

## Review on Genetics and Breeding of Tomato (*Lycopersicon esculentum* Mill)

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### Abstract

Tomato is considered as a member of the family *Solanaceae*. The botanical name of tomato is *Lycopersicon esculentum* Mill and is a diploid plant with  $2n=2x=24$  chromosomes. Great advances in tomato genetics have been achievable because of the understanding of mating systems and the possibility of controlled hybridization within and among species, the naturally occurring variability in the species, the occurrence of self-pollination that leads to the expression of recessive mutations, the lack of gene duplication, and the possibility to easily identify the 12 chromosomes. New methodological approaches like molecular mapping of important agronomical characters and the development of advanced-backcross and introgression lines have provided powerful tools for the improvement of the tomato crop and to understand the processes of domestication. The general breeding goals of tomato are fruit yield, fruit quality, and resistance to diseases and pests. Tomatoes are presented as a classical example for gene transfer from wild species into cultivated cultivars for improvement the qualitative traits. It was established that until now the achievements in tomato breeding are based on classical breeding-genetic methods and also, an essential change in the accelerated introduction of useful traits in the cultivars is not made. It is believable that conventional breeding wouldn't allow the increase of productivity in the future. The significant progress in molecular genetics and use of molecular marker techniques are established. Therefore, the combined application of traditional breeding and contemporary plant biotechnology methods including selection based on molecular markers marker-Assisted Selection might be valuable tools for tomato breeding.

**Keywords:** Chromosomes; Fruit quality; Fruit yield; Genome; *Lycopersicon esculentum*

### Introduction

Tomato (*Lycopersicon esculentum* Mill.) is one of the most important solanaceous vegetable crops grown worldwide under outdoor and indoor conditions. It has become an important commercial crop so far as the area, production, industrial values and its contribution to human nutrition is concerned. Tomato belongs to the family *Solanaceae*, which includes more than 3000 species. *Solanum* section *Lycopersicon* includes the cultivated tomato, *Solanum lycopersicum*, the only domesticated species, as well as a dozen other wild relatives [1]. The genetic diversity in wild tomatoes, especially the self-incompatible species such as *S. chilense* and *S. peruvianum* are extensive. Tomatoes originated in South America, in the general area of Peru and Ecuador, but they were first domesticated in Mexico. The Spanish took domesticated forms to Europe in 1523 and they had reached Italy by 1544, and England by 1597. The Spanish also took them to the Philippines and they were recorded in Malaysia in 1650. Tomatoes were taken to North America from Europe in the late eighteenth century. Today tomatoes are grown all over the world in areas that have at least three frost-free months each year. They are also one of the more popular greenhouse crops [2].

Tomato (*Lycopersicon esculentum* Mill.) possesses unique properties, as it is both an economically important crop, the first vegetable in production in the world, and a model plant species, due to its diploid, relatively compact, and recently sequenced genome and its

large genetic and genomic resources [3]. It is a widely grown vegetable throughout the tropics and subtropics and is an important source of vitamins A and C. Production of high value fruit and vegetables such as tomato offer some smallholders the opportunity to change from subsistence to commercial farming and substantially increase their incomes. The most widely cultivated vegetable crops in sub-Saharan Africa, grown for fresh market and sometimes for processing.

Tomato cultivars can also be distinguished on the basis of the indeterminate or determinate growing habit. Cultivars for processing purposes are determinate growing and plants have a compact growth habit with grouped fruits ripening at a single moment, which are suitable for a mechanical harvest. In addition, fruits for processing should have certain characteristics that are related to processing quality, such as high viscosity, dry extract, pH value and high value of total soluble acids, and so on. Indeterminate habit is typical of fresh market cultivars in a greenhouse. Important characteristics for fresh market cultivars are, for example, long shelf-life, external quality of fruits (like shape and color) and internal quality fruits (like flavor, sweetness, and juiciness) [4].

Tomato is one of the most widely grown and eaten food crops in the world, with an annual global production of about 50 million metric tons. It is one of the most popular vegetable garden crops. India is the second largest vegetable producer after china with 11% production share in the world. It is second largest producer of tomato followed by potato at global level [5]. It is a rich source of vitamins A, B and C. It has medicinal values and used for blood purification and cure of digestive ailments. Tomato is marketed and used either fresh or processed [6]. These two uses have resulted in two distinct industries

for the crop, each with its distinct set of cultivars and crop production and management systems. Fresh tomato is produced either in the field or in greenhouses (it is the leading greenhouse produced vegetable in the world). It is available year round and abundant in summer months in warmer regions of the world. In Western Europe and other colder regions, greenhouses are used to extend the availability of this crop. The surge in the popularity of tomato is attributable largely to the growth in the fast food industry and increased popularity of tomato-based foods such as a pizza [4]. The tomato is considered a protective food because of its particular nutritive value, as it provides important nutrients such as lycopene, beta-carotene, flavonoids, vitamin C and hydroxycinnamic acid derivatives. Furthermore, this crop has achieved tremendous popularity especially in recent years with the discovery of lycopene's anti-oxidative activities and anti-cancer functions [7,8]. Thus, tomato production and consumption are constantly increasing. It is noteworthy that tomatoes are not only sold fresh, but also processed as soups, sauces, juices or powder concentrates. The tomato ranks 7th in worldwide production after maize, rice, wheat, potatoes, soybeans and cassava, reaching a worldwide production of around 160 million tons on a cultivated area of almost 4.8 million hectares in 2011.

Owing to high food value, the request and demand on tomatoes is rising day after day. However its production is affected by many types of stresses (biotic and abiotic stress) like diseases that caused by fungi, bacteria, viruses and nematodes. There are many environmental stresses, which influence negatively on the growth and production of crops [9]. Moreover, there are various factors, which limited the production and growth of tomato such as high temperature, draught, salinity and its vulnerability to frequent insect and pest attacks. Diseases infestations are well known factors that decrease crop yields and expand production costs. The development and improvement of stress tolerance of crops are main objectives for plant molecular and genetic breeding. Genetic engineering techniques can play an important role in the development of disease resistant cultivars. Diseases infestation is mostly controlled by using of chemicals, which occasionally reaches the level of toxicity. So, currently it is evident that improvement of this crop is a critical task to overcome the constraints of tomato production.

## Genetics and Breeding of Tomato

### Floral biology

Grown under optimal conditions, tomatoes have a 95 to 115 day lifecycle. The first flowers will appear and open 7 to 8 weeks after seeding and mature fruits will follow 6 to 8 weeks later. Tomatoes have perfect flowers that contain both functional male and female parts. Flowering can occur for weeks, a feature of tomatoes that facilitates the ability to make crosses between varieties with distinctly different maturities. Normally at least 4 to 8 flowers are borne on each inflorescence, and a single tomato plant may produce as many as 20 or more inflorescences over a season, giving you ample opportunities for making crosses.

The tomato flower is normally perfect, having functional male (anthers) and female (pistil) parts. Present cultivated tomato varieties form a tight protective anther one surrounding the stigma, which greatly reduces the possibility for natural cross fertilization. Outdoors flower movement aided by wind is sufficient to release pollen, but under greenhouse conditions, manual variation of open flowers is required to effect pollination and fruit set. Genetic and environmental modification of stigma position can affect both fruit set and degree of

cross fertilization [10]. In older standard and heirloom varieties, and often in cherry types, the degree of natural cross-pollination can be much higher than the occurrence in modern standard varieties. Older standard and heirloom varieties often have longer styles, pushing the stigma either flushes with or sometimes beyond the tip of the anther cone. This arrangement facilitates higher rates of natural cross-pollination ([www.seedalliance.org](http://www.seedalliance.org))

Emasculation for the purpose of controlled pollination must be done approximately one day prior to anthesis of flower opening to avoid accidental self-pollination. At this time, the sepals have begun to separate and the anthers and corolla are beginning to change to from light to dark yellow, characteristics of fully ripen flowers. The stigma appears to be fully receptive at this stage, thus allowing pollination immediately after emasculation [11]. With favourable environmental conditions, 200 or more seed may obtain from a single pollination. Generally, under greenhouse conditions, no protection is required following emasculation prevent uncontrolled crossing. Making controlled pollinations under field conditions may be less efficient than under greenhouse environments because hot, drying winds may cause rapid desiccation of the exposed pistil before fertilization is achieved. Flowers are emasculated between 55 and 65 days after planting. Flower buds from the second cluster which would open within 2-3 days are selected for emasculation. Pollen is collected before it is shed. The anther cones are removed from the flowers and placed in suitable containers (e.g., glassine, cellophane, or paper bags) [12]. The stigma is ready for pollination when the corolla of the emasculated flower turns bright yellow. Repeat the pollination 2-3 times a week for 3-5 weeks. Usually, successful pollinations are visible within one week (fruit starts to enlarge). Thirty fruits should be allowed to develop per plant for large-fruited cultivars; the number of fruits may be up to 50 for small-fruited cultivars [13].

### Genetics of tomato

Tomato is considered as a member of the family *Solanaceae*. The botanical name of tomato is *Lycopersicon esculentum* Mill and is a diploid plant with  $2n=2x=24$  chromosomes. Great advances in tomato genetics have been achievable because of the understanding of mating systems and the possibility of controlled hybridization within and among species, the naturally occurring variability in the species, the occurrence of self-pollination that leads to the expression of recessive mutations, the lack of gene duplication, and the possibility to easily identify the 12 chromosomes [14]. New methodological approaches like molecular mapping of important agronomical characters and the development of advanced-backcross and introgression lines have provided powerful tools for the improvement of the tomato crop and to understand the processes of domestication.

The cultivated tomato genome has been selected as a model for the *Solanaceae* family due to its simple diploid genetics, small genome size, short reproduction period, adjusted transformation methodologies, and the availability of a great diversity of genetic resources within the cultivated species and in wild related species [2]. The tomato genome size (1C amount) is generally considered as approximately 95 pg of DNA [14]. Cultivated tomato has been chosen for an international sequencing project due to its small genome size compared with other species of the *Solanaceae*.

The cultivated tomato is extremely genetically poor, having suffered severe genetic bottleneck as the crop was transported from its center of origin and on its path of domestication through Central America to Europe. One estimate indicates that modern tomato contains less than

5% of the genetic variation of its relatives. Molecular genetic studies show a paucity of polymorphism in cultivated tomato [14].

Tomato genetics is quite advanced. Qualitative genes and quantitative trait loci (QTLs) for the domestication syndrome traits (growth habit and fruits traits) have been identified. One of the most dramatic changes in tomato through domestication is fruit size. Wild tomato has tiny berries while modern tomato cultivars are large and succulent. The locus codes for a negative repressor of cell division and mutations in the promoter sequences are responsible for the changes from small to large berries. Several loci have been identified for fruit shape. The ovate gene is responsible for the transformation from round to elongate or pear fruit shape, while the sun and fs 8-1 loci are responsible for elongated and square fruit shapes. Domestication has triggered a range of traits (morphological and physiological) that distinguish domesticated crops from their wild ancestor. Studies on the domestication process, not only of tomatoes but also in the cases of maize and rice revealed that rapid phenotypic divergence is often controlled genetically by a relatively small number of loci [15].

Self-incompatibility is a common feature of the wild relatives of the tomato, and is transmitted to hybrids with *L. esculentum*. Self-incompatibility is of the *Nicotiana* type conditioned by a single locus. Genetic male sterility has also been reported frequently within the genus and many loci producing male sterility have been identified and described [14]. The tomato has proved to be an ideal plant for genetic studies because of its relatively simple reproductive biology, its ease of culture, and the wealth of genetic variation in cultivated and wild forms. Natural genetic diversity is the fuel of evolution. No evaluative forces or adaptation to environment changes can apply without it [16].

### Tomato breeding

Breeding technologies are critical for improving crop production in our changing world with an exponentially growing population and in the face of extreme environmental changes [17]. The development of molecular biology and later of “omics” sciences and bioinformatics has offered substantial opportunities for enhancing the effectiveness of classical plant breeding programs. Molecular and bioinformatics tools can either be integrated into traditional breeding schemes to efficiently analyze large numbers of traits and crosses during the early seedling stage, or to generate new breeding schemes and programs previously not feasible. Among the fruit bearing plants, tomato has been preferentially selected to study the process of fruit development and significant progress in our understanding of the molecular basis of fruit set and development has been made due to advances in functional genomics techniques and molecular tools [18]. Advances in genetics and genomics improved the understanding of structural and functional aspects of plant genomes [19,20].

### Breeding objectives

**Fruit yield:** Yield is the most important breeding trait of crops. For fruit-bearing plants such as *Solanum lycopersicum* (tomato), fruit formation directly affects yield [21]. The final fruit size depends on the number and volume of cell layers in the pericarp of the fruit, which is determined by the degree of cell division and expansion in the fertilized ovaries. Thus, fruit yield in tomato is predominantly determined by the efficiency of fruit set and the final cell number and size of the fruits. Through domestication, tomato fruit yield has been markedly increased as a result of mutations associated with fruit size and genetic studies have identified the genes that influence the cell

cycle, carpel number and fruit set. Yield increase has been one of the most important objectives of tomato breeding programs. The exploitation of heterosis and the development of hybrids play a critical role in yield increases. Breeders prefer to develop F1 hybrids, not only for heterosis, but also for their uniformity and the protection against illegal reproduction [22].

**Resistance to diseases and pests:** One of the common breeding objectives in tomato is breeding for resistance to the most destructive pests and pathogens. With the release of tomato genome sequences, a significant advance in exploitation of polygenic resistance could be obtained if molecular markers to all the known genes for resistance are available [23]. The development of disease resistant tomato cultivars is perhaps one of the most important contributions of modern plant breeding to tomato improvement [23]. Selection process and the sequence of field, lab, greenhouse and molecular marker protocols applied by AVRDC-The World Vegetable Center (AVRDC) to a segregating population, which led to the development of fresh market tomato lines resistant to late blight, tomato yellow leaf curl disease, bacterial wilt, *Fusarium* wilt, gray leaf spot, and Tobacco mosaic virus (TMV) [24]. Resistance to some pests and pathogens has been transferred from the wild into cultivated species. For example, the resistance to *Cladosporium fulvum* was obtained from *S. pimpinellifolium*. Other diseases of interest to breeders include late blight resistances, *Fusarium* wilt, and tomato spotted wilt virus [23].

Insect resistant breeding in tomato has not been as successful as disease resistance breeding. The difficulty does not appear to be due to restricted variability for insect resistance, as a matter of fact, the genus *Lycopersicon* is replete with good reports on resistance to various mites and insect pests [25]. Several reasons attribute for lack of progress in insect resistance breeding; first of all insect resistance has traditionally received low priority in applied breeding programs because the use of pesticides has effectively controlled most of the major insect pests of tomato; in addition the screening and selection methods to exploit the existing genetic variability for insect resistance are difficult to develop [26].

**Tolerance to heat and drought stress tolerance:** Mutation breeding is an important breeding approach for abiotic stress tolerance in crop plants. In tomato, Firon et al. [27] reported that never ripe pollen grains exhibited higher heat-stress sensitivity manifested by a significant reduction in total number of pollen grains, reduction in number of viable pollen, and elevation in number of nonviable pollen, compared with wild-type plants. Heat- and drought-resistant tomato is required in tropical and subtropical environments; a combination of traditional breeding protocols and marker-assisted breeding will become routine for heat- and drought-resistant tomato production. For this to succeed, adequate and long-term research is necessary, scientific results have to be delivered, best approaches utilized, and effective methods sustained to overcome the effects of abiotic stresses on tomato [28].

**Fruit quality:** This breeding objective includes physical characteristics like size, shape, and color, as well as chemical factors like soluble solids, acidity, taste, and sensory factors. Fresh market producers are interested in the fruit ripening shelf-life of fruits. Fruit ripening affects other quality traits like color, flavor, and soluble solids content. Genetic manipulation of sugars and acids has resulted in the improvement of fruit flavor. Flavor is the sum of the interaction between sugars, acids and a set of approximately 30 volatile compounds [29]. Although flavor is a complicated trait, it has been shown that significant improvement in tomato flavor can be attained



by increasing the sugar and acid contents in tomato fruits by genetic manipulation. However, breeding for volatiles has not yet been performed intensively, as little is known about the relations between flavor, aroma and volatiles [30].

The nutritional quality of tomato is mainly determined by its lycopene and vitamin C and E contents. Most researchers at present focus on the increasing the level of lycopene, and transgenic approaches have been used in breeding with positive results. Wild tomato accessions rich in lycopene have been identified, making them a promising resource in tomato breeding programs [31]. For example, the average level of lycopene in *S. pimpinellifolium* is five times higher than that in cultivated tomatoes.

**Methods of tomato breeding:** The most breeding technique to improve tomato has been hybridization followed by pedigree selection. Back cross breeding has been the method of choice when desirable traits are to be transferred from the wild species to or from relatively unimproved cultivated varieties. In some breeding programs, combinations of methods such as pedigree breeding and single descent have been found to be a useful approach [32].

**Mass selection:** Mass selection involves selection of a number of phenotypically superior plants, fruits or seeds from the field population, harvesting and bulking their produce together for sowing the next year's crop and repeating this process till desired characters are achieved. This may be achieved by simply growing the variety in the field and roughing out the undesirable type. At maturity, the remaining plants (presumably the good plants) are bulked. A modification is tagging only the best plants in the field and bulk harvesting them at maturity. The two methods are essentially similar, the only difference being in the level of selection intensity. Modern plant breeding usually employs mass selection to preserve the characteristics of established varieties [33].

**Pedigree method:** The pedigree method of plant breeding involves making a controlled cross followed by several successive generations of single plant selections. The goal is to develop at least one new variety from a single cross [4]. Although the pedigree method is a reliable and successful means to developing new tomato varieties, it can be genetically restrictive for on-farm and diverse system breeding work [2]. The pedigree method involves visual selection among individual plants in early generations, because the pedigree method uses selection in each generation, and each generations must be known in an environment where genetic differences will be expressed (greenhouses and off season nurseries may not be useful). Pedigree selection produces new cultivars faster than mass selection and appropriate for tomato [1].

**Development of hybrid tomato varieties:** Hybrid varieties were originally popularized among cross pollinated crops such as maize but the idea has caught on among a number of self-pollinated crops, like tomato, even though the evidences on heterozygote advantage (heterosis) have not been unequivocal. It is true that F1 hybrids exhibit favorable traits such as uniformity and to some extent, better resistance to diseases, but their advantages over the standard cultivars have not been as great as in cross pollinating species. The development of F1 hybrids in self-pollinated crops follows to a large extent scheme used for cross pollinated species [34].

**Biotechnology in tomato breeding:** Conventional breeding techniques are still expected to be the mainstay most future breeding

efforts to exploit the variability in the cultivated and wild relatives of tomato. Additional improvements in the traditional techniques may be expected to facilitate the breeding process but, it is safe to say that the limits of conventional breeding methods have [35]. Traditional improvement methods are time-consuming and troublesome due to the time of breeding, and there is a problem with the choice of criteria appropriate for breeding purposes. Thus, the establishment of simple and efficient regeneration systems is a fundamental prerequisite of taking advantage of cell and tissue culture for genetic improvement (genetically transformed plants for commercial applications). The *in vitro* culture of the tomato has been successfully used in different biotechnological application including the clonal propagation of high-value commercial cultivars, virus-free plants, and genetic transformation [36-38].

In genetically improving tomatoes will have to explored, it appears that the promise of new field of biotechnology in tomato breeding. Advanced tomato breeding lines are now available that resist the major diseases such as bacterial wilt, tomato mosaic virus and nematode, are tolerant to the hot new tropical conditions, and bear fruits that are firm, improved size and resistant to cracking [39].

Since tomato is a relatively simple system for transformation with *Agrobacterium tumefaciens*. The first commercially produced genetically modified food crop was tomato, called the Flavr Savr. It was developed by the Calgene Company in 1992, after 10 years of breeding work. The fruits were slow to rot but skin softening was not altered, making it still susceptible to bruising and bursting during transportation and handling [31]. Another problem with the new product was that the tomato variety used in the breeding project was not very tasty to start with, making the transgenic tomato bland and less acceptable to consumers than the conventional types. Crossing the GM tomato with a tastier non-GM tomato may have corrected the problem [40].

Genetically modified technology is widely acclaimed as being able to produce upgraded crops, including tomatoes, more rapidly and efficiently than selection breeding and therefore has the potential to reduce food shortages [39]. The genetic engineering allowed for increased productivity by enhancing efficiencies of metabolic or photosynthetic pathways [41]. So far, transgenic tomato lines have been generated with enhanced resistance for wide range of stresses, including abiotic and biotic ones [42]. This has become possible through the over expression several genes or TFs. Additionally, understanding the underlying physiological process in response to different stresses could help in determining what promoter or TFs would be appropriate to use for transformation [43]. It should be pointed out that constantly expending knowledge regarding the physiological and genetics basis of stress tolerance, along with genetic transformation technologies, could allow for essential progress in the development of tomato cultivars with improving stress tolerance. Moreover, using GM technology, researchers are able to obtain tomato fruits with improved nutritional and organoleptic values [44].

## Achievements in Tomato Breeding

Several achievements in Tomato Breeding are summarised in Table 1.

Variety	Organization	Characteristics	Breeding method
Pusa Ruby	IARI New Delhi	Indeterminate, early, fruit flattened, medium size processing purpose	Hybridization
Pusa Early Dwarf	IARI NewDelhi	Plant dwarf, determinate, early maturing, table and processing purpose	Hybridization
Hisar Arun	Hau, Hisar	Extremely early and high yielding, concentrated flowering and fruiting, round	Hybridization
Hisar Anmol	HAU, Hisar	Field resistance to tomato leaf curl virus, plant determinate,	Hybridization
Pusa Hybrid-1	IARI	Fruit set at high night temperature	Hybridization
Pusa Divya	IARI	Developed using male sterile line	Hybridization
Arka Vikas	IIHR Bangalore	Plant indeterminate, suitable for fresh market, fruit suitable for drought condition	Selection
Roma	America	Determinate habit, pear shaped fruit, suitable for distant market	Introduction
Sioux	American	Suitable for growing in the hills	Introduction
Rakshita	IAHS	Indeterminate, medium sized fruit, suitable for hilly areas	Heterosis
Naveen	IAHS	Early, high yielding, processing hybrid	Heterosis
PKM 1	TNAU	Fruits are flat round and suitable for long distance transport, yield is 30-35 tonnes/ha	Mutation
NDT 5		Suitable for processing	Selection
Caro Red		10 time more beta carotene than the recurrent parent	Back cross
Flavr Savr	Calgene	Delayed softening	Biotechnology
8805R	BeijingUniversity	Delayed softening	Biotechnology
ARP tomato d2	MARC/EIAR (2012)		

**Table 1:** Achievements in Tomato Breeding. Source (Danailov [45]; Gerszberg et al. [39] advanced in tomato breeding).

## Summary and Conclusions

Tomato (*Lycopersicon esculentum* Mill.) is a self-pollinated diploid species with twelve pairs of chromosomes (2n=24). It belongs to the *Solanaceae* family with other frugally important crops such as pepper, eggplant and potato. Tomato is a rich source of vitamins (A and C), minerals (Ca, P and Fe) and a strong antioxidant against cancer and heart diseases. Cultivars for processing purposes are determinate growing and plants have a compact growth habit with grouped fruits ripening at a single moment, which are suitable for a mechanical harvest. In addition, fruits for processing should have certain characteristics that are related to processing quality, such as high viscosity, dry extract, pH value and high value of total soluble acids, and so on. Indeterminate habit is typical of fresh market cultivars in a greenhouse. Important characteristics for fresh market cultivars are, for example, long shelf-life, external quality of fruits (like shape and color), and internal quality fruits (like flavor, sweetness, and juiciness).

Tomatoes have perfect flowers that contain both functional male and female parts. The cultivated tomato genome has been selected as a model for the *Solanaceae* family due to its simple diploid genetics, small genome size, short reproduction period, adjusted transformation

methodologies, and the availability of a great diversity of genetic resources within the cultivated species and in wild related species.

The general breeding goals of tomato are fruit yield, fruit quality, and resistance to diseases and pests. Tomatoes are presented as a classical example for gene transfer from wild species into cultivated cultivars for improvement the qualitative traits. It was established that until now the achievements in tomato breeding are based on classical breeding-genetic methods and also, an essential change in the accelerated introduction of useful traits in the cultivars is not made. It is believable that conventional breeding wouldn't allow the increase of productivity in the future. The significant progress in molecular genetics and use of molecular marker techniques are established. Therefore, the combined application of traditional breeding and contemporary plant biotechnology methods including selection based on molecular markers marker-Assisted Selection might be valuable tools for tomato breeding.

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