phase can revert to patches or longitudinal stripes of the green phase. All selfed progeny from any of these phases are solely of *gh* phenotype. Although this mutant has elicited great interest as a possible example of transposable element activity, such activity has not been proven.

Experience with the tomato since the turn of the century has revealed that, despite a relatively high chromosome count ($n = 12$), it behaves genetically as a strict diploid. Further, automatic self-pollination responsible for reproduction under most conditions guarantees rapid appearance of recessive mutants. As a consequence, the tomato is replete with mutants with sharply defined expression (hence clear-cut segregation) affecting many morphological, physiological, biochemical, and behavioral characters. A rather large share of the known mutants has been discovered as spontaneous variants in the seedling stage in nursery culture or in mature plants in gardens or commercial fields. An important additional group has been induced by radiation or chemical mutagens. With increasing intensity of research, the discovery and description of new mutants has greatly accelerated in recent years. According to periodic summaries, the number of known mutant genes stood at 9 in 1917, 20 in 1931, 49 in 1947, 118 in 1956, 690 in 1967, about 800 in 1975, and, currently, about 1200.

Tomato genes amount to far more than mere geneticists' playthings. Various mutants have proven essential for experiments of plant physiologists, evolutionists, and breeders of commercial and home-garden tomatoes. It is therefore appropriate that this material be collected and preserved—a goal of the Tomato Genetics Stock Center (TGSC), Department of Vegetable Crops, Univ. of California, Davis. Here is maintained a collection of about 800 monogenic mutants, as well as various compound stocks of such markers (linkage testers, etc.), primitive Latin American cultivars, chromosomal variants, wild species, and other special types. Totaling about 2500 accessions, the TGSC is currently supported by a grant from the National Plant Germplasm System, ARS/USDA. Duplicate seed samples are also preserved at the National Seed Storage Laboratory at Fort Collins, Colo. Available stocks are listed periodically in Reports of the Tomato Genetics Cooperative, which also serves as an important medium for announcing new mutants and reporting research on various mutants. Seed samples are available from the TGSC on request by investigators.

Extensive use of mutants from the TGSC collections has been made to expedite research on the nature of the tomato genome. Such studies embrace a wide range of subjects: transmission and lethality phenomena, gamete competition, physiological and developmental genetics, linkage mapping and recombination, gene distribution, gene duplication, genetic control of chromosome behavior, spontaneous and induced mutation, modifications of pollination systems, and parasexual hybridization. Thanks to the wide array of available mutants, the tomato has become one of the best-mapped species of flowering plants.

Recent genetic research has emphasized the use of molecular markers. The inherent advantages of enzyme variants (allozymes) has led to their extensive use to promote mapping, and various applications have been made of linkages between such markers and other major genes as well as those determining quantitative characters. The prospects for using DNA markers, as generated by restriction enzymes, appear even brighter, and widespread applications can be anticipated.

Fig. 1. Mature plants of determinate (*sp*) (left) and normal type (right). Both plants are 5.5 months old and were grown under comparable greenhouse conditions. Note the compact growth and termination of branches in inflorescences of *sp* and unlimited growth of normal.

Tomato mutants have greatly abetted research on the physiology of plant development. The role of growth regulators has been elucidated by studies of the overwilting mutants *flc, not,* and *sit*, as well as the remarkable geotropically neutral *dgt*. Some other areas of investigation thus facilitated are: biosynthesis of phenolics by a dozen mutations that modify anthocyanin, and carotenoids by a series of mutations affecting fruit pigmentation; the fruit ripening process by various obstructing mutants; and mineral transport and metabolism by various inherited defects.

The tomato is a classic example of exploitation of monogenic traits for breeding improved cultivars. Large numbers of highly useful mutant genes have established themselves in the breeders' repertoire. Probably no other mutant matches determinate habit (*sp*) for its impact on tomato breeding. Discovered in 1914 as a spontaneous mutant by a Florida physician, *sp* was regarded at first as a curiosity. Later, and particularly in the 1940s and, more recently (with interest becoming more serious), *sp* has been widely incorporated in breeding programs. It has fundamentally altered tomato production by providing an orderly, compact plant with greatly concentrated flowering and fruiting. For example, nearly all of the plantings in the vast tomato acreage in California are of *sp* cultivars. The absence of any other gene conditioning equivalent modification of plant habit further underscores the indispensability of this gene.

Other genes that have proven their use include uniform fruit ripening (*u, ug*), jointless pedicel (*j, j-2*), some 50 male-sterile mutants, genes affecting fruit flavor constituents, and an impressive array of monogenically controlled disease resis-

*Continued on inside back cover*

Front cover:
Ghost mutant, a monogenic variant of the tomato.

tances. Recently, breeding activities have been promoted by tight linkages between allozyme markers and genes controlling economically important traits, for example, between *Aps-1* and *Mi*, the widely used gene for resistance of root-knot nematode, and between *Prx-2* and *ms-10*, one of the more useful male-sterile mutants.

Control of disease by inherited resistance is a well-advanced area in tomato research. A surprisingly high proportion of the resistances are determined monogenically, with most of the alleles derived from related wild species and incorporated into advanced horticultural lines. Certain of these genes defy the concept that monogenic vertical resistance is restricted to a narrow range of pathogenic races. In the case of nematode resistance, *Mi*, derived from *L. peruvianum*, conveys resistance to several species of *Meloidogyne* and many races of *M. incognita*. The $Tm\text{-}2^2$ gene for resistance to TMV, also derived from *L. peruvianum*, has proved effective against virtually all strains of the virus. On the other hand, certain other genes code for vertical resistance against a limited range of pathogenic variants, as in the case of leaf-mold resistance, for which at least 7 different genes of the *Cf* series have been identified. With respect to multiple resistance, the tomato is also a classical example. Resistance to as many as 5 different diseases has been combined in certain pure-breeding, commercially acceptable cultivars and to as many as 10–12 diseases in $F_1$ hybrid cultivars. Such genes obviously play a key role in the activity of tomato breeders.

The contribution of mutation to the home gardener must not be overlooked. To a very large extent, genes (such as those for disease resistance, high fruit set and quality, etc.) that appeal to the commercial grower are also prized by the amateur, but the latter also covets novelty—the extreme being ''ornamental'' variants (i.e., *Wo*, wooly foliage; and *Cu*, the exotic Curl mutant). The fruit color variants—yellow (*r*, *at*), pink (*y*) ''white'' ($r + y$), tangerine (*t*), Beta orange (*B*)—have their advocates and are often claimed to have better flavor than the standard scarlet tomatoes. One of the oldest known tomato mutants, dwarf (*d*), dating back to the 19th century (although seldom making its mark in commercial cultivars), plays a key role in the ''patio'' type for container culture and miniature gardens.

Perhaps this tiny sample conveys an idea of the wealth of available genetic variation and diversity of use. The more variants that are discovered, the more we appreciate what nature can provide, as revealed in monogenic mutants of the tomato.

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