4 Tomato Breeding

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INTRODUCTION

The cultivated tomato (*Lycopersicon esculentum* Mill.) is a relatively recent addition to the world's important food crops. Within the past century, it has become one of the most popular and widely consumed vegetable crops, with an annual world production approaching 50 million MT (Table 4.1). It is also America's most popular and pampered home garden vegetable, occupying space in more than 90% of the home gardens planted in the United States (*6*). Per capita consumption in the United States has more than tripled in the past 50 years to approximately 56 lb per person. Its versatility in fresh or processed form has played a major role in its rapid and widespread adoption as an important food commodity.

The tomato is a tender perennial that is almost universally cultivated as an annual. Despite its susceptibility to frost, the tomato can be grown outdoors successfully from the equator to as far north as Alaska. Cultivars have been developed for a variety of different environments, methods of production, and food uses. Its adaptation to fit many diverse

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TABLE 4.1. World Production of Tomatoes[a]

	Area ($\times 10^3$ ha)	Production ($\times 10^3$ MT)	Yield (MT/ha)
World	2,404	49,201	20.5
Continent			
Africa	354	4,769	13.5
North and Central America	314	9,847	31.3
South America	135	2,854	21.2
Asia	706	11,251	15.9
Europe	490	13,871	28.3
Oceania	10	208	21.3
Leading countries			
1. United States	182	7,663	42.1
2. USSR	395	6,400	16.2
3. Italy	126	4,294	34.1
4. China	284	3,930	13.8
5. Turkey	108	3,136	29.2
6. Egypt	139	2,421	17.5
7. Spain	64	2,050	32.0
8. Greece	40	1,669	41.8
9. Brazil	56	1,500	26.6
10. Rumania	72	1,393	19.3

[a]After Yamaguchi (*122*).

uses and environments is a reflection of the great wealth of genetic variability existent in the genus *Lycopersicon* and the relative ease with which this diversity can be exploited in applied breeding programs.

Tomatoes are readily available in the U.S. marketplace in fresh and processed form throughout the year. The fresh and processed tomato industries are distinct entities, and cultivars and systems of crop management are generally unique for each.

Fresh Tomatoes

Fresh tomatoes are available in the United States in greatest supply during the summer months (June–September). Although almost all states grow fresh tomatoes to some extent, Florida, California, and Mexico provide the bulk of annual supplies, largely as a result of their long cropping seasons and/or mild winters (*54*). Fresh tomatoes also rank as the leading greenhouse-produced vegetable; however, less than 5% of the annual fresh production in the United States is derived from this source. In Western Europe climatic limitations require more extensive use of greenhouse facilities to extend availability of fresh tomatoes throughout the year.

Processed Tomatoes

Processed tomato products reach the consumer in a variety of forms or as ingredients in a wide array of processed commodities. A major portion of the per capita increase in tomato consumption in the United States during the past four decades is attributable to increased use of processed tomato products (Table 4.2). The dramatic growth of the fast-food industry and the rapid rise in popularity of food items containing tomato, such as pizza, have fostered a steady rise in consumption of processed tomato products.

TABLE 4.2. Fresh and Processing Tomato Production and Yields in the United States (1940–1983)[a]

	Fresh market		Processing	
Period	Volume (cwt × 10^6)	Yield (cwt/acre)	Volume (tons × 10^6)	Yield (tons/acre)
1940–1943	14.6	66	3.4	5.4
1944–1947	17.1	64	3.5	5.8
1948–1951	17.6	75	3.2	8.2
1952–1955	19.3	84	2.8	10.1
1956–1959	19.5	93	3.0	12.1
1960–1963	20.2	127	4.4	15.3
1964–1967	20.6	135	4.7	16.3
1968–1971	18.8	130	5.6	19.8
1972–1975	19.7	152	6.8	21.2
1976–1979	21.8	172	6.9	21.6
1980–1983	26.2	209	6.6	23.7

[a]Adapted from Brandt *et al.* (*17*) and Sullivan (*104, 105*).

California is by far the leading producer of tomatoes for processing, supplying more than 85% of the processed tomato products manufactured in the United States each year. Italy, Spain, and Greece are major suppliers of processed tomato products to the world marketplace. Production in these areas is favored by long, dry growing seasons that facilitate crop management, improve predictability of supplies, and provide a consistent quality of raw product for processing purposes.

The tomato does not rank high in nutritional value. By virtue of volume consumed, however, it contributes significantly to dietary intake of vitamins A and C as well as essential minerals. Its popularity is due in large measure to its versatility and the variety it lends to our diet. As an ingredient in numerous foods, from lasagna to a well-spiced Bloody Mary, the tomato has truly become a dietary staple.

ORIGIN AND EARLY HISTORY

Numerous wild and cultivated relatives of the tomato can still be found in a narrow, elongated mountainous region of the Andes in Peru, Equador and Bolivia as well as in the Galapagos Islands. These primitive relatives of the edible tomato occupy diverse environments based on latitude as well as altitude and represent an almost inexhaustible gene pool for improvement of the species (*2*).

Domestication and cultivation of the tomato appears to have first occurred outside its center of origin by early Indian civilizations of Mexico. The cultivated tomato is common in Peru today; however, it is used as a food primarily by the non-Indian population. Where it is cultivated by the native Indians of Peru, it appears to be a recent addition to their diet. Quite the contrary is true in Mexico, where the tomato is widely used by Indians and great diversity is evident in cultivars being grown. Furthermore, the name "tomato" comes from the Nahuatl language of Mexico, and variants of this name have followed the tomato in its distribution throughout the world (*40*).

The first written account documenting the arrival of the tomato in the Old World appeared in 1554 by the Italian herbalist Pier Andrea Mattioli. The first cultivars introduced to Europe probably originated from Mexico rather than South America. These early introductions were presumably yellow, rather than red in color, since the plant was first known in Italy as *pomi d'oro* or golden apple. It was also known as the love apple, *pomme d'amour,* in France. This appealing name did little, however, to hasten its acceptance as a food crop. In most places, the tomato was remarkably slow to gain acceptance, except as an ornamental curiosity. Apparently the tomato's similarity to familiar poisonous members of the nightshade family such as mandrake and belladonna caused concern over its safety as a food. Such unfounded superstitions persisted widely, even into the twentieth century and undoubtedly had a major impact in slowing its adoption as a useful and nutritious food crop.

The first recorded mention of the tomato in North America was made in 1710. It was apparently brought from the Old World by early colonists but did not gain widespread acceptance, presumably because of the persisting view that its fruits were unhealthy and poisonous. Thomas Jefferson wrote of tomato plantings in Virginia in 1782 and makes frequent reference to its planting and culinary uses in later writings. However, it was not until 1830 that the tomato began to acquire the popularity that has made it the indispensable food commodity it has become today. Its history as a commercially processed commodity began at Lafayette College at Easton, Pennsylvania, in 1847, where the commercial ''canning'' possibilities of the ''love apple'' were first demonstrated. From this humble beginning, the tomato has become the leading processed vegetable crop in the United States today.

The increasing popularity of the tomato resulted in a rapid proliferation of new cultivars. In 1863, 23 cultivars were known; however, within two decades the number of cultivars available to growers had increased to several hundred (*61*). Liberty Hyde Bailey of the Michigan Agricultural College initiated a testing program in 1886 to clarify the classification of tomato cultivars and reported that much of the confusion was a result of indiscriminate renaming by seed suppliers (*61*).

Livingston was probably the first American to recognize the need for constructive breeding. Between 1870 and 1893, he introduced 13 cultivars developed by single plant selection to meet specific requirements of tomato producers and consumers. The worth of useful new cultivars was clearly appreciated during this early history of the tomato as evidenced by the fact that seed of the cv. Trophy was sold for 5 dollars per packet of 20 seeds when it was introduced in 1870.

The early progress of tomato breeding in the United States is poorly documented and is best illustrated by the length of time cultivars remained in demand and listed by seed suppliers (*61*). On this basis, the cvs. Red Cherry, Red Pear Shaped, and Trophy represented the most important, popular, or persistent cultivars during the early history of the tomato in the United States. Few, if any, of these cultivars are of commercial significance today; however, they represent the foundation upon which modern-day cultivars were developed.

Extensive efforts are under way to maintain old cultivars and the invaluable wild relatives that have served as the progenitors of the present-day tomato. The U.S. Seed Storage Laboratory in Fort Collins, Colorado, has the responsibility of maintaining seed of old cultivars. Tomato introductions from foreign countries and from germplasm collection expeditions are maintained by the North Central Regional Plant Introduction Station at Ames, Iowa, and are available to private and public breeders working on tomato improvement.

TABLE 4.3. The Species of the Genus *Lycopersicon*[a]

Species	Common name	Somatic chromosome number	Reproductive features[b]
L. esculentum	Common tomato	24	SP
L. pimpinellifolium	Currant tomato	24	SP + CP
L. cheesmanii	Wild species	24	SP
L. parviflorum	Wild species	24	SP
L. chmielewskii	Wild species	24	CP
L. pennellii	Wild species	24	SI
L. hirsutum	Wild species	24	SF, SI
L. chilense	Wild species	24	SI
L. peruvianum	Wild species	24	SI

[a]Adapted from Rick (*81*).
[b]SP, self-pollinated; CP, cross-pollinated; SF, self-fertile; and SI, self-incompatible.

BOTANICAL CLASSIFICATION

The tomato is a member of the nightshade family (Solanaceae) and the genus *Lycopersicon,* which contains several species commonly divided into two subgenera. The subgenus *Eulycopersicon* includes red-fruited species and *Eriopersicon* mostly green-fruited types. At present, nine species are recognized as distinctive entities within the genus (Table 4.3). Controversy still exists, however, regarding taxonomic classification of the wide variability found within the genus *Lycopersicon.* All members of the genus are annual or short-lived perennial herbaceous diploids with a somatic chromosome number of 24. Essentially all cultivated forms of the tomato belong to the species *esculentum.*

The relatives of the cultivated tomato have proven to be an invaluable source of germplasm for plant improvement (*76*). Interspecific crosses between *L. esculentum* and *Lycopersicon pimpinellifolium* are easily made and show few, if any, barriers to gene exchange. Both members of the subgenus *Eulycopersicon* are also compatible with members of the subgenus *Eriopersicon,* but in some cases only when the latter functions as the pollen parent (Table 4.4). Where such unilateral incompatibility exists, the F_1 interspecies hybrid can be crossed to *L. esculentum* only when the F_1 functions as the male, and to the wild parent only when the F_1 is used as female. The self-incompatibility common to many of the wild species is also transmitted to interspecies hybrids, and aberrant genetic segregation is common in such wide crosses (*58*). Embryo abortion may occur in crosses of *L. esculentum* with *Lycopersicon peruvianum,* but this barrier can be overcome by use of

TABLE 4.4. Survey of Intra- and Interspecific Breeding Barriers in *Lycopersicon*[a,b]

♀\♂	*L. esculentum*	*L. pimpinellifolium*	*L. hirsutum*	*L. chilense*	*L. peruvianum*
L. esculentum	+	+	+	EA	EA
L. pimpinellifolium	+	+	+	EA	EA
L. hirsutum	+, UI	+, UI	+, SI, UI	?	EA
L. chilense	UI	UI	?	SI	EA
L. peruvianum	UI	UI	UI	EA	SI

[a]Adapted from Hogenboom (*45*).
[b]+, No serious barrier; SI, self-incompatibility; UI, unilateral incompatibility; EA, embryo abortion; ?, no research results known.

embryo culture (*92*). Thomas and Pratt (*106*) have recently shown that hybridization between *L. esculentum* and *L. peruvianum* can be enhanced by regenerating plants from embryo callus rather than direct embryo culture. Backcrosses of the embryo callus hybrids to the *L. esculentum* parent were also produced in this fashion to facilitate introgression between these two species. Successful intergeneric crosses have also been made between *L. esculentum* and the closely related *Solanum* species *S. lycopersicoides* (*75,118*). A relatively free (although sometimes difficult) exchange of genes between species is thus possible, although it may require the use of special techniques.

REPRODUCTIVE BIOLOGY

The cultivated tomato has been a favored crop for genetic studies because of the wealth of variability within the species and the ease with which it can be manipulated. It is normally highly self-pollinated; flowers are easily emasculated and pollinated; and individual crosses may yield as many as several hundred seed. Rates of natural cross-pollination in temperate zones vary from 0.5 to 4% (*80*); however, much higher rates occur in Peru, presumably as a result of native insect vectors that can transfer the pollen. Rick suggests that the change from moderate cross-fertilization to almost exclusive self-fertilization occurred following introduction to Europe, and was accompanied by a change in stigma position from outside to within the anther cone.

The tomato flower is normally perfect, having functional male (anthers) and female (pistil) parts (Fig. 4.1). Several (usually four to eight) flowers are borne in each compound inflorescence and a single plant may produce as many as 20 or more successive inflorescences during its life cycle. This feature facilitates crosses between cultivars that represent extremes in variation for maturity since flowering occurs over a long period of time.

Present cultivated varieties form a tight protective anther cone 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 vibration of open flowers is required to effect pollination and fruit set. Genetic or environmental modification of stigma position can affect both fruit set and degree of cross-fertilization.

Emasculation for the purpose of controlled pollination must be done approximately 1 day prior to anthesis or 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 from light to dark yellow, characteristic of fully opened flowers. The stigma appears to be fully receptive at this stage, thus allowing for pollination immediately after emasculation. With favorable environmental conditions, 200 or more seed may be obtained from a single pollination. Generally, under greenhouse conditions no protection is required following emasculation to 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. Cool, dry, and relatively wind-free weather is preferred for high success rates with outdoor crossing, and protection of flowers with glassine bags may be necessary to avoid chance crosses.

Under optimal temperature and growth conditions, the tomato will complete its reproductive cycle in 95–115 days, depending upon cultivar (*18*). The first flowers open 7–8 weeks after seeding, and an additional 6–8 weeks elapse from first flower to ripe fruit.

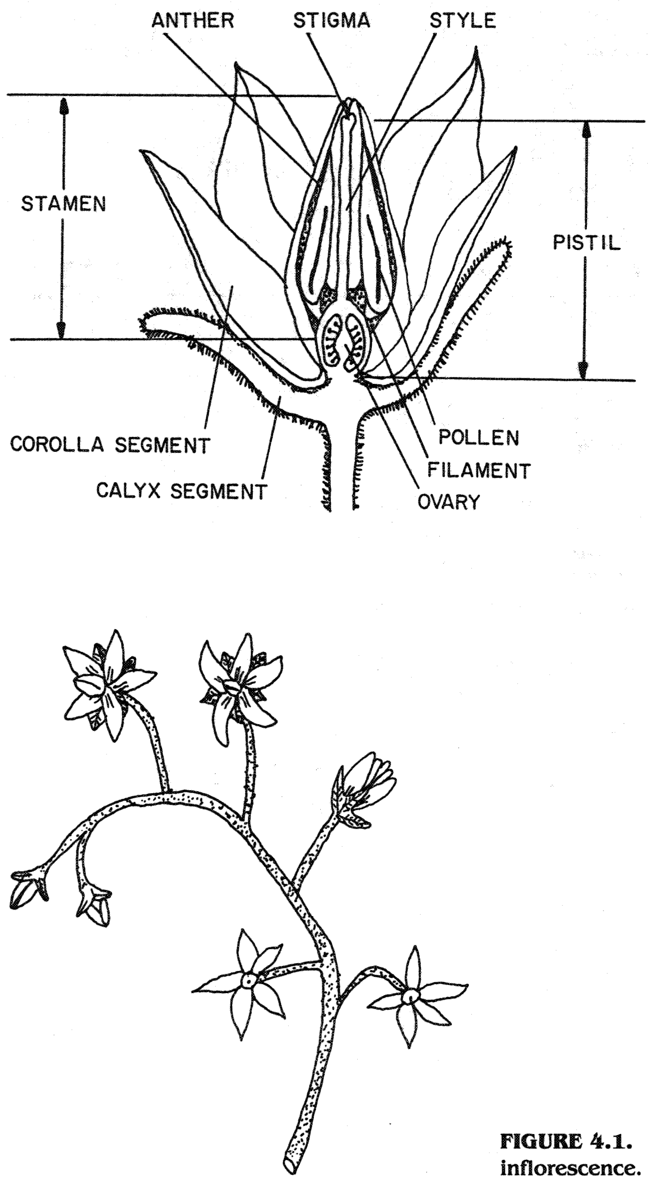

FIGURE 4.1. Tomato flower and inflorescence.

Seed is physiologically mature when the fruit reaches full ripeness. This makes it theoretically possible to complete three reproductive cycles a year using greenhouse facilities for off-season plantings.

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 (*74*).

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

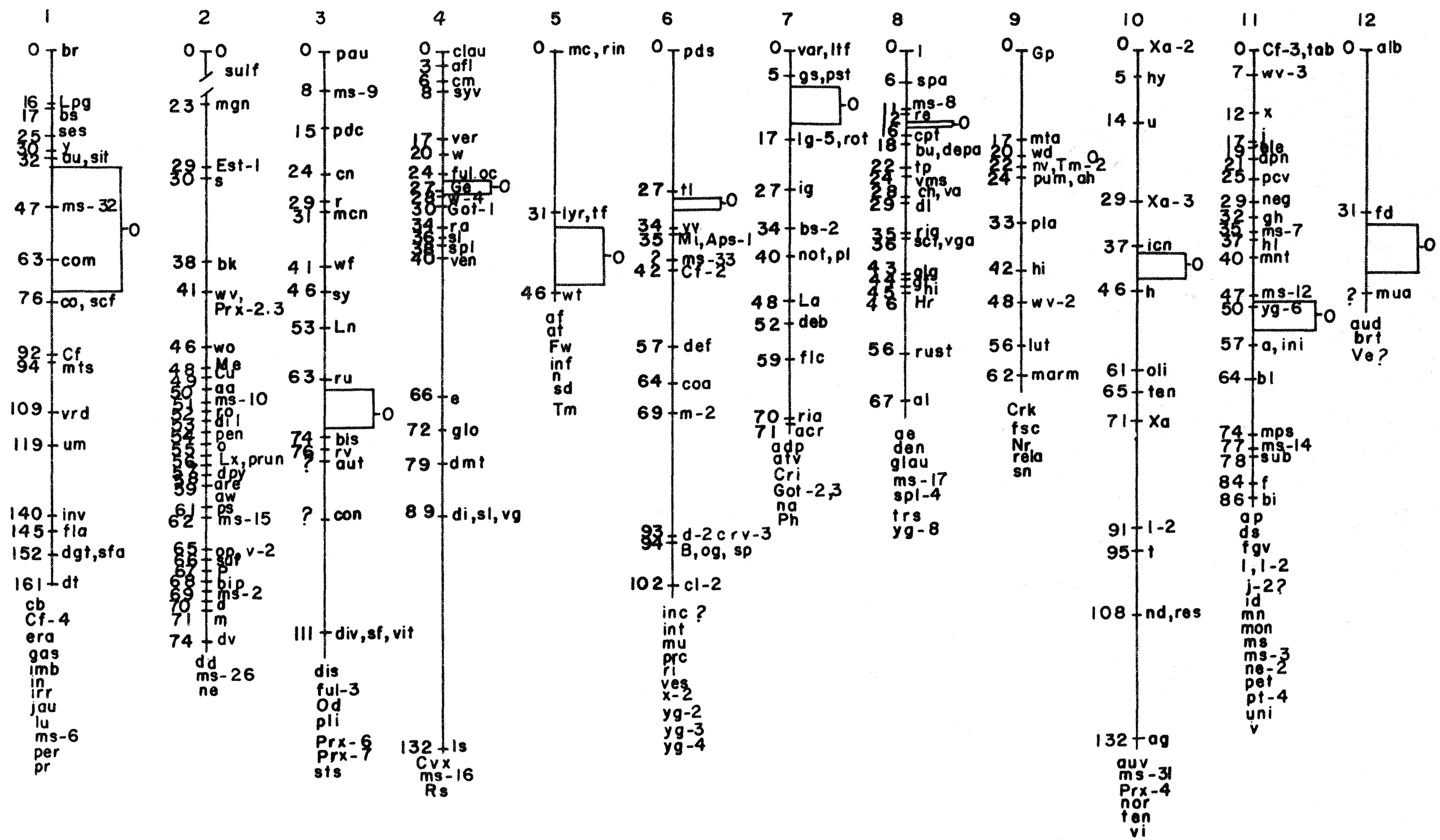

FIGURE 4.2. Linkage map for the tomato.

cultivated and wild forms. It has been more extensively studied genetically than any other major food crop (excepting possibly maize), and more than 970 genes had been reported by 1979. The Tomato Genetics Cooperative, established in 1951 by Dr. C. M. Rick, University of California at Davis, has provided an invaluable service to the many workers in tomato genetics by coordinating gene nomenclature and mapping efforts. The annual report of this organization[1] also provides brief research reports on tomato genetics as well as new cultivar pedigrees. In addition, descriptive lists of new genes are published periodically to update workers on the rapidly accumulating information on the genetics of the genus *Lycopersicon.*

The extensive genetic information that has accumulated from many years of research has permitted the development of genetic maps showing the relative location of many genes controlling a wide variety of traits (Fig. 4.2). Such maps have proven useful in the design and planning of breeding programs since linkage distances can be used to predict the probability of recombination between linked genes.

BREEDING HISTORY

The earliest written record of attempts to select and develop improved tomato cultivars date to the mid-nineteenth century in Europe. Livingston, in 1870, is generally recognized as the first tomato breeder in North America. However, as is the case with most cultivated crops, much of the very early improvement can be credited to those who first domesticated, cultivated, and consumed the crop. In the case of the tomato, the Indians of Mexico must certainly be credited for improvements that fostered its adoption as a new food crop in Europe and later in North America. As its popularity grew in the twentieth century, intensity of improvement efforts increased accordingly. During the past four decades, efforts by both public and private plant breeders have resulted in spectacular improvements in yield and other characters (see Table 4.2). New cultivars grown under improved methods of crop culture and management have resulted in fourfold increases in yield per hectare for California processing tomatoes since 1940. Without this progress, processed tomato products would undoubtedly be a commodity that only a select few could afford.

Many hundreds of new cultivars have been developed within the past 40 years to meet the diverse needs and varied situations and climates under which the tomato crop is grown. The recent trend has been toward development of cultivars to meet specific uses rather than multipurpose cultivars to meet several needs. For example, fresh-market and processing cultivars are distinct today, largely as a result of the different quality requirements for intended use. Likewise, cultivars for greenhouse culture generally differ from their outdoor counterparts because of the vastly different cultural systems used in production. Many breeding situations encountered today in tomato (as well as other crops) involve fitting the crop to its intended environment, cultural system, method of harvest and/or handling, and proposed food use.

The research and development in the 1950s and 1960s that converted processing tomatoes from a hand-harvested to an almost exclusively machine-harvested crop (Fig. 4.3) are an example of cooperative efforts among several disciplines to achieve a successful system. The development of the first machine-harvestable cultivar by G. C. Hanna at the University of California at Davis involved a major redesign of standard cultivar

[1]Report of the Tomato Genetics Cooperative, Department of Horticulture, Purdue University, West Lafayette, IN 47907.

FIGURE 4.3. Machine harvest of processing tomatoes in California.
Courtesy of Johnson Farm Machinery Co., Woodland, CA.

characteristics. The new crop type had a small vine, concentrated fruit set, and adequate firmness to withstand machine handling in addition to having the required yield, disease resistance, and quality characters. Accompanying changes in crop culture and management and the design of an efficient machine to harvest the crop were equally important elements in the system. Success in modern-day plant breeding requires imagination, cooperation with other disciplines, and an intimate knowledge of the environmental and cultural aspects of production of the crop to be improved.

Several "highlights" mark the short history of tomato improvement and its dramatic increase in popularity to the status of a food staple. Foremost among these is the fact that fruit quality has remained a major focus of most tomato breeding programs (despite contrary assertions in the popular press) while cost to the consumer has declined in real terms as a result of increased efficiencies of production.

Several simply inherited genetic characters have had important impacts on the improvement of new cultivars and the changes in culture made possible by their development (*73*). One such gene is *sp* (self-pruning), which appeared as a spontaneous mutation in Florida in 1914 and has been used in the vast majority of cultivars developed during the past two decades. This recessive allele conditions determinate habit of growth, which results in two or fewer nodes between inflorescences (as opposed to three or more in indeterminate types). This results in more compact growth and early, more concentrated flowering, a feature essential for machine-harvestable cultivars. This single feature made possible the use of higher plant populations to increase yield per unit area and the reduction of the number of times the crop had to be harvested. The same innovative process, popularly referred to in the early 1970s as "the green revolution" for wheat and rice, had been applied to tomato improvement and production several years earlier.

Numerous simply inherited characteristics are part of the architecture of modern-day tomato cultivars (Table 4.5). Single genes also control resistance to many of the common diseases, and dominance of resistance has facilitated the development of F_1 hybrids with resistance to as many as eight different pathogens (*35*). Much of these disease resistances originated in the wild relatives of the tomato and were transferred by recurrent backcrossing to adapted cultivars of *L. esculentum*. Bohn and Tucker (*15*) pioneered work that identified the dominant allele *I*, controlling resistance to fusarium wilt in *L. pimpinellifolium*. The first resistant cultivar developed from this interspecies hybrid was appropriately named Pan American to reflect the North and South American parentage in its pedigree (*69*).

TABLE 4.5. Examples of Single Genes That Have Been Useful for Tomato Improvement

Gene designation	Gene symbol	Variety
	Growth habit	
Self-pruning	*sp*	Many
Brachytic	*br*	Redbush
Dwarf	*d*	Epoch, Tiny Tim
Potato leaf	*c*	Geneva 11
Jointless pedicel	*j-1*	Penn Red
	j-2	Many
	Pest resistance	
Leaf mold resistance	*Cf-1*	Sterling Castle
	Cf-2	Vetamold
	Cf-3	V_{121}
	Cf-4	Purdue 135
Fusarium immunity		
race 1	*I-1*	Pan American
race 2	*I-2*	Walter
Verticillium resistance	*Ve*	VR Moscow
Septoria resistance	*Se*	Targinnie Red
Late blight resistance	*Ph-1*	New Yorker
Alternaria resistance	*Ad*	Southland
Stemphylium resistance	*Sm*	Tecumseh, Chico III
Tobacco mosaic resistance	*Tm*,*Tm-2*,$Tm\text{-}2^2$	
Curly top virus	?	C5, Columbia
Spotted wilt virus	Several genes, race specific	Pearl Harbor, Rey de los Tempranos
Nematode resistance	*Mi*	Rossoll, VFN Bush
	Fruit characters	
Uniform ripening	*u*	Heinz 1350
High pigment	*hp*	Redbush
Green stripe	*gs*	Tigerella (novelty)
High beta	*B*	Caro-Rich
Old gold crimson	og^c	Vermillion
Low total carotene	*r*	Snowball
Tangerine	*t*	Sunray, Jubilee
Colorless peel	*y*	Traveller
Nonripening	nor^A	Long Keeper
Male sterility	many genes	Some F_1 hybrids
Parthenocarpic fruit	*pat-2*	Severianin

Pan American and its offspring served as a primary source of resistance to this disease until 1960, when a new race of the pathogen appeared in Florida. Resistance to this new race (designated race 2) was quickly identified in a plant introduction (PI 126915), and the cv. Walter with resistance to both races was released in 1969 (*103*). Recently, a third race of the *Fusarium* organism has been reported in Australia for which tolerance has been identified in *L. pimpinellifolium* (PI 124034) as well as two *L. esculentum* breeding lines, US 629 and US 638 (*57,116*).

Disease resistance has been a major contribution of past breeding efforts, and current varieties generally possess resistance to one or more pathogens. Host resistance has been particularly important for control of soil-borne pathogens such as verticillium and fusarium wilts, for which chemical control has been relatively ineffective or costly. Virtually all important present-day cultivars possess resistance to one or both of these diseases.

The use of F_1 hybrid varieties has increased dramatically in recent years, particularly for fresh-market and home garden production. Hybrid cultivars generally do not show large yield advantages when compared with inbred varieties; their advantage appears to derive from improved earliness and better consistency of performance, particularly under less than optimal growing conditions (*123*). Virtually all hybrid seed production is done manually, thus requiring skilled yet inexpensive labor. Taiwan has become a leading producer of hybrid tomato seed (*7*).

BREEDING GOALS

Effective crop improvement programs require clearly defined objectives and a well-conceived breeding strategy to accomplish established goals. Improved yield and quality are universal goals of most breeding programs; however, selecting for yield per se is seldom very effective. Instead, the plant breeder must often define the production system and the individual components that contribute to yield or quality and emphasize selection for those individual attributes. This may mean that primary emphasis is placed on selection for such characteristics as disease resistance, earliness, habit of growth, or some novel feature rather than yield per se. Frequently, plant improvement involves adapting the crop to changes in culture and management, to the vagaries of weather and pests, or to anticipated future needs of the producer, processor, or consumer. The effective plant breeder must therefore be intimately acquainted with industry and consumer needs (as well as the genetic diversity of the crop to be improved) to establish relevant and realistic goals.

Four distinct uses and/or methods of culture characterize the tomato industry, and breeding objectives will depend upon the intended use of the new cultivar. Whereas a decade or so ago, most tomato cultivars served multiple purposes, modern cultivars are developed specifically for processing, fresh-market, greenhouse, or home garden use. This has occurred largely because the quality and/or cultural requirements may be quite distinct for each of these four uses.

Processing Tomatoes

Processing tomatoes are grown on large acreages with highly mechanized production systems (Fig. 4.3). Direct field seeding and harvest mechanization, which require high plant populations to achieve the concentrated fruit set needed for mechanical harvest, have fostered the development of compact, highly determinate processing cultivars to fit the systems of culture and harvest used. These features must be combined with other essential horticultural characteristics—disease resistance, firm fruit, earliness, ability to set fruit at adverse temperatures, resistance to rain-induced cracking of fruit, tolerance to major ripe-fruit rots, ease of fruit separation from the vine, and adequate vine cover—which are needed for adaptation to the environment in which the cultivar will be grown.

Fruit quality has also been a very important consideration in processing-tomato breeding programs. Several individual parameters of quality—color, pH, total acidity, soluble solids, total solids, and viscosity—are recognized and their relative importance depends upon the processed product for which the cultivar is to be used. Improved fruit quality has been a major objective of breeding programs supported by the food processing industries since it influences both quality and "case yield" (number of cases of processed product per unit of raw fruit) of the finished product.

Case yield, in turn, depends upon specific quality attributes that influence the amount of fruit required to produce a unit of processed product. Tomato paste standards, for example, are based upon final soluble-solids content of the finished product. As a consequence, high-soluble-solids cultivars yield more cases per ton and require less energy in concentration than do low-solids cultivars. For a product such as catsup, in contrast, viscosity (or consistency) may be the primary quality attribute influencing the number of cases of finished product produced per ton of fruit. In the highly competitive food industry, varietal or location differences in case yield may be the difference between success and failure in producing a particular processed product.

Fresh-Market Tomatoes

Quality requirements and methods of crop management for fresh use have become sufficiently distinct from processing use that cultivars seldom serve both purposes. The marketplace demands large, round fruit (to fit a hamburger bun conveniently?) with adequate firmness and shelf life for shipping to distant markets; uniform fruit size, shape, and color; and freedom from external blemishes or abnormalities. These features must be combined with the required horticultural characteristics—earliness, growth habit, disease resistance, and adaptation to environment—to make a successful cultivar.

In recent years, fresh-tomato quality has come under criticism by the consuming public, and the tomato breeder has been held accountable for many of the deficiencies of this favored vegetable crop. The issue illustrates the complex, yet subjective, nature of our perception of quality. Taste panel studies carried out at the University of California at Davis have clearly shown that free sugars, organic acids, and the sugar : acid ratio are the major identifiable determinants of flavor preference. Color, appearance, and texture, however, also contribute to perception of quality. In a study at Purdue University, taste panelists judged orange-fruited cultivars as inferior in flavor to red cultivars unless the color differences were masked by colored lights. We apparently perceive flavor with our eyes as well as our taste buds and have been conditioned by past experience to decide what represents superior quality.

Appearance has probably received more emphasis in breeding programs than flavor or other sensory aspects of quality. The recent view that modern tomato cultivars are inferior in quality to their predecessors is, however, difficult to document. The expectation that this fresh commodity be harvested (usually "green mature") and shipped thousands of miles during the winter months and still have a taste equivalent to a fully mature fruit freshly picked from the home garden may be more than modern technology can provide.

Greenhouse Production

Cultivar requirements for controlled-environment or glasshouse tomato production are quite different from those for outdoor culture. Whereas the majority of cultivars for outdoor commercial production are determinate in growth habit and produce for a relatively short period of time, greenhouse cultivars are generally indeterminate and will produce for several successive months (Fig. 4.4). In addition, certain disease problems that do not frequently cause serious losses in outdoor culture—tobacco mosaic virus (TMV), leaf mold (*Cladosporium fulvum*), gray mold (*Botrytis cinerea* Pers.), and whitefly (*Trialeurodes vaporariorum* Westwood)—may be serious problems under intensive greenhouse production.

Escalating energy costs for greenhouse heating have prompted recent efforts to develop cultivars that would perform at lower temperatures and light intensities. European and Canadian workers have been particularly active in glasshouse tomato breeding, largely because protected-environment production in these areas represents a major source of supply of this commodity during times of the year when outdoor production is not possible.

Home-Gardening Cultivars

Home-gardening cultivars constitute a particularly diverse assortment of types. This diversity provides a measure of the environmental as well as personal preference differences that characterize home gardens and their keepers throughout North America. The tomato is unquestionably the most popular and pampered garden vegetable, and many cultivars have been developed to meet the unique needs and desires of the home gardener. Several fresh-market and processing cultivars have achieved popularity among the home-gardening population. Earliness, appropriate disease resistance, large fruit size, high fruit quali-

FIGURE 4.4. Hydroponic production of greenhouse tomatoes.

ty, and continuous production throughout the gardening season are important attributes of cultivars destined for home garden use. In addition, novelty is frequently a desirable characteristic, and the use of yellow- and orange-fruited cultivars (some of which are nutritionally superior to red-fruited cultivars) has been largely restricted to home gardens. The American consumer has apparently been conditioned to believe that tomatoes should be red and the marketplace offers, in the vast majority of cases, only red-fruited types. The home gardener, on the other hand, is often willing to experiment with novel variants, and several unique cultivars are available strictly for such home garden use. Extremely dwarf cultivars have been developed for use by ''high-rise'' gardeners whose only area may be a window box or hanging basket. For those who wish to savor the fruits of their gardening efforts well after the last frost, long-storing cultivars are being developed to extend fresh-fruit shelf life.

SPECIFIC BREEDING OBJECTIVES

Earliness

Earliness is of particular importance in short-season areas to extend the production or gardening season. The recent trend to establish commercial plantings by direct field seeding rather than by transplants has further increased the importance of earliness. Three main components contribute to earliness: time from planting to flowering, time from flowering to the initiation of ripening, and the concentration of flowering (or number of flowers produced per unit of time). Wide variation exists for each of the above components of earliness (*50*). The earliest cultivars will, under optimal conditions, produce mature fruit less than 90 days after seeding.

Growth Habit

Many genes affecting growth habit have been identified and described. Certainly the most important has been the self-pruning (*sp*) gene, which conditions determinate habit of growth. This recessive gene has been used in the vast majority of cultivars released in the past two decades. It contributes to smaller vine size, since inflorescences are borne closer than at every third node (or more), as in indeterminate types. Genes controlling dwarf (*d*) and brachytic (*br*) habits of growth have also been used; however, their acceptance has been limited to unique production situations (e.g., pot culture). These very compact vine types may offer greater potential in cultivars of the future, particularly where use of high plant populations and/or machine harvest is anticipated.

Machine Harvestability

The development of tomato cultivars for machine harvest has involved a major redesign of plant structure to fit both the machine and the cultural systems required for harvest mechanization. The most important design changes have involved development of cultivars with compact growth habit and concentrated fruit set. Vine storability, or the ability of fruit to remain sound and usable on the vine following ripening yet retain adequate firmness to withstand the rigors of mechanical handling, has also been essential for successful machine harvest cultivars. These changes to accommodate machine harvest compromised certain quality attributes (particularly fruit soluble solids), and a major focus of recent improvement efforts has been directed toward enhancement of this component of processing quality.

In humid areas, the challenge of developing tomato cultivars for machine harvest has been considerably more difficult than in the arid west. Resistance to rain-induced fruit cracking (*72*), tolerance to major fruit rots (*11,12*), and improved concentration of fruit set have been necessary in these areas to minimize field losses for once-over destructive harvest. Very compact vine types used at high populations seem to offer the greatest potential for success in such areas, where rainfall may interfere with harvest scheduling.

Disease Resistance

Without question, the greatest contribution of modern plant breeding to tomato improvement has been through the development of cultivars resistant to common pathogens. For certain organisms (notably soilborne fungi responsible for fusarium and verticillium wilts), production would be considerably more difficult and costly in the major production areas without host resistance. Breeding for resistance remains a major goal as new diseases achieve significance or new races of existing pathogens become established. The dynamic interplay of host and pathogen provides job security and a guaranteed challenge to tomato breeders serving major production areas.

Host resistance has been identified and described for most of the major pathogens of tomato, and in many cases the inheritance of resistance is clearly known (Table 4.6). Early progress was fostered by cooperative efforts in the early 1950s to screen germplasm collections for reaction to major tomato diseases. Voluntary cooperative screening by cooperators in both the public and private sector resulted in a major national program to exploit variability for disease resistance within the wild relatives of tomato (*3*). Single dominant genes specifically confer resistance to several of the major tomato diseases, and inbred cultivars and F_1 hybrids with multiple resistance are now widely used where host resistance is necessary. A noble (but presently unachieved) goal would be the elimination of the extensive need for pesticides in tomato production by use of host resistance. Such an objective would require considerably more effort and expenditures in tomato breeding than is currently available.

Host resistance has often been derived from the wild relatives of tomato and incorporated into adapted cultivars by backcross breeding. For certain pathogens, several distinct races of the organism are known and new types may appear following the introduction of resistant cultivars. Surprisingly rapid evolution of new pathotypes of the organism responsible for the common greenhouse disease "leaf mold" (*Fulvia fulvum*) has provided greenhouse tomato breeders a "high degree of job security" (*51*). Fortunately, this disease is not widespread under field conditions and when it occurs, chemical control is relatively effective and is the chosen method for control. Such has not been the case for new races of the organism causing fusarium wilt for which the only effective means of control involves host resistance. In such cases, the identification of a new biotype is followed immediately by redirection of program objectives to locate and incorporate sources of resistance.

The wealth of genetic diversity in the genus *Lycopersicon* is clearly evident in the host resistance that has been reported for this extensively studied crop. Three examples will serve to illustrate how this resistance is identified and utilized.

Fusarium Wilt

The recent appearance in Australia of a third race of the organism causing fusarium wilt has fostered international cooperation to locate sources of resistance. It is expected that this new race (or a similar pathotype) will inevitably appear in other major tomato

TABLE 4.6. Sources of Resistance and Inoculation Techniques for Screening Tomato Diseases[a]

Disease	Causal organism	Source of resistance	Inoculation techniques	References
Fusarium wilt	*Fusarium oxysporum* f. sp. *lycopersici* (Sacc.)	Pan American (race 1), Walter (race 2)	Dip roots in inoculum and transplant to flats	*69,103*
Verticillium wilt	*Verticillium albo-atrum* Reinke & Berth.	VR Moscow	Dip roots in inoculum and transplant to flats	*117*
Late blight	*Phytophthora infestans* (Mont.) DBy.	West Virginia 63	Inoculate leaves with swarmspore suspension by atomization	*30*
Early blight	*Alternaria solani* (Ell. & G. Martin) Sor.	(on foliage) 68B134	Inoculate with atomized spore suspension	*10*
		(collar rot) Southland	Dunk tops and stems of seedlings into inoculum and transplant to a depth of 3 in.	*71*
Septoria leaf spot	*Septoria lycopersici* Speg.	Targinnie Red	Atomize conidial suspension onto plants	*5,14*
Gray leaf spot	*Stemphylium solani* Weber	Manalucie	Atomize spore suspension onto plants	*42*
Leaf mold	*Fulvia fulvum* Cke.	Sterling Castle	Inoculate by spraying lower-leaf surfaces with spore suspension	*51*
Foot and stem rot	*Didymella lycopersici* Kleb.	*L. hirsutum* 66087 (IVT 61292)	Apply 3 ml of inoculum around the stem base of 4-week-old seedlings	*16*
Brown root rot (corky root)	*Pyrenochaeta lycopersici*	PI 260397	Plant to fields infested with the causal organism	*45,115*
Anthracnose	[*Colletotrichum phomoides* (Sacc.) Chester] *C. coccodes* (Wallr.) Hughes	PI 272636	Inoculate fruit by atomization or puncture	*12*
Rhizoctonia soil rot	*Rhizoctonia solani*	PI 193407	Place mature green fruit on infested soil	*11*
Bacterial wilt	*Pseudomonas solanacearum* (E. F. Sm) E. F. Sm.	PI 127805A, Saturn, Venus	Cut roots on one side; pour bacterial suspension into soil trench	*1,41*
Bacterial canker	*Corynebacterium michiganense* (E. F. Sm.) H. L. Jens.	Bulgarian 12, Utah 737	Inoculate cut made by excising first true leaf at point of attachment with bacterial suspension	*24,108*
Bacterial speck	*Pseudomonas tomato*	Ontario 7710	Atomize suspension of *P. tomato* on both sides of leaf	*4,68*
Tomato mosaic	Tobacco mosaic virus	Ohio M-R9	Apply expressed inoculum with an air brush; inoculate again 10 days later	*4,65*
Spotted wilt	Spotted wilt virus	Pearl Harbor	Place seedlings in a disease nursery and encourage thrips	*29*
Curly top	Curly top virus	CVF4	Release viruliferous leafhoppers into screened greenhouse 2 or 3 times at 1-week intervals	*55*
Yellow leaf curl	Yellow leaf curl virus	*L. pimpinellifolium* (LA 121)	Release viruliferous whitefly females onto caged tomato seedlings; allow feeding for 72 hr	*67*

[a]Adapted from Webb *et al.* (*120*).

producing areas of the world, thus justifying cooperative efforts to stay ahead of the organism's ability to evolve new races capable of infecting resistant cultivars. Several sources of resistance have been identified, and genetic studies are in progress to establish the breeding strategy most appropriate to utilize this resistance and identify the most effective resistance sources (*57,116*).

Anthracnose Fruit Rot

The adoption of mechanical harvest has had a major influence on the importance of resistance and/or tolerance to fruit rots, since ripe fruit must be held on the vine for up to 3 weeks for once-over destructive harvest. The most significant ripe fruit rot in the midwestern United States is anthracnose, caused by several species of *Colletotrichum*. An ambitious program to locate sources of resistance, develop screening procedures, and transfer resistance from small-fruited wild species to commercially acceptable germplasm was initiated by the USDA (*12*). This program has resulted in promising germplasm sources, which are currently being used by both public and private tomato breeders to develop cultivars with high levels of field tolerance to this disease.

Tobacco Mosaic Virus

The tomato is susceptible to many virus diseases. Greenhouse tomatoes are particularly prone to losses from tomato mosaic, caused by the tobacco mosaic virus (TMV), which may be mechanically transmitted during growing and harvesting operations. Host resistance has proven to be a most effective and reliable means of control (*46*). Several distinct strains of the virus are recognized, and the resistances identified for these strains are race specific as well as environment dependent (*21*). Dominant genes at two loci (*Tm-1* and *Tm-2*) have been used in tomato improvement. A third allele ($Tm\text{-}2^a$) at the *Tm-2* locus is completely dominant at 20°C, but mild necrosis of hybrids occurs with certain virus strains at 30°C (*39*). Tolerance to TMV is widespread among the wild relatives of the tomato; these species will undoubtedly serve as a valuable reservoir of germplasm to meet future needs in breeding for mosaic resistance.

Insect Resistance

Insect resistance has received considerably less attention than disease resistance breeding, and very few commercial cultivars have been developed with specific resistances to problem insect pests. This situation is not a result of inadequate genetic variability but rather the low priority given to insect resistance in applied breeding programs and the difficulty of developing breeding and selection procedures to use this variability effectively. Use of pesticides has efficiently controlled most major insect pests and the tomato crop value justifies extensive use of this method. As an unfortunate consequence, little effort has been expended to utilize genetic resistance to facilitate insect control. We hope this situation will change as integrated pest management research attempts to develop viable alternatives to the use of pesticides for insect control.

Resistance or tolerance has been reported to most of the major insect pests of tomato (Table 4.7). McKinney, in 1938, was the first to report insect resistance, which he attributed to entanglement of the insects (aphids and thrips) in a gumlike exudate from the tomato foliage (*59*). Gilbert *et al.* (*36*) reported that certain Hawaiian cultivars showed resistance to spider mites (*Tetranychus telarius*). Reduced oviposition was later shown to be related to the frequency of glandular hairs on the foliage (*100*). A similar mechanism appears to influence resistance to whiteflies (*33,119*) and flea beetles (*Epitrix hirtipennis*) (*32*). In the latter case, glandular hair secretions appear also to influence the observed resistance, since washing leaves with 75% ethanol reduced resistance. In subsequent work, resistance to both mites and tobacco hornworm (*Manduca sexta*) has been associated with leaf trichome frequencies, type, and levels of 2-tridecanone (a methyl ketone) secreted from glandular leaf trichomes. Knowledge of the nature of resistance to specific insect pests will certainly facilitate screening and selection to utilize this variability (*89*).

The tomato fruitworm (*Heliothis zea*), also known as corn earworm, cotton bollworm, and soybean podworm, may be a devastating pest in commercial tomato plantings

TABLE 4.7. Sources of Insect Resistance Reported in the Genus *Lycopersicon*

Insect pest	Resistance source	Species	Reference
Flea beetle (*Epitrix hirtipennis*)	PI 126449	*L. hirsutum* f. glabratum	32,79
Potato aphid (*Macrosiphum euphorbiae*)	PI 129145	*L. peruvianum*, *L. pennellii*	*31,70*
Spider mite (*Tetranychus telarius* L.)	Anahu	*L. esculentum*	*36,101*
Carmine spider mite (*Tetranychus cinnabarinus*)	Several cultivars	*L. hirsutum*	*100*
Colorado potato beetle (*Leptinotarsa decimlineata*)	PI 134417	*L. hirsutum*	*87*
Pinworm (*Keiferia lycopersicella*)	PI 127826	*L. hirsutum*	*89*
Leaf miner (*Liriomyza munda*)	PI 126445 PI 126449	*L. hirsutum* *L. hirsutum* f. *glabratum*	*90,121*
Fruitworm (*Heliothis zea*)	PI 126449	*L. hirsutum* f. *glabratum*	*27,28*
Tobacco hornworm (*Manduca sexta* L.)	PI 134417	*L. hirsutum* f. *glabratum*	*49*
Whitefly (*Trialeurodes vaporariorum*)	IVT 74453 IVT 72100	*L. hirsutum* *L. pennellii*	*25*

throughout North and South America. Fery and Cuthbert found that leaves of *Lycospericon hirsutum* contain a factor highly detrimental to development of fruitworm larva, resulting in high larval mortality (*28*). Since early larval stages feed on leaf tissues as their primary food source, it was concluded that this would be a valuable source of resistance.

The species *hirsutum* and *pennellii* appear to be particularly valuable sources of insect resistance, and efforts to exploit this variability deserve greater future support to reduce losses to insect pests. Such efforts offer particular promise in tropical and developing areas, where insect control via chemical means may be difficult and costly and insect transmission of virus diseases represents an added threat from inadequate control (*48*).

Nematode Resistance

Nematodes may cause devastating losses where these pests are endemic. Further, they may be widely transported on transplants and cause serious losses from introduction on infected planting stock. Seven species of the root-knot nematode (*Meloidogyne* spp.) are known to attack tomato. Yield losses from severe infestations may be almost complete and predisposition to attack by other pathogens may be increased by the presence of nematodes.

Resistance to the root-knot nematode *Meloidogyne incognita* was first reported in *L. peruvianum* (PI 128657) by Bailey (*8*). Through the use of embryo culture, this resistance was successfully transferred by backcrossing to adapted *L. esculentum* cultivars (*92*). Resistance derived from this source is conditioned by a single dominant gene (*Mi*) located on chromosome 6 (*9,34*). This gene fortunately also provides resistance to three other prevalent nematode species (*Meloidogyne javanica, Meloidogyne arenaria* and *Meloidogyne acrita*). Many fresh-market cultivars and hybrids now possess this resistance, and new efforts are under way to incorporate nematode resistance into processing and greenhouse cultivars where it is necessary or desirable (*99*).

Fruit Quality

Fruit quality must be an important consideration in any tomato improvement program (*94*). In certain cases, efforts are made simply to maintain quality while emphasis is given to higher priority objectives. Recent criticism of fresh-tomato quality by the popular press and long-term interest by processing industries in improving quality and increasing "case yield" have encouraged recent efforts to improve genetically both fresh- and processing-tomato quality.

Breeding for improved fruit quality initially requires a definition of the major parameters that contribute to it. Since perception of quality is highly subjective and a result of both visual and sensory stimuli, taste panel evaluations to quantify the importance of individual quality parameters must precede improvement efforts to define the relative importance of each.

Tomato fruit are 94–95% water. The remaining 5–6% is predominantly organic constituents, which give the fruit its characteristic flavor, aroma, and texture (Fig. 4.5). During fruit maturation, dramatic changes in chemical composition of the fruit occur. As a consequence, careful sampling to ensure that fruit to be compared are at approximately similar physiological maturity is required for meaningful comparisons of different genotypes.

Appearance

Size, shape, external color, smoothness, uniformity, and freedom from defects are of major concern for fresh use but are of less significance in tomatoes to be crushed and concentrated for pizza sauce or other similar products.

The tomato is highly susceptible to rain-induced fruit cracking which may render fruit unmarketable for fresh or processing use. Significant progress has been made to develop firm cultivars highly resistant to fruit cracking (*72,91*).

Fruit Color

Many genes affecting tomato fruit color have been identified and described (*23*). For practical breeding purposes, the crimson (og^c) and the high-pigment (*hp*) genes have been of particular interest to enhance fruit color (*107*). The og^c gene increases lycopene at the expense of β-carotene, resulting in fruit with lower vitamin A levels. The *hp* gene, in contrast, increases total fruit carotenoids, resulting in excellent color and improved vitamin A levels. Unfortunately, several undesirable apparent pleiotropic effects associated with *hp* (slow germination and growth, premature defoliation) have limited its use for tomato improvement (*85*). Both of these genes can be identified visually (with practice); however, colorimetric measurements may be preferred when quantitative measures of color are desired. The Hunterlab Color Difference Meter provides a measure of redness (a), yellowness (b), and lightness (L) of raw juice (*47*). These values may be used to calculate standard estimates of juice color.

Texture and Firmness

Fruit texture, notably firmness and the ratio of fruit wall to locular contents, plays an important role in quality as perceived by the consumer of fresh tomatoes (*91*). This particular facet of tomato quality has been soundly criticized by the popular press during

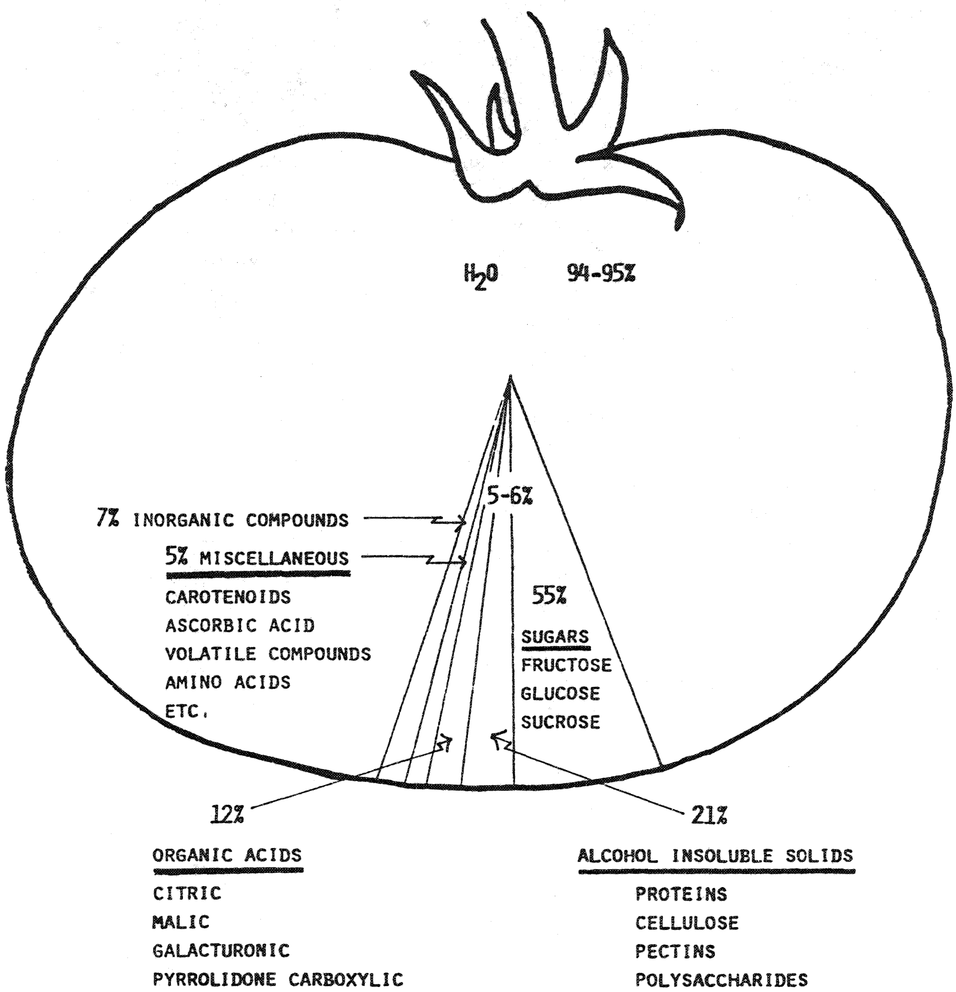

FIGURE 4.5. Constituents of a typical mature tomato fruit.

the past decade and plant breeders have borne the brunt of the blame. A 1974 article reflects opinions of fresh-tomato quality that have been restated in numerous subsequent articles appearing in the popular press. For example, "Not so long ago, tomatoes were soft and juicy and tasted of tomato. Several varieties available in today's supermarket are rubbery gobs of cellulose that taste of nothing. They are bred that way for mechanical picking" (*60*, p. 240). Such articles have reinforced the view that firm fruit precludes flavor and quality.

This view represents an oversimplification of a problem commonly encountered in the handling and marketing of perishable commodities. Consumers would like fresh tomatoes during midwinter with the same fresh quality they find in fruit harvested from their home gardens during the long days of summer, but this is still not possible. Harvesting immature fruit for long-distance shipping and producing the crop under the short photoperiods of winter are equally important factors that contribute to winter tomato quality. Criticism by consumers has fostered cooperative efforts by postharvest physiologists and plant breeders to find solutions to this problem.

Flavor

Studies by Stevens *et al.* (*96,98*) have clearly established that sugars and organic acids are important determinants of tomato flavor. Apparently the proper balance of these fruit constituents (sugar : acid ratio) is required to give optimal flavor, whereas intensity of flavor (sweetness or sourness) is a result of the relative levels of each. Volatile constituents also contribute to ''tomato-like'' flavor. The importance of the individual fruit volatiles to flavor is still poorly understood, due in large measure to the very complex array of these constituents in tomato fruit. Since a single constituent is not responsible for the predominant flavor identified with fresh or processed tomatoes, it is difficult to assign minimum acceptable levels of any single constituent for ''good flavor.''

Nutritional Value

The tomato is a significant source of vitamins A and C in human nutrition. Wide genetic variation exists in tomato for the levels of these nutrients, and conscious efforts to exploit this variation have resulted in several nutritionally superior cultivars.

Plant carotenoids, which represent the major pigments in tomato fruit, are the primary dietary source of vitamin A. For example, oxidation of β-carotene (an orange pigment) yields two molecules of vitamin A. Compounds that are converted in vivo to vitamin A are termed provitamin A. Certain carotenoids in tomato fruit also may be converted to vitamin A, but, lycopene, the major pigment of red-fruited cultivars, has no provitamin A activity. Some orange-fruited cultivars, on the other hand, have much higher vitamin A activity than red-fruited cultivars. A single dominant gene *B* favors β-carotene synthesis (at the expense of lycopene) and results in orange fruit with provitamin A levels 8–10 times higher than in red-fruited cultivars (*109,114*). Genes that enhance total carotenoids may also increase provitamin A activity [for example, high pigment (*hp*)] and genes that enhance lycopene [for example, the crimson (og^c) gene] decrease provitamin A content. The widely held consumer view that ''redder is better'' presents a dilemma to the tomato breeder concerned with nutritional value.

There is also a wide range of fruit ascorbic acid (vitamin C) levels in the genus *Lycopersicon* (10–120 mg/100 g fresh wt) (*43,52*). Linkage or pleiotropy between high ascorbic acid and small fruit size has limited use of this wide variability largely to maintenance of acceptable levels. The high-pigment (*hp*) gene offers possibilities to enhance both vitamins A and C; however, undesirable linkage or pleotropic effects of this gene on growth rate, yield, and fruit size have severely limited its use for simultaneous improvement of color and nutritional value (*85*).

Processing Quality

Fruit characters that contribute to processing quality and case yield (cases of final product per ton of fruit) have been well studied and defined. Five distinct parameters are commonly used to evaluate processing quality. The purpose of each is to quantify raw fruit quality to meet standards established for specific processed products. Careful fruit sampling is important in obtaining reliable measures of fruit quality. Undermature and/or overripe fruit may give erroneous values for certain quality parameters since fruit is continuously changing during ripening and senescence. A moderate-sized sample (5–7 lb) of uniform fruit is desirable to minimize environmental variation in estimating quality.

Color

Fruit color is often a key quality parameter used in grading raw fruit to reimburse producers. In addition to providing a measure of fruit maturity, color also influences the grades and standards of the processed commodity. Colorimetric measurement of raw color is now a standard practice in most tomato processing establishments.

Fruit pH

Fruit pH affects the heating time required to achieve sterilization of the processed commodity. Longer times are required as product pH increases. Values above pH 4.5 are considered unacceptable for fruit destined for unconcentrated products in which sterilization is achieved by preprogrammed heating times. For cultivar and breeding line comparisons, pH is measured directly with fresh juice prepared from a uniform sample of fully ripe fruits. Overmature fruit will give erroneously high pH values.

Titratable Acidity

Titratable acidity provides a measure of organic acids (total acidity) present in a fruit sample, which in turn estimates tartness. Total acidity and pH are not always closely correlated due to differences in the degree of buffering of pH by other fruit constituents. To determine titratable acidity, 10 ml of fresh raw juice is diluted to 50 ml with distilled water. The volume of 0.1 *N* NaOH required for titration to pH 8.1 is multiplied by a correction factor (0.064) to estimate titratable acids as percentage of citric acid (*62*).

Soluble Solids

Quality standards for processed tomato pulp and paste are defined in terms of soluble-solids content. This parameter of quality directly influences flavor and the degree of concentration required to manufacture products in which standards of quality are determined by solids content. High-soluble-solids cultivars give more cases of finished product per ton of raw fruit and thus require less energy in concentration. As a consequence, this parameter of quality has been of major interest to the processing industries that manufacture concentrated tomato products (*53*). Soluble solids are measured by placing two or three drops of filtered juice on the prism of a refractometer and directly reading the percentage of soluble solids.

Tomato fruit solids content is influenced by both environmental and genetic factors. High light intensity, long photoperiods, and dry weather at harvest favor high fruit solids. Small fruit size and indeterminate habit of growth also favor high solids content (*26*). As a consequence, selection for high yield or compact growth habit frequently results in sacrifices in solids content.

Tomato solids are comprised of a soluble and insoluble fraction. The soluble fraction is made up largely of free sugars and organic acids (see Fig. 4.5). The insoluble fraction (made up of proteins, pectins, cellulose, and polysaccharides) contributes to the viscosity (consistency) of processed tomato products. Stevens and Paulson have shown that the polygalacturonides are the most important component of the insoluble fraction contributing to viscosity (*95*).

Viscosity (Consistency)

For many processed tomato products, viscosity is an important parameter of established grades and standards. Perceived quality of items such as juice, catsup, tomato sauces, soup, and tomato paste is influenced by consistency. Advertising emphasis for products such as catsup reflects the importance of this quality attribute. Viscosity potential of raw fruit will influence processed product consistency and the amount of raw product required to achieve a desired consistency (case yield).

Several methods are used to determine viscosity potential (*37*). The acid efflux method is commonly used to evaluate raw fruit samples originating from variety trials or breeding plots. Approximately 2 kg of fully mature fruit is blended in 30 ml of concentrated HCl to inactivate pectic enzymes. This preparation is then passed through an extractor fitted with a 400-mesh screen to remove skin and seeds. The resulting extract (juice) is then deaerated under vacuum for 3 min and used immediately to estimate viscosity. The flow rate through a standard viscometer is timed and viscosity expressed as the time required for 100 ml to flow through the viscometer column. Alcohol-insoluble solids (AIS) also provide a measure of fruit viscosity potential (*97*). A major challenge has been to combine high soluble solids with improved alcohol-insoluble solids and high yield. Apparently, increasing solids occurs at the expense of yield.

Several other quality attributes are recognized for specific processed products. Crack resistance and fruit rot tolerance are required in humid production areas. Firm fruit indirectly improves processing quality by reducing mechanical damage. For canned whole tomatoes, uniform color, size and shape, small core size, and jointless pedicel *j-2* are essential attributes where a high percentage of raw fruit is desired for peeling purposes.

Physiological Traits

Many physiological characters contribute to the wide adaptation of the tomato. Early tomato improvement efforts emphasized disease resistance; however, more recently, attempts have been made to understand and utilize the more subtle variation contributing to crop adaptation and development. Considering the diversity of ecological niches occupied by the wild relatives of tomato, it is not surprising that substantial variation exists for a variety of adaptive features.

Low-Temperature Germination and Growth

Low-temperature germination and growth have been examined to improve emergence at the low soil temperatures frequently encountered with direct field seeding (*63*). The glasshouse tomato industry has had a major interest in developing cultivars adapted to lower light and temperature environments to reduce energy inputs into winter crop production. Patterson *et al.* (*64*) have examined *L. hirsutum* introductions originating from different elevations and have shown marked quantitative differences in germination, growth, and susceptibility to chilling injury as a function of the elevation of origin. Obvious variation thus exists, and techniques are being developed to exploit this variation in applied breeding programs.

Fruit Set

Fruit set under temperature extremes has been an improvement goal in production areas where high and/or low temperatures may interfere with pollination and fruit development. Schaible (*86*) was among the first to show that genotypic variation for ability to set fruit at low temperatures also favors high temperature setting. Not surprisingly, much of the known variation in cultivars of *L. esculentum* has originated from breeding programs in regions with very short seasons or with extreme summer temperatures. Such regions have apparently permitted rigorous field screening, which is not always possible in areas with temperatures more favorable to tomato fruit set.

Recently, the use of genetic parthenocarpy has been examined as a method to alleviate environmental limitations on fruit set (*66*). Several sources of parthenocarpy have been identified in *L. esculentum;* the most promising originated in the Russian cv. Severianin and is controlled by a single recessive gene, *pat-2*.

Chilling Injury

Chilling injury may occur under field conditions but is most commonly regarded as a fruit storage disorder that severely limits tomato shelf life. In addition, seedling injury may result from prolonged exposure to low temperatures. Patterson *et al.* (*64*) have examined various low-temperature responses in *L. hirsutum* originating from different altitudes to identify potentially useful variability for improving crop performance at low temperatures.

Salt Tolerance

Salt tolerance is commonly observed among certain wild relatives of the tomato in their native habitat (*77*). Rush and Epstein (*82,83*) have compared the tolerance of susceptible and tolerant species and efforts have been initiated to introgress the tolerance from wild species into adapted cultivars (*84*).

Drought Tolerance

Drought tolerance is found in *Lycopersicon chilense* and *L. pennellii,* both of which occur in native habits of low annual rainfall. Rick (*80*) suggests that the physiological basis for drought tolerance in *L. chilense* may be related to its deep vigorous root system. *L. pennellii,* in contrast, has a limited root system and the basis for its tolerance to drought is presumably related to its ability to conserve moisture during periods of limited rainfall.

Fruit Ripening

Fruit ripening is under genetic control and recent studies have identified and described several genes with striking effects on the ripening process (*111,113*). Two of these [ripening inhibitor (*rin*) and non-ripening (*nor*)] virtually inhibit the changes that accompany ripening, including color development, fruit softening, ethylene production, and respiratory changes. Their effects on enhancing fruit shelf life in homozygotes or heterozygotes have prompted interest in their use in applied breeding programs, particularly for fresh tomatoes destined for long-distance shipping (*102,112,113*).

BREEDING PROGRAM DESIGN

Hybridization followed by pedigree selection has been the most commonly used breeding method for tomato improvement. Backcross breeding has been the method of choice in wide crosses or for interspecies gene transfer. In certain situations, a combination of pedigree selection and backcross breeding has proven useful to exploit the advantages of each method.

In recent years, time has been recognized as an important element in plant improvement efficiency and off-season breeding nurseries have become an integral part of many tomato improvement programs. In this way, tomato breeding becomes a year-round activity with two (or in some cases three) generations each year. Winter programs are now virtually essential in the competitive race to develop improved cultivars; it is no longer possible to store seed for 7 or 8 months and keep current with changing needs.

The use of single-seed descent (SSD) has been examined as an alternative to pedigree selection for use where facilities or funds do not permit maintenance of winter breeding nurseries. We have compared pedigree selection and SSD and found combinations of early-generation pedigree selection followed by SSD to be most efficient in both time and progress under selection (*18*). Obviously, the merit of each method will depend upon breeding objectives and heritability of the trait(s) under selection (*110*). Computer simulation studies indicate pedigree selection to be most efficient with high heritabilities, whereas SSD is favored for characters of low heritability since a broader genetic base is maintained to advanced generations (*19*). Where several characters are under selection simultaneously, which is frequently the case, a combination of the two methods appears desirable. Pedigree selection is practiced in early generations (F_2 ad F_3) for highly heritable traits, followed by selection among SSD-derived inbred F_6 or F_7 lines for characters of lower heritability. We have used this procedure for several years and feel it combines the desirable features of the two methods. Obviously, the plant breeder must choose the appropriate breeding method to fit the established improvement objectives.

Currently, there is considerable interest in the use of genetic engineering and related biotechnologies for tomato improvement. The popular press has optimistically proposed some rather spectacular possibilities from this technology, including improvement of tolerance to drought and salinity, low temperature adaptation, improved disease resistance, and increased soluble solids. These suggestions of short-term benefits and unusual accomplishments minimize the problem of physiological limitations and techniques that remain to be developed before this technology can be applied to crop improvement. Techniques evolving from research in biotechnology may provide useful adjuncts to, rather than replacements for, conventional plant breeding (*93*). Sex is not only the spice but also the essence of life, for without sexual reproduction, evolutionary progress in higher organisms is severely restricted. Since plant breeding is simply a directed form of plant evolution, use of the sexual cycle appears essential and will remain the future technique of choice to exploit induced or natural variability for crop improvement purposes.

The organization and methods for handling breeding populations and maintaining records vary considerably from program to program. A typical scheme used for tomato improvement is illustrated in Fig. 4.6. Several key elements in program organization and implementation deserve comment.

Choice of Parents

In virtually all cases, one of the parents used to develop hybrid populations for selection is an adapted cultivar that requires improvement for one or more characteristics. The second parent should complement the weaknesses of the adapted cultivar to ensure adequate segregation for the character(s) under selection. Wise choice of parents is a key decision, which requires an intimate knowledge of germplasm sources available for tomato improvement.

F_1s may be evaluated for horticultural and quality attributes in their area of intended use, and only promising combinations retained for selection in F_2 and subsequent generations.

Selection in Segregating Generations

Single plant selection is initiated in F_2 and is continued through successive generations until stable lines are obtained (generally F_7–F_{10}). Since within-line segregation decreases with each generation of inbreeding, with pedigree selection, population sizes for selection are reduced by 50% each generation. During generation advance, selection emphasis is shifted from individual plant performance in early generations to line performance in more advanced generations. In practice, selection in early generations generally emphasizes

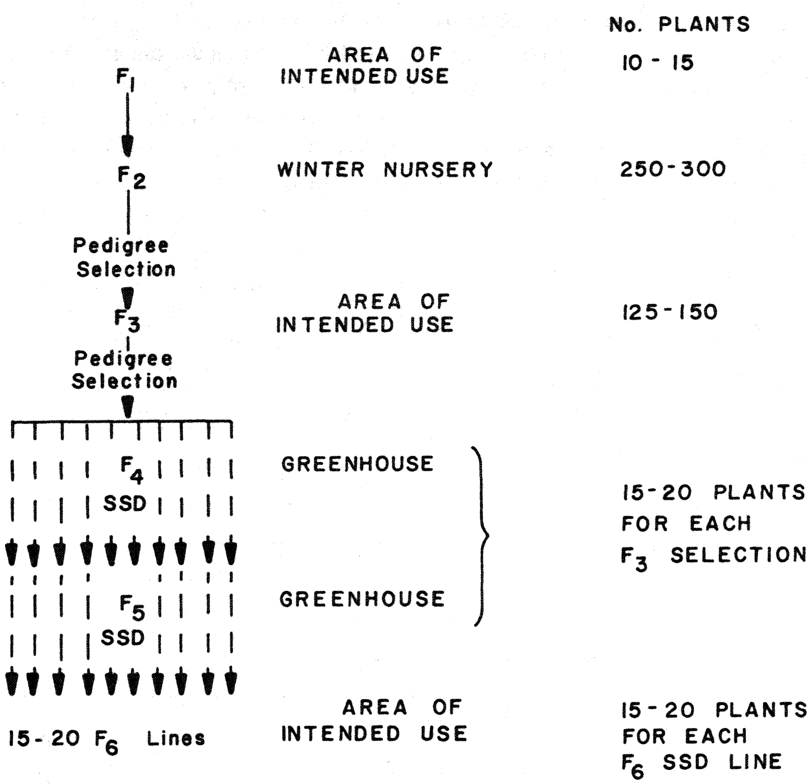

FIGURE 4.6. Breeding scheme combining pedigree selection and SSD.

highly heritable characters (disease resistance, growth habit, fruit characteristics, etc.), whereas selection emphasis may be shifted to less highly heritable characters in more advanced generations. For this reason, it is important to maintain a broad genetic base through early generations to maintain adequate variability among selected lines for selection in later generations. Combining pedigree selection in early generations with SSD following F_3 or F_4 seems to accomplish the desired balance between stringent selection and maintaining a broad genetic base. This balance is important since it is relatively easy to accumulate more breeding lines than can be properly evaluated in a short period of time or with limited space.

Maintaining Pedigrees and Records

Efficient, simple, and rapid methods of record keeping are essential in an active breeding program. Various systems have been devised and used by tomato breeders. As an example, the system used at Purdue University illustrates the essentials of an efficient system.

All field records for a single line or selection are maintained on a single record page (Fig. 4.7). These sheets are printed on light blue heavy paper to facilitate field work. (Light blue is easier on the eyes in bright sunlight; heavy paper does not get mutilated on windy days!) Preprinted columns for all characteristics to be evaluated are included on each record page to simplify record keeping. These are kept in a hard-backed, two-ring notebook until season's end, when they are cut and filed (Fig. 4.8).

Pedigrees are identified by an arbitrary field number assigned to each line prior to planting (See Fig. 4.7). This number (e.g., 83-2-406) identifies the planting year (1983), the specific project (2 = vitamin C breeding), and a sequential field number (406). Its pedigree identifies it as cross 102 made in 1980 and the seed source as SSD plant 17-2 grown in the greenhouse (prefix 6) during 1982–1983. This system provides a simple method of tracing records of selections for their entire period of development.

Field records must be taken in the relatively short time period during the growing

Pedigree 83-2-406

F_6 of cross 80102 (V 6724 x PU 74-32)

Seed Source 82-83-6-17-2 SSD

	Earliness	Cracking	Firmness	Color	Vine Cover	Stylar Scar	Stem Scar	Core	Texture	(Set)	Genes
①	3.5	2	2	3	2	3	3	2	2	4	j^+
	①		①		Vit. C	-272					
pH	4.27	V	R								
SS	5.1	F_1	R								
Col	71.2	F_2	-							Discard	
Visc	112.0	SI	S								

Pedigree 83-2-407

F_6 of cross 80102 (V6724 x PU 74-32)

Seed Source 82-6-17-3 SSD

	Earliness	Cracking	Firmness	Color	Vine Cover	Stylar Scar	Stem Scar	Core	Texture	(Set)	Genes
pH		V									
SS		F_1									
Col		F_2								Discard	
Visc		SI									

FIGURE 4.7. Field record sheets used to evaluate breeding lines and selections.

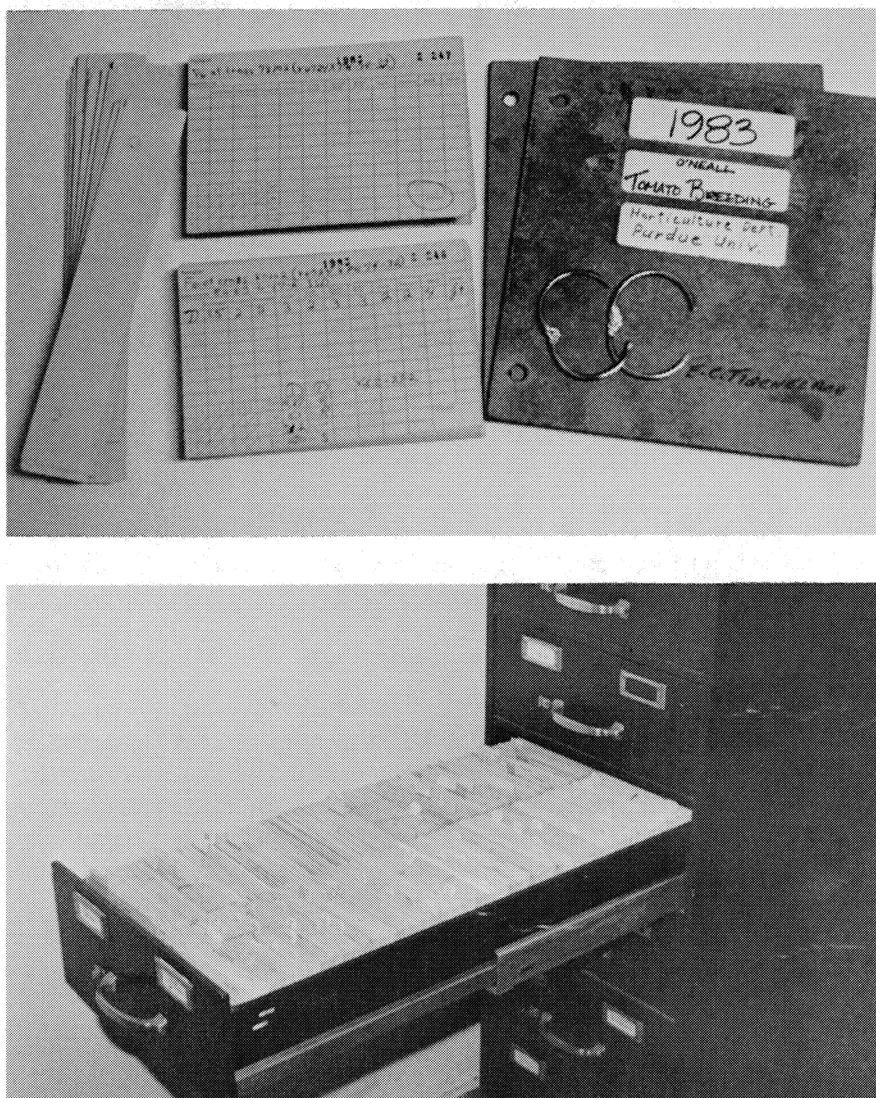

FIGURE 4.8. Filing system used to maintain field records.

season when expression of the characters to be selected is optimal. Breeding populations are usually observed several times before final selections are taken. Field records generally involve subjective evaluations against a standard cultivar using a simple number system [e.g. 1 (poor) to 5 (excellent)]. In this way, selected lines may be compared with a standard as well as with each other and progress measured over successive years.

Fruit Quality Evaluation

Environment and stage of maturity influence the major parameters of quality, thus necessitating careful sampling for reliable measures of fruit quality. Ideally, all fruit should be at an approximately similar stage of maturity for valid comparisons of cultivar quality differences. This may be difficult to achieve with material of widely differing maturities; the simplest procedure involves harvesting all ripe fruit and then waiting several days and harvesting again for quality determinations. This ensures that fruit is relatively uniform and largely eliminates the confounding effects of cultivar earliness on quality determinations.

Disease Resistance

Breeding for disease resistance generally requires artificial screening procedures that ensure uniform exposure to the pathogen. This seldom occurs under field conditions, and so artificial inoculation is commonly used (either in the field or laboratory) to identify resistant genotypes. The common procedures used for screening the major tomato diseases are given in Table 4.6.

Nematode Resistance

Breeding for resistance to the root-knot nematode (*Meloidogyne* spp.) has been simplified by the recent observation of isozyme differences in resistant and susceptible genotypes (*78*). Electrophoretic separation of seedling proteins provides a rapid, nondestructive test to screen large populations for the *Mi* gene, which controls resistance.

Early- versus Advanced-Generation Selection

In view of the large number of individual attributes that must be considered, early-generation selection frequently emphasizes characters with relatively high heritability and for which single-plant selection is relatively effective. If a broad genetic base can be maintained to advanced generations, selection for traits of lower heritability may be most effective in advanced generations when selection emphasis can be shifted to family performance. We consider this to be a major advantage of combining early-generation pedigree selection with SSD. Two or three generations of pedigree selection minimize the number of undesirable lines retained, whereas SSD effectively maintains a broad genetic base to advanced generations. Complex characters such as yield and quality are evaluated at this time. Where several hundred advanced SSD lines are developed each year, defect elimination (i.e., discarding lines that do not meet standards) throughout the season may be an effective method of selecting for specific characteristics and of maintaining manageable numbers of lines from one season to the next.

Monitoring Progress

Records are maintained during generation advance to monitor progress and establish the merits or faults of a particular parent, population, or individual breeding line. Simple regression of offspring on parent provides a measure of the progress with selection for a particular selected trait and yields useful information on the specific merits of a line before final testing and evaluation are initiated.

Trials of Advanced Lines

Testing of breeding lines begins when a line appears stable and shows sufficient merit to warrant yield and quality trials (generally F_7–F_{10}). Seed from a single-plant selection is generally adequate to perform transplanted trials at several locations and also to initiate a preliminary small seed increase. Testing should be performed at as many locations as is feasible within the intended area of use before release is considered. Cooperative testing programs involving exchange of advanced breeding lines for evaluation over a broad geographical area are conducted annually for cultivars intended for fresh-market or processing use. The Southern Tomato Exchange Program (STEP), Northern Tomato Exchange Program (NTEP), and All-American Vegetable Trials are designed for this purpose. The STEP trials involve largely fresh-market cultivars, whereas the NTEP trials emphasize processing cultivars. The All-America Vegetable Trials serve both fresh and home garden cultivars. Such broad-based trials expose potential new cultivars or hybrids to many different environments and evaluators. This broad exposure prior to release is essential to ensure wide adaptation and consistent performance over different seasons.

RELEASE PROCEDURES

Both public and private institutions are actively involved in tomato improvement. The seed industry has historically provided the delivery system for improved cultivars via multiplication and sale of new cultivars. Public institutions, on the other hand, have been involved in basic genetic and breeding methods research as well as cultivar development. The major tomato processing industries have also maintained active and productive tomato cultivar development programs for several decades.

Few, if any, standard guidelines exist regarding release procedures for new tomato cultivars. Virtually anyone can develop and/or release a new variety; however, to obtain plant variety protection (PVP) to patent a new cultivar, uniqueness must be clearly demonstrated. Many public institutions have established variety release procedures; however, in the final analysis, the marketplace determines the ultimate usage of a new cultivar.

The true merit of a new cultivar is ultimately determined by the grower and consumer. As a consequence, small-scale grower trials should be an integral part of prerelease testing. A truly superior cultivar "sells itself" and rapidly establishes its position in the marketplace. Consistency of performance under diverse environments is the mark of a worthy cultivar.

FUTURE PROSPECTS

The vast reservoir of genetic variability within the genus *Lycopersicon* and the "favored status" of the tomato as a crop for genetic and physiological studies have been factors that have fostered the impressive improvements that have occurred in the past. Despite this progress, plant breeders have merely scratched the surface in redesigning this crop to meet the needs of the grower, processor, and consumer. An almost inexhaustible supply of unexplored diversity exists within the wild taxa of *Lycopersicon* (*2,22,77*), which to date have served primarily as sources of resistance to major disease pests. This germplasm source has been virtually unexploited in tomato improvement for insect resistance, tolerance to environmental stresses, fruit quality, or other valuable traits. The building blocks for future improvements are clearly available with the genus *Lycopersicon* and expanded efforts to conserve and evaluate this variability are crucial to its future utilization.

The recent view expressed by Griesbach *et al.* (*38*) that new techniques are required in genetic manipulation "due to lack of sufficient gene reserves" grossly underestimates the vast diversity found in the wild species of most of our cultivated crops. The array of variation in cultivated *L. esculentum* is limited when compared with the wild taxa of *Lycopersicon* (*56,81*) and greater future efforts will be required to exploit the useful diversity from the wild species. The long-term nature of such programs will require greater public support for conventional genetic and physiological studies of this diversity to facilitate its use. Continued progress is certain if improvement goals are clearly defined and established and appropriate breeding strategies are employed. Mother Nature has been exceedingly generous in providing the raw materials for improvement of this favored crop.

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