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REVOLUTIONARY GENES IN THE GENUS LYCOPERSICON

Ruben L. Villareal

Professor and Dean, College of Agriculture, U.P. Los Banos, College, Laguna 4031

ABSTRACT

Tomato, an obscure ornamental plant from South America, is one of the most popular and widely grown vegetable crops in the world today. It has been ranked first among vegetable crops by various groups of scientists, policymakers and farmers because of its great potential to generate rural employment, stimulate urban employment, expand exports, improve nutrition of people, increase the income of farmers and save energy. Without doubt the remarkable transformation of this obscure ornamental plant to its current form is largely due to the numerous revolutionary genes which affect disease resistance, growth habit, fruit characters and adaptation. Some promising genes which are likely to influence the further development, of the dynamic tomato industry in the tropics include: genes that promote parthenocarpic fruit development, delayed ripening genes that improve storage life of tomatoes, genes that influence the breeding of genes that influence the breeding of low input cultivars and genes that govern drought resistance.

Introduction

The cultivated tomato originated in the New World where it reached a fairly advanced stage of domestication before it was transported to Europe and Asia (13). Its most likely ancestor is the wild cherry tomato (*L. esculentum* var. *cerasiforme*) which was found first throughout tropical and subtropical America and later in the tropics of Asia and Africa. In Asia, it is possible that the cultivated tomato was introduced in the Philippines by the Spaniards from Europe either shortly after its discovery by Ferdinand Magellan in 1521 or from Mexico at the initiation of the Galleon Trade between Acapulco and Manila in 1750. Very likely, trade between the Philippines and the neighboring countries of Japan, China, Malaysia, Indonesia and others was responsible for the spread of tomatoes in those places (21).

Tomato is grown in 2.8 million hectares over the world. In 1990, developed countries produced 55 percent of the total tomato production (38 million tons), although they occupied only 41 per cent of the growing areas (3). Developing countries, on the other hand, planted tomatoes in 1.7 million hectares producing 31 million tons representing 45 per cent of total production. The wide commercial growing of tomatoes attest to the successful utilization of the genus *Lycopersicon* germplasm in plant breeding. This germplasm has played a vital role in transforming tomato from an obscure ornamental plant into the most popular and widely grown vegetable in the world today (22). The same germplasm has been the source of numerous genes which have largely revolutionalized the development of a dynamic tomato industry throughout the world. For this reason, these genes are called revolutionary.

The primary purpose of this paper is to review such revolutionary genes and their utilization in tomato improvement with emphasis on tropical conditions.

THE GENUS LYCOPERSICON

The major source of variation being used until now for tomato improvement has been the cultivated tomato (*Lycopersicon esculentum* Mill) which is generally characterized as a genetically well-endowed species of the potato family (*Solanaceae*). Equally important sources of variation are the wild taxa of *Lycopersicon* which have been sources of useful genes including the following: *L. esculentum* var *cerasiforme* (Dun.) A. Gray, *L. pimpinellifolium* (Jusl. Mill., *L. cheesmanii* Riley, *L. chmielewskii, L. parviflorum, L. pennellii* (Corr.) D'Arcy (formerly *Solanum pennellii Corr.*), *L. hirsutum* Humb. & Bonpl., *L. peruvianum* (L.) Mill, and *L. chilense* Dun.

L. ESCULENTUM var *cerasiforme* (Dun.) A. Gray (15)

This botanical variety is small and cherry-fruited in both its wild and cultivated forms. The interior of a ripe fruit is red. It is widespread throughout the tropical and sub-tropical regions of the world.

L. PIMPINELLIFOLIUM (Jusl.) Mill. (15)

So far, this species is the most closely related to *L. esculentum* with respect to morphology and crossability. In fact, it crosses readily with *esculentum* and produces viable and fertile F_1's and subsequent generations. The fruits of this species are small, grow in clusters and turn to bright red when ripe. The interior of a ripe fruit is red. This species is also widely distributed throughout the tropical and sub-tropical regions of the world.

L. CHEESMANII Riley (9)

Unique because of its yellow-to-orange fruit and other morphological characters, this species is endemic to the Galapagos Islands. It crosses readily with *esculentum* but segregating generations are subject to low viability and reduced fruitfulness.

L. CHMIELEWSKII (12)

This species has slender stems, simple form of leaves and inflorescences. The interior of a ripe fruit is either green or whitish. It is native to a restrictive zone in the intercordilleran region of Apurimac and Ayacucho, Peru and prefers mesic conditions at mid-altitudes.

L. PARVIFLORUM (12)

This is a sibling species of *L. chmielewskii,* with which it shares many similar morphological traits, except for *L. parviflorum's* smaller flower and tendency to inhabit lower and more moist conditions. It occupies the same territory in Peru but extends farther northward, approaching the Ecuadorean frontier.

L. PENNELLII (Corr.) D'Arcy (15)

This is another green-fruited species that crosses easily but unilaterally with *L. esculentum.* Distribution of *L. pennellii* is limited to mid-elevations in the western drainages of Central Peru.

L. HIRSUTUM Humb. and Bonpl (15)

L. hirsutum has large robust plant size, dense hair and strong odor that distinguish it from all other species of *Lycopersicon.* The interior of a ripe fruit is either green or whitish. The species is native to the western watersheds of Peru and Ecuador but also extends its range east of the continent dividing Ecuador and Northern Peru.

L. PERUVIANUM (L.) Mill. (15)

This species has a green or whitish interior when ripe. It is self-incompatible, variable and so difficult to cross with *L. esculentum* that it is less exploited by plant breeders. *L. peruvianum* is widely distributed in Peru along the coast and western drainages, extending southward into northern Chile and northeastward irregularly into the canyon of Rio *Marañon.*

L. CHILENSE Dun. (15)

L. chilense closely resembles *L. peruvianum* but can be distinguished by several morphological traits. It is also self-incompatible and variable like *peruvianum.* Hybridization with *esculentum* are easier with *chilense* than with *peruvianum.* They overlap in their ranges but the range of *chilense* extends farther south in Peru. Although their ecological preferences are similar, *L. chilense* prefers dryer conditions.

The abovementioned, cultivated and wild taxa of *Lycopersicon* may be obtained upon request from the Asian Vegetable Research and Development Center (AVRDC). The Center maintains the largest collection of more than 5,000 accessions, including modern cultivars, older outmodeled cultivars, and primitive cultivars; wild forms of the cultivated species, and related wild species in addition to numerous breeding lines adapted to tropical environment (20). Moreover, the Tomato Genetic Stock Center at the Department of Vegetable Crops, University of California at Davis, stores at least 1,600 items and specializes in tomato species, genetic and cytological lines (15).

THE REVOLUTIONARY GENES

There are hundreds of tomato genes which greatly influenced the evolution of the current domesticated tomato and the subsequent development of the tomato industry. However, in this paper, only the most important genes representing disease resistance, growth habit, fruit character, adaptation, and other useful traits for the tropics will be reviewed.

Disease Resistance

Perhaps the greatest achievement in tomato breeding is the improvement of the disease resistance of the cultivated tomato. Collective efforts of scientists throughout the world resulted in the identification of resistant genes from wild taxa of *Lycopersicon*, understanding their inheritance, and successfully transferring them to tomato varieties that are grown both in the temperate and tropical countries. Most of these resistant genes were derived from wild relatives of the cultivated tomato (Table 1).

The behavior of a given wild allele in the *esculentum* background will not be known until it is transferred there (15). It takes enormous time and effort before the behavior of a wild gene is fully understood, and eventually utilized in a breeding program. In many instances, a desirable wild gene is associated with several undesirable traits and it takes several years and great difficulty to separate them.

The bacterial wilt resistance gene is a case in point. Scientists of the North Carolina State University spent at least 35 years before such gene from *L. pimpinellifolium* was transformed into a more usable form for practical breeding programs. Indeed, it is important to promote developmental plant breeding for purposes of utilizing useful genes from wild taxa. The developmental plant breeder in this case, incorporates the new genes in a relatively advanced form which is far more useful to the plant breeder than the original accession in which the desired genes were first discovered.

Table 1. Common tomato diseases in the tropics, source of resistances genes, and their mode of inheritance (15 & 24).

Diseases	*Source of gene(s)*	*Mode of inheritance*
Bacterial wilt	*L. pimpinellifolium*	complex
Bacterial canker	*L. pimpinellifolium*	complex
Bacterial spot	*L. pimpinellifolium*	complex
Early blight	*L. esculentum var. cerasiforme*	single incompletely dominant
collar-rot phase		
leaf spot phase	*L. esculentum var cerasiforme*	two or more recessive genes
Gray leaf spot	*L. pimpinellifolium*	complex
Late blight	*L. pimpinellifolium*	single dominant and complex
Leaf molds	*L. pimpinellifolium*	single dominant gene, pathogen is very mutable
Septoria leaf spot	*L. hirsutum*	single dominant plus one or more modifiers
Fusarium wilt race 1	*L. pimpinellifolium*	single dominant
Fusarium wilt race 2	*L. pimpinellifolium*	single dominant
Verticillium wilt	*L. esculentum var. cerasiforme*	single dominant
Spotted wilt virus	*L. pimpinellifolium*	single dominant
Tobacco etch virus	*L. pimpinellifolium*	single dominant
Tobacco mosaic virus	*L. peruvianum*	single dominant
Root-knot nematode	*L. peruvianum*	single dominant

Understanding how the different resistant genes are inherited has enabled plant breeders to utilize appropriate breeding techniques for transferring specific genes from wild sources to a horticulturally acceptable variety (Table 1.) Thus, it is now common to see in seed catalogues, especially in the U.S.A., Japan, Germany, the Netherlands and other developed countries, tomato F_1 hybrids or varieties with resistance to form 5 to 10 different diseases. Each of these are based on intelligent manipulation of an even larger number of genes that affect other traits of the hybrid or cultivar.

Growth Habit

In rice, the dwarfing gene from Dee-geo-woo-gen is known to have ushered the Green Revolution. The semi-dwarfing gene produces plants with short, stiff stems that help to resist lodging; short, upright leaves that allow the penetration of sunlight; and a heavy tillering capacity that aids in producing more panicles. Therefore, when grown under good management, the rice plant could yield 4 to over 8 t/ha which is more than twice the normal yield of the tall lodging susceptible rice varieties being grown by Asian rice farmers (1, and 24). In the tomato, the self-pruning (sp) plant habit has been principally responsible for revolutionalizing and saving form extinction the tomato industry in California, USA., when labor for handpicking tomatoes became scarce.

The determinate growth characteristic or self-pruning controlled by a single recessive gene (*sp*) is a spontaneous mutation which occurred in Florida in 1914 (13). Before the discovery of this mutant, processing tomato varieties had indeterminate growth habit. Thus, they were grown widely spaced and little fertilized, resulting in low yield per hectare. The mutant gene was successfully transferred to Sta. Clara Canner, an indeterminate processing variety. Determinate progenies from the cross of the determinate and indeterminate types resulted in the predominat tomato processing varieties used in California from the 1940's to the 1960's (21). Today all of California's tomatoes for processing are machine-harvested. California accounts for at least 85 per cent of the production in the United States.

The gene *sp* causes the plant to grow in an orderly, compact and determinate fashion that terminates with flower clusters. This gene also induces the plant to flower more abundantly, and to ripen faster than the normal or indeterminate type, thus allowing first the machine harvesting of processing tomatoes, and later of fresh market tomatoes, as well. Where manual labor is not a problem, it is common to harvest processing tomatoes from 3 to 7 times, as against once for machine-harvested tomatoes. Compact growth permits closer spacing and more judicious use of fertilizers, resulting in higher yield per hectare. Yield of processing tomatoes in the USA was 20 t/ha in the early 1960s; today, it is 65 t/ha. The same gene allows the Asian farmers to intercrop tomatoes with surgarcane and corn and efficiently grow them even with fruit trees like mangoes and papayas (21).

The indeterminate type (*Sp*), on the other hand, permits successful greenhouse production of trellised tomatoes in Europe, Japan and North America. This dominant gene allows trellised tomatoes to be trained with one or two stems and are grown for almost a year so that very high yields are obtained. For example, in Denmark and in the Netherlands where most tomatoes are grown in greenhouses, average yields were 318 to 361 t/ha in 1990 (3).

relates to case yields of products (i.e. the higher the solids, the higher the case yield). Breeders have been involved in programs to increase soluble-solids content in high-yielding cultivars. The high-solid breeding lines developed (11) from an inter-specific cross with *L. chmielewskii* has been used for this program.

Adaptation

Plant explorers have found wild relatives of the tomato in the tropical rain forests of South America, as well as in arid regions of its native Mexico (21), indicating wide adaptability of the tomato. In fact, tomatoes thrive at many latitudes and under a wide range of soil types, temperatures and methods of cultivation. Nevertheless, for optimum production, tomatoes require special genes to adapt to environmental stresses such as heat, wetness (excessive moisture), or dry and salty conditions as in coastal areas.

Heat tolerance – The AVRDC scientists have evaluated more than 4,616 accessions for their fruit-setting ability under hot humid conditions (19). Only 38 accessions coming from 15 countries and representing 1% of the total showed good to excellent potential as parents for heat tolerance breeding programs. Most of the aforementioned accessions belong to *L. esculentum* and *L. pimpinellifolium*. Fruit-setting ability under hot humid condition is due singly or in combination to the following characters: low stylar exertion, high pollen production and viability, high stigma receptivity, and good ovule viability. This observation suggests that the heat tolerance strengths of the different accessions should be combined into a single cultivar.

Moisture tolerance – Cultivars with the ability to set fruits at high temperatures also need moisture tolerance since the period of high temperature coincides with the period of high rainfall (21). Thus, the 38 heat tolerant accessions mentioned earlier could be used for moisture tolerance breeding programs. Another useful germplasm for this trait is the var. *ceresiforme* which is the only taxon of *lycopersicon* that survives, grows to maturity and produces fruits under extremely wet conditions (15).

Salt tolerance – In the Philippines, there are at least 125,000 hectares coastal saline soils (4) which can be made productive, if only salt-tolerant crop cultivars are available. Such possibility exists in the case of tomato. *L. cheesmanii* contributes this gene for salt tolerance (16). This species can withstand concentrations of up to 100 per cent sea water. The Institute of Plant Breeding in the Philippines has successfully transferred such gene, into some locally adapted cultivars and are now awaiting further evaluation.

Fruit Characters

Firmness – With mechanized harvesting of tomato, it is necessary to develop firm-fruited cultivars in view of the severe handling that the tomatoes would undergo (17). For example, in the hand-pick days, the fruits were transported in boxes which held less than 23 kg. With mechanical harvest, bins holding up to 680 kg were used. Today, large bulk tanks which contain about 11 tons of fruit are being used. A distinguishing characteristic of firm-fruited cultivars is their ability to remain in good physical condition for several weeks after becoming fully red. This trait has been controlled by genes that govern high levels of the alcohol-insoluble components of the fruits, a thicker outer pericarp, and a smaller-locular area. *L. cheesmanii* has been the source of gene for thick pericarp (15).

Removal from vine – The ease of fruit removal from the vine is another important trait for machine-harvest tomatoes since those difficult to remove remain attached to the vines even after passing through the shakers.

Pedicel retention – Pedicel or stem retention on the fruit is undesirable since pedicels damage other fruits in the bin by inciting wounds on the fruits. These wounds serve as entries for pathogens and eventually affect the flavor of the processed product. The jointless character (*j2*) from *L. cheesmanii* has been bred into processing cultivar to reduce stem retention (12). Jointless lines, however, leave a slight yield disadvantage and the *j2* gene makes separation of fruit from the vine difficult since the gene increases stem adhesion to the fruit (17).

Color – Color is controlled by several independent genes. Some of these genes are: 1) uniform gene (*u*) which eliminates the dark green shoulder of unripe fruit, its dominant allele (*U*) imparting the dark green shoulder of unripe fruit (8); 2) high beta-carotene gene (*B*) which makes the color of fruit more orange (8); 3) high pigment gene (*hp*) which intensifies chlorophyll, cartenoids and ascorbic acid content of fruits; and 4) the crimson gene (*og*) which partly suppresses synthesis of beta-carotene and thus improves color for certain products (2). The gene tangerine (*t*) makes the fruit flesh and stamens orange (8). The fruit skin, when colorless or lacking pigmentation (y), makes the fruit pink; when pigmented (y) it makes the fruit color red (8). The abovementioned genes were derived from spontaneous monogenic mutations of the cultivated tomato.

Unlike fresh market tomatoes in which color preferences differs from person to person, processing tomatoes require the more specific color of intense deep red to come up with the desired quality product. The combination of crimson (*og*) and high-pigment (*hp*) characters results in ripe fruit with beautiful intense red and with Vitamin A content which is 25% higher than that in standard cultivars (17). Associated with this combination, however, are the lack of seedling vigor and an open vine that allows sun damage.

Sugar – The most prevalent organic components of tomatoes are the reducing sugars fructose and glucose which constitute at least 50% of the total solids of most cultivars. Thus, processors are interested in soluble-solids content because it

PROMISING GENES IN THE TROPICS

Parthenocarpic Genes

Parthenocarpy is the production of fruits without fertilization, resulting in seedless fruits. In tomatoes, the development of parthenocarpic fruit is governed by a single recessive geen (*pat* or *pat-2*). One exciting possible application of this gene is to improve the yields of unfruitful cultivars where heat tolerant cultivars are unsuccessful due to excessive temperatures. These genes can also be incorporated into cultivars grown under protected cultivation (i.e. greenhouses and plastic tents) where unfruitfulness results due to high temperature and poor pollination.

Delayed Ripening Genes

The discovery of the nonripening (*nor*), ripening inhibitor (*rin*), alcobaca (*alc*) and never ripe (*Nr*) genes in mutants of *L. esculentum* shows promise of improving the storage life of fresh market tomatoes. These genes may be incorporated into tomato varieties bred for tropical growing conditions (i.e. heat tolerant with resistance to specific pests and diseases) to develop lines with extended shelf life. In the absence of adequate postharvest facilities in the country, regulation of ripening through genetic means is one way of reducing losses and increasing the percentage of marketable fruits; thus increasing production and profit.

Nonripening (nor) – The *nor* mutant was identified from an introduction, "Italian Winter" initially obtained by E.A. Kerr of the Horticultural Research Institute of Ontario (18). Other mutants, nor^2 and nor^3 have also been reported by Italian workers. The *nor* gene affects carotene synthesis and fruit softening. Sound fruits with this gene remain firm and green for a long time.

Ripening inhibitor (rin) – The *rin* mutant was first described by R.W. Robinson and M.L. Tomes in 1968 in an F_4 breeding line developed by H.M. Munger at Cornell University (18). It was the result of a spontaneous mutation at the *rin* locus and is linked with large sepal size (a condition termed as macrocalyx). Mature fruits with the *rin* gene remain firm and in good condition for several months after harvest.

Alcobaca (alc) – The alc is a slow ripening mutant described by N.R. Leal in 1973 and thought to have originated from Portugal (18). The time required to ripen mature green fruit on the vine was doubled in the alcobaca parent. Fruits picked before being mature green did not ripen. The gene imparts long storability of 20-90 days after ripening. Increased storability is accompanied by a sharp decrease in the rate of fruit softening during the storage of red ripe fruit (6).

Never ripe (Nr) – The *Nr* mutant was first described by L.L. Moris of the University of California at Davis (18). This gene permits fruits to turn red at normal times, but they develop red pigmentation slowly and never become deep red regardless of how long they stay on the plant or in storage. Fruits also retain the texture and low sugar content of mature green fruits.

Plant breeders of the Institute of Plant Breeding and the Department of Horticulture, UPLB College of Agriculture, are now undertaking a breeding program to transfer the aforementioned ripening genes to selected commercial and promising varieties with tropical adaptations (i. e. heat tolerance, resistance to major insect pests and diseases).

LOW INPUT GENOTYPES

The high cost of chemical inputs (i. e. fertilizers, fungicides, insecticides) has been a deterrent to the widespread use of modern varieties. This raises the question of whether we can develop tomato varieties that might produce more acceptable yields than traditional varieties with only a minimal increase in inputs. This means that high dependence on chemical inputs can be reduced through breeding of pest-resistant and stress-tolerant varieties as well as varieties which are efficient utilizers of nutrients in the soil.

Multiple disease resistance - A natural consequence of planting disease-resistant cultivars is the reduction in the use of chemical pesticides. The more resistance genes that are incorporated into a commercial cultivars, the more is the savings in the cost of pesticides. As discussed under the section DISEASE RESISTANCE, there are now several genes which have been transformed into a more usable form for easy use by plant breeders. Thus, cultivars or breeding lines with appropriate genes (i. e. leaf molds, bacterial spot, septoria leaf spot and gray leaf spot) should be transferred to selected local commercial varieties with tropical background. in the case of the bacterial wilt problem, the classification of *P. solanacearum* into, Biovars I, III and IV by IPB's pathologists, has explained why resistance in different cultivars varied with location. This means that it is possible now to breed for more location-specific tomato that carries resistance to a specific wilt biovar. For instance, Biovar I is more prevalent in cooler areas indicating that tomatoes grown in this area should carry resistance genes to Biovar I. Thus, commercial varieties with tropical background should be provided with resistant genes to Biovar I. Biovar III and Biovar IV of *P. solanacearum* since current cultivars (i.e. those developed by AVRDC and IPB) are susceptible to these biovars.

Low-nutrient requirement – The concept of genetic control of efficiency of nutrient utilization in tomatoes was investigated within naturally occurring variation among 146 strains comprising 81 plant introductions, 44 plant selections and 21 commercial cultivars (7). Results of this study show that efficient strains produced as much as 45% more dry weight than inefficient strains, an indication that tomato strains vary in the efficiency of N utilization. This study should be of considerable interest to plant breeders, producers and consumers, especially in developing countries for at least three reasons: current high cost of fertilizers (organic or inorganic), energy conservation, and possibility of extending similar studies to other important nutrients such as P, K, Mg, Ca and others.

Drought resistance - Assured irrigation water is desirable in growing tomatoes in the tropics. Even during the rainy season, rainfall distribution can be erratic. The problem is aggravated in the dry season when precipitation is almost non-existent. Thus, growing a commercial crop of tomatoes in the dry season is impossible, unless farmers have supplemental water available. Moreover, farmers risk in growing tomatoes is reduced if they can plant cultivars with resistance to drought. Such can happen if drought resistance from *L. pennellii* is bred into commercial cultivars. A recent study confirmed the drought resistance of *L. pennellii* (5). For example, all *pennellii* accessions had at least 57% fruit set compared to none in the check cultivar when the entries were irrigated every other week. This species can cope with dryer conditions through the capacity of its leaves to resist water loss (15).

Conclusion

The development of the cultivated tomato from its ornamental status into the more popular and widely grown vegetable crop has been a long and arduous process. The increasing cultivation of this crop both in terms of hectarage and volume of production in different parts of the world attests to its importance as source of income in the sector involved with the tomato industry.

The growth of the tomato industry was significantly due to the identification and utilization of revolutionary genes among the different taxa of the genus *Lycopersicon* by plant scientists/breeders from different countries. Through skillful breeding work, they were able to utilize those revolutionary genes to produce varieties that possess desirable characteristics. These genes include those that impart disease resistance, genes that control the growth habit of the plant to suit different growing conditions, genes responsible for the expression of desired fruit characters such as firmness, color, removal from vine, and sugar content, and genes that control the plant's adapatability to varied growing conditions (e.g. saline and drought environments). There are also a number of promising genes that can truly revolutionize the tomato industry in the tropics, such as genes that promote parthenocarpic fruit development, delayed ripening genes that improve storage life of both processing and fresh market tomatoes, genes that influence the breeding of low input cultivars and genes that govern drought resistance in order to minimize the risk of growing tomatoes were irrigation water is uncertain.

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