3
Pepper Breeding

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Although peppers (*Capsicum* spp.) are one of the lesser vegetable crops in dollar terms, they are an important constituent of many foods, adding flavor, color, vitamin C, and pungency, and are therefore indispensable to the United States and world food industries. Mexican foods (over 60 kinds) are the fastest growing line of ethnic foods in the United States. Grocery store sales have increased from $60 million in 1970 to over $300 million in 1980. The Economics and Statistics Service of the United States Department of Agriculture (USDA) reports that the United States produced an annual average of 261,000 tons of green peppers for the fresh market and for processing from 1978 to 1980 (Tables 3.1 and 3.2). These peppers were worth over $109 million yearly. The five major producing states are Florida, California, Texas, New Jersey, and North Carolina. Texas, New Mexico, Arizona, and California produce most of the hot chili peppers in the United States.

Production of bell peppers in the United States from 1978 to 1980 is shown in Table 3.1. According to Marshall (*91*), the United States produced a total of 686,000 tons of all kinds of peppers in 1976 on 111,000 acres (Table 3.2). This was second only to China's 1,310,000 tons produced on 319,000 acres.

TABLE 3.1. Green Pepper Production for Fresh Market and Processing in the United States, 3-Year Average 1978–1980[a]

	Acres harvested	Tons	Tons/ acre	Price		Value (×$1000)
				$/ton	$/100 lb	
Seasons						
Winter (Florida only)	5,303	31,742	6.0	469	23.4	14,888
Spring	12,409	59,434	4.8	542	27.1	32,204
Summer	23,801	94,957	4.0	304	15.2	28,888
Fall	13,776	74,781	5.4	445	22.2	33,272
Total (or average)	55,289	260,932	4.7	419	20.9	109,252
Major producing states						
Florida	17,747	94,050	4.9	469	26.0	48,854
California	8,073	72,351	9.0	286	14.3	20,657
Texas	8,439	36,000	3.8	573	28.7	20,626
New Jersey	6,939	22,451	3.2	328	16.4	7,361
North Carolina	6,805	13,050	1.9	325	16.3	4,245
Total (or average)	49,003	237,902	4.9	428	21.4	101,743

[a]After USDA (*2*).

TABLE 3.2. Estimated Acreage, Production, and Grower Value of Pepper Cultivars Grown in the United States, 1976[a]

Pepper type	Harvested acres	Production (tons)	Value (×$1000)
Bell	68,167	415,215	109,409
Paprika	15,940	143,475	24,310
Pimiento	12,900	42,270	8,935
Jalapeno	2,880	32,525	7,357
Cayenne	1,786	6,685	2,850
Small Yellow Pickling	1,685	14,935	6,040
Cherry	1,640	7,750	2,855
Cubanelle	1,405	8,250	2,040
Hot Banana	1,255	7,440	1,710
Tabasco	1,200	2,740	1,715
Small Chili	760	1,515	440
Sweet Banana	565	2,315	505
Pepperoncini	235	535	365
Mexican	170	350	175
Serrano	95	570	305
Total	110,683	686,570	169,011

[a]After Marshall (*91*).

ORIGIN OF *Capsicum*

Authorities are generally agreed that *Capsicum* originated in the New World tropics and subtropics. Safford recovered dried pepper pods from 2000-year-old burials in Peru (*129*). De Candolle traced the origin of cultivated plants and concluded from a lack of reference to this genus in ancient languages that no *Capsicum* was indigenous to the Old World (*40*). Peppers were unknown in Europe until the sixteenth century, having been introduced into Spain by Columbus on his return trip in 1493. Cultivation spread from the Mediterranean region to England by 1548 and to Central Europe by the close of the sixteenth century (*14*). The Portuguese carried *Capsicum* from Brazil to India prior to 1885 and cultivation was reported in China during the late 1700s.

TAXONOMY AND CENTERS OF ORIGIN

The genus *Capsicum* of the nightshade family Solanaceae comprises some 20–30 species of the New World tropics and subtropics. Modern taxonomists recognize five major cultivated species (Fig. 3.1): *Capsicum annuum* L., *Capsicum frutescens* L., *Capsicum chinense* Jacquin, *Capsicum pendulum* Willdenow, and *Capsicum pubescens* Ruiz & Pavon. Eshbaugh has proposed that *C. pendulum* and the closely related species *Capsicum microcarpum* Cavanilles be reclassified as botanical varieties of *Capsicum baccatum*. The latter species was originally described by Linnaeus. In this classification, the larger fruited cultivar *C. pendulum* Willd. becomes *C. baccatum* L. var. *pendulum* (Willd.) Eshbaugh and the smaller fruited wild *C. microcarpum* Cav. becomes *C. baccatum* L. var. *baccatum* (*53*).

The five major cultivated species are derived from different ancestral stocks found in three distinct centers of origin. Mexico is the primary center for *C. annuum*, with Guate-

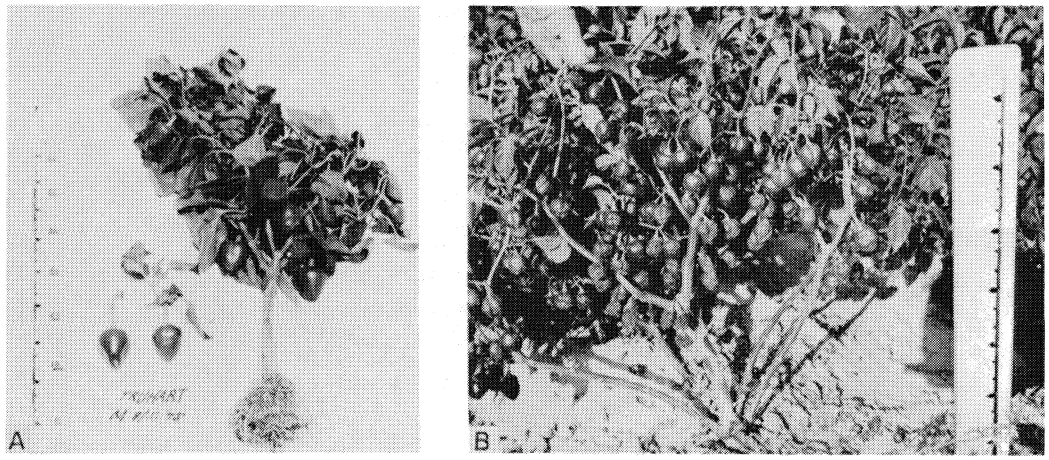

FIGURE 3.1. Representative varieties of five major *Capsicum* species. (A) *C. annuum* L. *cv.* Truhart Perfection Pimiento; (B) *C. chinense* Jacquin Acc. 1555. Scales are in inches.

mala a secondary center; Amazonia for *C. chinense* and *C. frutescens,* and Peru and Bolivia for *C. pendulum* and *C. pubescens. C. annuum* and C. frutescens are widely distributed from Mexico through Central America and throughout the Caribbean region. *C. chinense* is the most commonly cultivated species in South America. Wild forms exist of all but *C. pubescens,* which is known only in cultivation (*141*). The most comprehensive modern sourcebook on the genus *Capsicum* is by Jean Andrews (*1a*).

In the United States *C. annuum* is the major cultivated species. Only Tabasco and Greenleaf Tabasco, both *C. frutescens,* are grown to a limited extent in Louisiana for

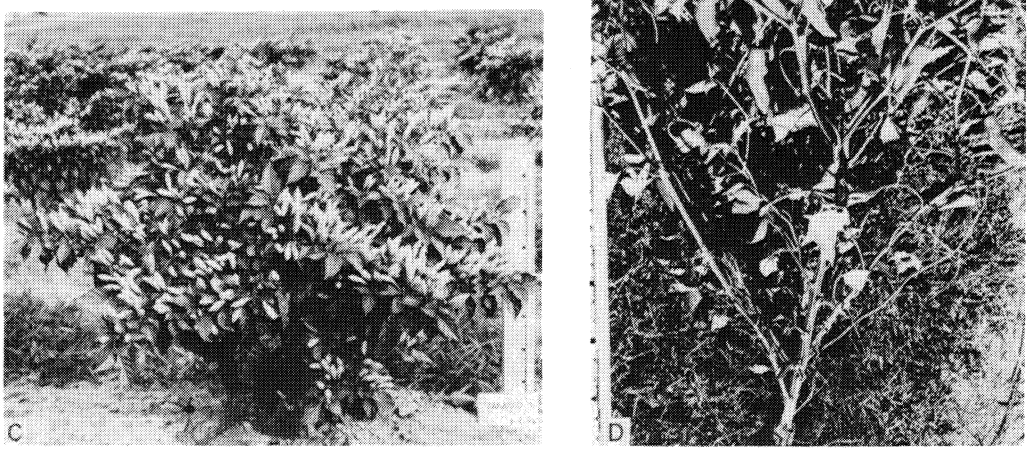

FIGURE 3.1. (*Cont'd.*) (C) *C. frutescens* L. *cv.* Tabasco; (D) *C. baccatum* var. *pendulum* (Willd.) Eshbaugh. Scales are in inches.

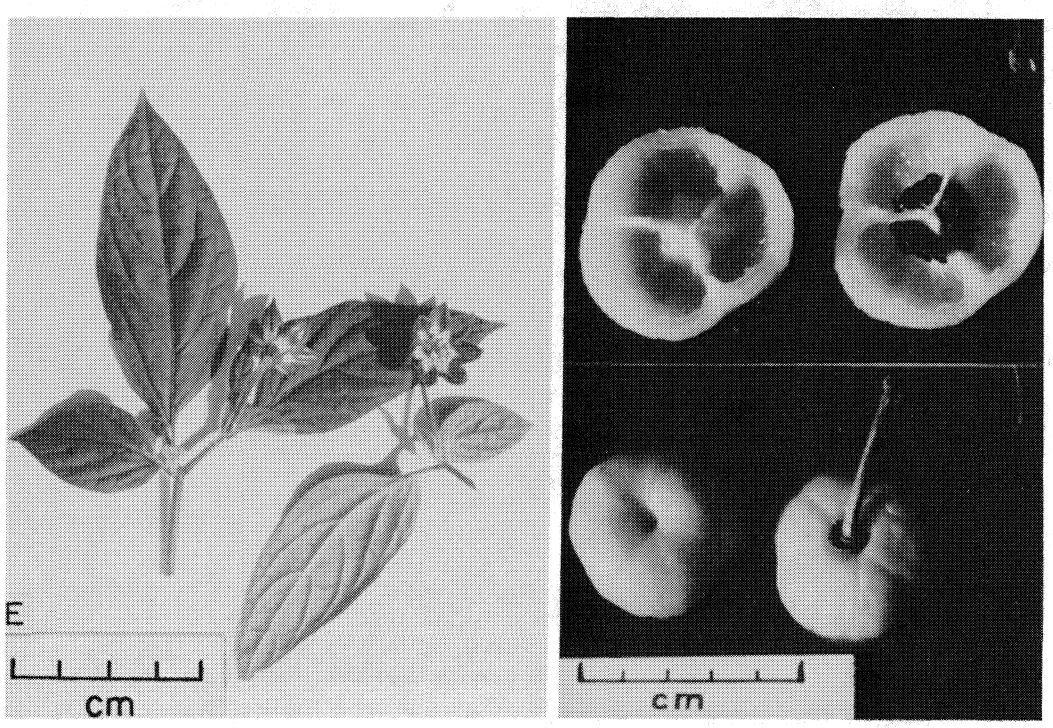

FIGURE 3.1. (*Cont'd.*) (E) *C. pubescens* Ruiz et Pavon. Scale is in centimeters.

making Tabasco sauce from the red ripe fruit and vinegar sauce from the yellow–green immature peppers pickled in vinegar. *C. pendulum* is the third species grown to a very limited extent in California for pickling in the mildly pungent immature yellow–green stage and sold under the brand name Mild Italian. Modern pepper breeders must acknowledge the achievements of the native Indian cultivator–breeders, probably women, who developed from the wild species a wide range of fruit shapes and sizes, from the small fiery Tabasco to the sweet giant bell type, by the time the Spaniards arrived. This development is thought by Pickersgill to have occurred during the last 4000 years (*113*). A probable contemporaneous development, corn (*Zea mays*) from its fully interfertile wild ancestral species *Euchlaena mexicana* (teosinte), is thought by Beadle (*8*) to have taken place between 8000 and 15,000 years ago, probably in Mexico. This time period is based on the earliest corn yet identified from archaeological finds in the southwestern United States and Mexico, which has been dated back 7000 years.

Species Characteristics

The five major cultivated species of *Capsicum* can usually be distinguished by a combination of flower and fruit characteristics (Table 3.3). *C. annuum,* the commonly cultivated species in the United States, has white flowers, blue to purple anthers, a toothed calyx, and typically single-fruited nodes with the possible exception of an occasional double-flowered axil in a lower main fork. *C. frutescens* has greenish flowers, a non-toothed, non-constricted calyx that encloses the fruit base, blue anthers, and mostly single-fruited nodes but with a few double-flowered nodes on each plant, as in Tabasco, unless the

TABLE 3.3. Taxonomic Characters Distinguishing *Capsicum* Species[a]

Species	Corolla color	Corolla throat spots	Corolla shape	Anther color	Calyx teeth	Seed color	Flowers/ node
C. annuum	White	None	Rotate	Blue–purple	Present	Tan	1
C. frutescens	Greenish white	None	Rotate	Blue	None	Tan	1–3[b]
C. chinense	White to greenish white	None	Rotate	Blue	Present	Tan	1–5
C. galapogense	White	None	Rotate	Yellow	None	Tan	1
C. chacoense	White	None	Rotate	Yellow	Present	Tan	1
C. schottianum	White	Yellow	Rotate	Yellow	None	Black	5–7
C. baccatum	White	Green–yellow	Rotate	Yellow	Present	Tan	1–2
C. praetermissum	White to lavender	Yellow	Rotate	Yellow	Present	Tan	1
C. eximium	White to lavender	Yellow	Rotate	Yellow	Present	Tan	2–3
C. pubescens	Purple	None	Rotate	Purple	Present	Black	1
C. cardenasii	Blue	Greenish yellow	Campanulate	Pale blue	Present	Tan	1–2

[a]After Lippert *et al.* (*89*).
[b]Certain wild forms may produce up to five flowers.

plants are stunted. Certain wild forms of *C. frutescens* apparently produce up to five fruits per node. *C. chinense* has white or greenish white flowers, blue anthers, a constricted, toothed calyx, and typically from one to three fruits per node. *C. pendulum* is easily identified from the white flowers with the yellow corolla throat spots, yellow anthers, and the long, curved, characteristically pendant fruit pedicels and leaf petioles. *C. pubescens* with its larger, showy purple flowers, soft pubescent leaves, yellow–orange fruits, and black seeds is unique.

Species Crossability and Hybrid Fertility

When recording crosses the accepted convention is always to write the female parent first. *C. annuum* and *C. frutescens* will cross reciprocally with *C. chinense,* producing partially fertile hybrids. With *C. chinense* as the bridge, these three species can form a common gene pool. The crossability of *Capsicum* species and the fertility of their hybrids is shown in Fig. 3.2 and Table 3.4. Dumas de Vaulx and Pitrat reported the successful hybridization of two cultivars of *C. annuum*—Doux Long des Landes (DL), a sweet, long-fruited cayenne type, and Yolo Wonder (YW)—with two Acc. of *C. baccatum* var. *pendulum* by two new methods: (1) Double pollination, first with *C. baccatum* pollen followed with pollen of *C. annuum* cv. Nigrum. The best results with this method, two to three hybrids per pollinated flower of DL and 0.4 of YW, were obtained when the second pollination followed the first 3–4 days later. (2) The second method, nitrous oxide (N_2O) gas treatment of the female gametophyte in a pressure chamber at 6 atm for 4 hr prior to pollination with *C. baccatum* pollen, yielded seven hybrids per pollinated flower (*49*). It is a general rule that wide crosses are more successful when the smaller fruited wild type is used as the female.

All *Capsicum* species have $2n = 24$ chromosomes. The F_1 hybrid *C. chinense* PI 152225 × *C. frutescens* var. Tabasco will illustrate the chromosome pairing relationship and fertility level to be expected in F_1 hybrids between *C. annuum, C. chinense,* and *C. frutescens.* In this cross, chromosome pairing is surprisingly regular, with 12 bivalents usually forming at metaphase I (MI) of meiosis and with mostly regular disjunction at MI and MII, resulting in 12 chromosomes being distributed to most pollen grains in the pollen

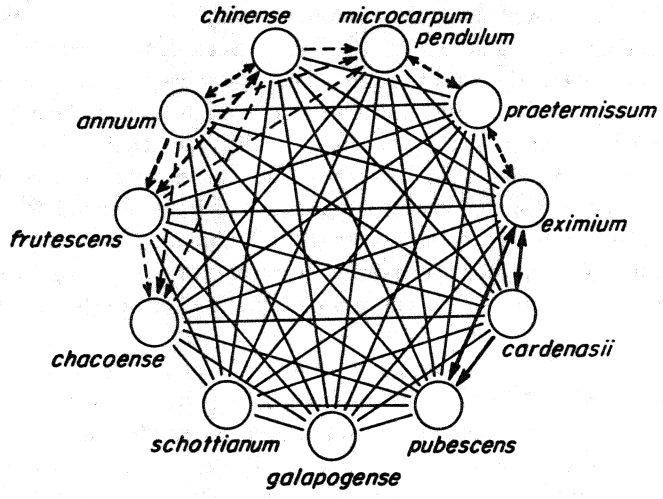

FIGURE 3.2. Cross compatibility of *Capsicum* species. —, Highly fertile F_1; ———, partially fertile F_2; —, highly sterile F_1; ———, no viable F_1 seed.
After Lippert *et al.* (*89*).

tetrads. Pollen fertility, however, as determined by staining with iron acetocarmine, was only about 21% as compared to 80–90% in the parents. Seed fertility is correspondingly reduced, with the F_1 hybrid, Tabasco, and *C. chinense* averaging 6.3, 21.1, and 28.1 seeds per fruit, respectively. A number of F_2 seedlings emerged only partially from the seed coat. Many of these, extricated manually, developed abnormally. Those that survived grew slowly into highly abnormal dwarf plants with thick and malformed leaves. Such partially sterile interspecific F_2 populations would not be expected to produce Mendelian ratios as do intraspecific crosses. For example, there was a deficiency of

TABLE 3.4. Crossability of *Capsicum* Species and Hybrid Fertility[a]

Cross	Initial cross	Viability		
		F_1 seed	F_2 seed	Backcross seed
C. annuum × *C. frutescens*	−			
C. annuum × *C. chinense*	++	++	++	++
C. annuum × *pendulum*[b]	E	E	+	−
C. annuum × *C. pubescens*	−			
C. frutescens × *C. annuum*	+	+	+	+
C. frutescens × *C. chinense*	+	+	+	+
C. frutescens × *C. pendulum*	++	++	+	+
C. chinense × *C.* × *frutescens*	+	+	+	+
C. chinense × *C. annuum*	+	+	+	+
C. chinense × *C. pendulum*	+	+	−	−
C. chinense × *C. pubescens*	E	E	−	−
C. pendulum × *C. pubescens*	−			

[a]After Smith and Heiser (*141*). E, seed germinated by embryo culture only; −, no viable seed; +, few viable seed; ++, many viable seed.

tobacco etch virus (TEV) resistant plants in the F_2 from *C. chinense* PI 152225 (resistant) × Tabasco (susceptible) due to zygote abortion resulting from gene imbalance (genic sterility). During meiosis in the F_1 hybrid, pairing and crossing-over between homoeologous chromosomes having small structural rearrangements would produce gametes with chromosomes having duplications, deficiencies, or both. Whereas the union of such gametes would often result in nonviable F_2 zygotes, their gene imbalance is usually covered by the normal gametes from the backcross parent, thus producing viable zygotes and nearly normal Mendelian ratios in the backcross (BC). Stebbins ascribed the cause of this type of sterility, common in interspecific hybrids, to *cryptic structural hybridity* since it is not revealed by the seemingly normal chromosome pairing relationship in meiosis (*64,148*).

The F_1 hybrid Tabasco × *C. pendulum* is an example of a more highly sterile cross with only about 3% good pollen. Meiosis is again surprisingly regular, but less so than in the cross *C. chinense* × Tabasco. Some chromosome bridges are observed at MII and laggard groups of chromosomes give rise to micronuclei. Hence this hybrid exhibits both chromosomal and genic sterility, but gene imbalance appears to be the major cause of gamete abortion.

Karyotype and Species Crossability

Ohta presented the idiograms of six species (Fig. 3.3). Of these, *C. frutescens, C. pendulum,* and *C. microcarpum* have similar karyotypes, each with three similar, readily distinguishable chromosomes, namely, one large satellited (Sat-I), one smaller satellited (Sat-II), and one with a subterminal constriction and a heterochromatic (non-staining) distal region. The remaining nine chromosomes, all with median centromeres, are similar in size and could not be distinguished. The similarity in karyotype of the species corresponds with their crossability (*105*).

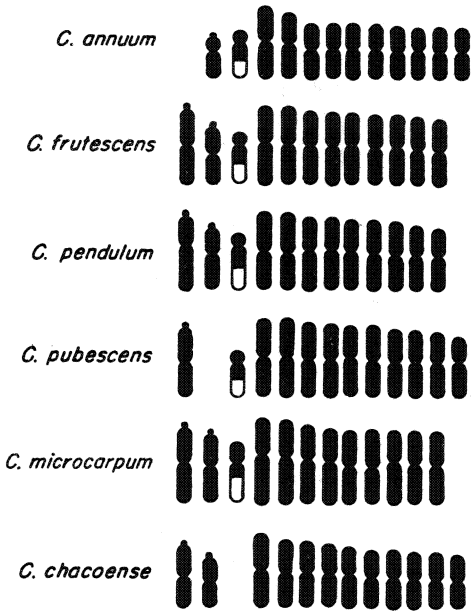

FIGURE 3.3. Karyotypes of *Capsicum* species. Top to bottom: *C. annuum* L., *C. frutescens* L., *C. baccatum* var. *pendulum* (Willd.) Eshbaugh, *C. pubescens* Ruiz & Pavon, *C. baccatum* var. *microcarpum* (Cav.) Eshbaugh, and *C. chacoense* Hunziger.
After Ohta (*105*).

FLOWER STRUCTURE AND POLLINATION

The flowers of wild *Capsicum* species are pentamerous, but large-fruited cultivars have five to seven corolla lobes. The stamens alternate with the petals and correspond with them in number (Fig. 3.4). While crosses can be made at any time during daylight hours, the best times are in the early morning or in the late afternoon when the flowers are in the mature bud stage and have not been disturbed by insects. The necessary tools are a bottle of 95% ethyl alcohol with a screw cap, a pair of sharp-pointed forceps, a spear needle, a 14-power hand lens, a plastic squeeze bottle filled with water and fitted with a fine-tipped nozzle, a roll of cheesecloth, a pair of scissors, some lightweight cotton string, and several balls of different colors of thread to mark the pollinated flowers.

Crossing and Selfing

The stigma of the flower chosen for crossing is first carefully examined with the hand lens and, if found contaminated with pollen, is pinched off. If the flower has already been visited by bees, the pollen will appear evenly distributed over the stigma and the flower must be discarded.

If some pollen is present on the style but not on the stigma, or if contamination occurred during manipulation of the flower, the flower may still be saved for crossing if the anthers are first removed with forceps, the stigma and style washed off, the excess water blown off by mouth, and any droplets remaining on the stigma gently blotted off with the thumb and fingers. The stigma is then again carefully examined with the hand lens and, if free from signs of earlier pollen penetration as evidenced by swelling and puffiness, it may be pollinated. Pollen is gently transferred to the stigma either from mature undehisced anthers by scooping it out through the lateral sutures with the spear needle, or by touching a freshly dehisced anther to the stigma with the forceps.

Several flowers are usually emasculated and prepared for pollination at one time to speed up the process. The hands and tools must be disinfected between different crosses or selfs, and care must be taken that the fingers are not damp with alcohol when the stigmas are blotted free of water droplets. Pollinated flowers are marked by loosely tying colored thread around the delicate pedicels, preferably enclosing a leaf petiole for protection. Different colors of string can be used for different crosses on the same plant, and white for

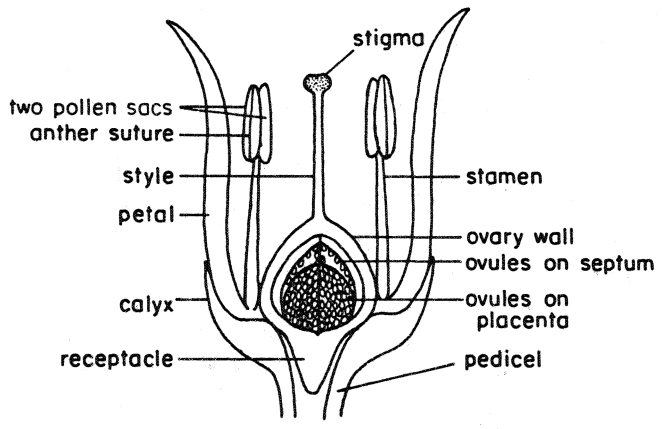

FIGURE 3.4. Diagram of *Capsicum* flower.

the selfs. Pollinated flowers must be protected from bees by a double layer of cheesecloth, loosely wrapped around the branch, enclosing leaves and flowers, and securely fastened. Appropriately marked plastic labels (insects will chafe paper) describing the cross, with the date, are attached to a bamboo stake marking the chosen plant. Pollinated flowers should be periodically checked and the cheesecloth removed in 4–6 days. Fruits should mature in about 45 days.

In an insect-screened greenhouse, several plants can be quickly selfed by touching the flowers of each with a different fingertip before again disinfecting the hands with alcohol. Pollen in mature, undehisced anthers can be stored at −5°C and 97% relative humidity for about 10 days (*112*).

Natural Crossing

There is considerable natural crossing in peppers by bees, which probably accounts for some of the variability found in pepper cultivars. Odland and Porter reported from 7.6 to 36.8% crossing in the field, with a mean of 16.5% (*103*). They transplanted single plants of each of six cultivars possessing recessive fruit and plant characters into the middle of solid block plantings of Harris Early Giant, a cultivar with all dominant traits. Variance analysis showed that the cultivars differed significantly in the amount of natural crossing. The differences were probably due to differences in flower structure, such as proximity of the anthers to the stigma and to the kind and number of insect visitors. In an open field, the minimum safe isolation distance for peppers is estimated at 600 ft.

Time Scale of Female Gametogenesis

Dumas De Vaulx has provided a time scale of embryo sac development in *C. annuum* from meiosis to the first division of the zygote, based on his cytological studies on the origin of haploids (*47*). A knowledge of the time sequence of the reproductive stages is important for hybridization and cytological studies (Fig. 3.5).

HORTICULTURAL CLASSIFICATION OF PEPPER VARIETIES

This classification system for peppers was developed by Dr. P. G. Smith, Department of Vegetable Crops, University of California, Davis. The system is based on grouping cultivars that are horticulturally similar in major characteristics such as fruit shape, size, color, texture, flavor, and pungency, as well as in uses, and hence may provide alternate sources for various processed products of the pepper industry. This classification is useful because it makes order out of a seemingly unlimited diversity of cultivars. Although intended primarily for cultivars of *C. annuum,* this system can encompass cultivars of the other four cultivated species.

With Dr. Smith's approval, his text is reproduced with only minor modifications and additions, except for certain additional cultivars and of one new group, the Squash Group. Representative cultivars of the 13 groups are shown in Fig. 3.6. All fruit measurements are length (depth) × width in inches.

This classification is limited to the more important forms of *C. annuum* and to one cultivar of *C. frutescens* (Tabasco) grown in the United States, and to one exotic cultivar of *C. chinense* (Rocotillo). *C. annuum* is the most important cultivated species of the northern hemisphere, with its center of domestication in Mexico. Within this one species the fruit range from less than ¼ to over 10 in. long, and from very slender to more than 4

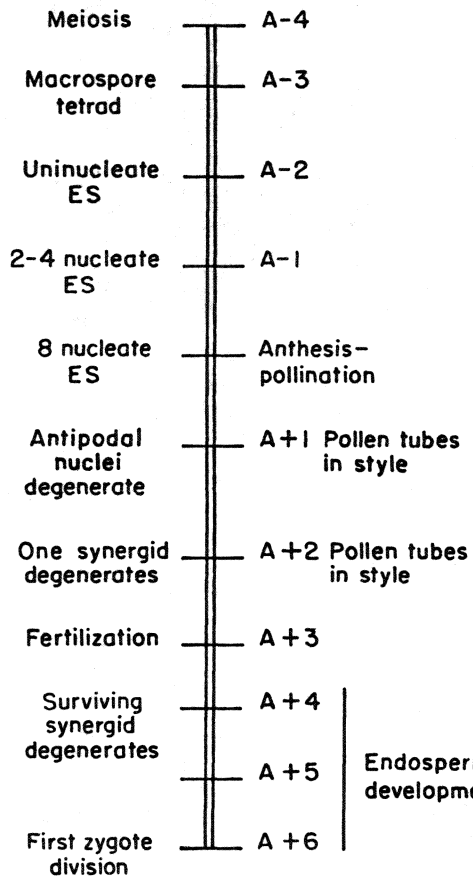

FIGURE 3.5. Time scale of female gametogenesis from meiosis to the first zygote division in *C. annuum.* ES, embryo sac; A − 4, 4 days before anthesis; A + 6, 6 days after anthesis.
After Dumas De Vaulx and Pitrat (*49*).

in. wide. Some are smooth, others are rough and irregular. Immature color may be varying shades of green to yellow, and the mature fruit, while most commonly red, may also be orange, yellow, brown, or even green.

Terminology may be confusing. The word *pimiento* is Spanish for any pepper, but in the United States it, or pimento, refers specifically to a large, sweet, thick-walled heart-shaped group of cultivars. Chili (chilli in European literature) is derived from the Mexican word *chile,* which in Mexico and Central America means any pepper. In Europe and the United States, chili refers to most pungent peppers, but not to non-pungent cultivars. The American Indian word *aji* (pronounced *ah-hee*), meaning hot pepper, was recorded by Columbus in his journal in 1493.

In recent years the Mexican influence has been felt by the increasing use of the term Long Green Chile for the Anaheim Chili cultivar group, and by the increased use of the name Ancho for the Mexican Chili. The use of Mexican names may be expected to increase.

The following classification is proposed:

Bell Group

Fruit large (3–5 in × 2–4 in.), smooth, thick-fleshed, blocky, blunt, three to four lobed, square to rectangular, or tapering in longitudinal sections. Color usually green when

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immature, turning red at maturity. A few minor cultivars are yellow when immature and others become orange–red at maturity. Mostly non-pungent, although a few pungent forms are known.

Common cultivars. Non-pungent; green, turning red when ripe: California Wonder (various strains), Yolo Wonder (various strains), Florida VR2, Florida VR2-34, Florida XVR3-25, Keystone Resistant Giant (various strains), Early Calwonder, Ruby King, World Beater, Miss Belle, Bell Boy, Big Bertha, Golden California Wonder (orange–yellow when ripe). Yellow, turning red when ripe: Golden Bell, Rumanian. Yellow-green turning red when ripe: Gypsy. Pungent: green, turning red when ripe: Bull Nose Hot. Yellow, turning red when ripe: Rumanian Hot. *Uses:* fresh market, salads, stuffed, sauteed, pizza, meat loaf, dehydrated (dried) processed meats, canning.

Pimiento Group

Fruit large, heart-shaped (2½–5 in. × 2–3 in.), green, turning red, smooth, thick-walled, non-pungent.

Common cultivars. Pimiento, Pimiento Select, Pimiento Perfection, Pimiento Truhart, Pimiento Truhart-D, Pimsan, Pimiento L., Pimiento Bighart. *Uses:* fresh market, salads, soups, meat loaf, cheese, stuffed olives, processed meat, canning.

Squash or Cheese Group

Fruit small to large, wider than deep, scalloped or rounded, flat or semipointed, smooth or rough and involuted (1–2 in. × 2–4 in.), medium- to thick-walled, non-pungent. Medium green or yellow to mature red.

Common cultivars. Cheese, Yellow Cheese, Frommage, Sunnybrook, Tennessee Cheese, Gambo (Israel), Norron de Conserva (Spain), Antibois (France). *Uses:* processing, canning, pickling, stuffing, culinary. Mildly pungent: Rocotillo (*C. chinense*), from Peru is flavorful eaten raw in salads, or used as a garnish.

Ancho Group

Fruit large, heart-shaped (4–6 in. × 2–3 in.), smooth, thin-walled, stem indented into top, forming cup, mildly pungent.

FIGURE 3.6. Fruits of 30 representative pepper cultivars reduced to ¼ natural size. Country of origin follows the cultivar name. Synonyms are in parentheses. Fruits are borne erect or pendent as shown.

(1) Greenleaf Tabasco (Tabasco G), U.S. (2) Cherry Sweet, U.S. (3) Cascabella, Mexico. (4) Serrano Chili, Mexico. (5) Red Chili, U.S. (6) Santaka, Japan. (7) Cayenne Long Slim, U.S. (8) Cayenne Large Red Thick, U.S. (9) Hungarian Sweet Wax, Hungary. (10) Sweet Banana (Long Sweet Hungarian), Hungary. (11) College 64 L, U.S. (12) Anaheim TMR 23, U.S. (13) Pasilla, Mexico. (14) Aconcagua, Argentina. (15) Fresno Chili Grande, U.S. (16) Santa Fe Grande, U.S. (17) Caloro, U.S. (18) Jalapeno M., Mexico. (19) Golden Greek, Greece. (20) Cubanelle, U.S. (21) Long Spanish Bell (PI 164564), Spain. (22) Ancho 101, Mexico. (23) Rumanian Hot, Rumania. (24) Rumanian Sweet, Rumania. (25) Pimiento L., U.S. (26) Pimiento Bighart KL, U.S. (27) Gypsy (F_1 hybrid), U.S. (28) Emerald Giant (selection from Keystone Resistant Giant), U.S. (29) Big Bertha (F_1 hybrid), U.S. (30) Cheese, U.S.

I am indebted to Dr. K. W. Owens of PetoSeed Company for the inclusion and measurements of the cvs. Cheese and Golden Greek.

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Common cultivars. Ancho, Mexican Chili, green, turning red to red-brown at maturity. Mulato, black-green, turning brown-black at maturity; imported from Mexico, little grown in the United States. *Uses (Ancho and Mexican Chili):* powder, whole pod (all). *Uses (Mulato):* dried whole or powdered or fresh roasted and peeled; distinctive flavor.

Anaheim Chili Group (Long Green Chile Group)

Pods long, slender (5–8 in. × ¾–1¾ in.), tapering to a point, smooth, flesh medium thick, medium to dark green, turning red. Moderately pungent to sweet.

Common cultivars. Moderately pungent: Sandia, Big Jim. Mildly pungent: Anaheim Chili, California Chili. Very slightly pungent: Mild California, New Mexican Chili. Non-pungent: Paprika (Bulgaria). In the United States paprika is a product, not a cultivar. Non-pungent (or nearly so) Anaheim types are used in the western United States to make this product. These cultivars are often called Paprika locally. *Uses:* dehydrated whole pods, powder (usually mixed with spices), color (especially paprika), canned (green pods), sauces (both green and red pods), many Mexican dishes.

Cayenne Group

Fruit long, slender (5–10 in. × ½–1 in.), thin-walled, medium green, turning red, characteristically wrinkled and irregular in shape, highly pungent.

Common cultivars. Mature fruit red: Cayenne Long Red, Cayenne Long Slim, Cayenne Long Thick. *Uses:* fresh market, dried, powder, hot sauce, pickling. Pasilla: long, glossy, dark blue-green, turning chocolate brown at maturity; imported from Mexico; used dried and toasted in sauces, distinctive, rich flavor. Non-pungent: Centinel and Doux Long des Landes (France). *Uses:* fresh, in salads, culinary.

Cuban Group

Fruit (3–6 in. × ½–2 in.), yellowish green, turning red, thin-walled, irregular, blunt, mildly pungent.

Common cultivars. Cuban, Cubanelle, Aconcagua, Golden Greek. Non-pungent, immature fruit green: Pepperoncini (Green Italian). *Uses:* fresh market, salads, pickled, frying. Golden Greek and Pepperoncini are harvested when fruits are 1½–2 in. long for use in salad bars; mature fruit are 3–4 in. long.

Jalapeno Group

Fruit elongated (2–3 in. × 1–2 in.), rounded cylindrical shape, smooth, thick-walled, dark green, turning red, with or without corky network on skin of mature fruits, variable in shape, highly pungent.

Common cultivars. Jalapeno (various strains). *Uses:* as green pepper, canned (in oil and spices), fresh market, mature-dried, sauces.

Small Hot Group

Fruit slender (1½–3 in. × ¼–1 in.), medium- to thin-walled, green, turning red, highly pungent.

Common cultivars. Fresno Chili (several strains) and Serrano (several strains) are

harvested in green stage only; Red Chili, Chile de Arbol, Japanese Chili, Santaka, Hontaka. *Uses:* fresh green, dried powder for seasoning and for sauces.

Cherry Group

Fruit small, spherical (½–2 in.) to somewhat flattened, thick flesh, green, turning red, pungent.

Common cultivars. Red Cherry Large, Red Cherry Small. Non-pungent: Sweet Cherry. *Uses:* pickling.

Short Wax Group

Fruit (2–3 in. × 1–2 in.), yellow, turning orange–red, smooth, medium to thick-walled, tapered.

Common cultivars. Pungent: Floral Gem, Cascabella, Caloro, Santa Fe Grande. Non-pungent: Petite Yellow Sweet. *Uses:* fresh, pickling, processing, sauces, cooking.

Long Wax Group

Fruit (3–5 in. × ¾–1½ in.), yellow, turning red, pointed or blunt.

Common cultivars. Pungent: Hungarian Yellow Wax. Non-pungent: Sweet Banana, Hungarian Sweet Wax, Long Yellow Sweet. *Uses:* fresh, pickled, sauces, relishes, canning.

Tabasco Group

Fruit slender (1–2 in. × ¼ in.), yellow or yellow-green to red, highly pungent, of the species *C. frutescens.*

Common cultivars. Tabasco, Greenleaf Tabasco. *Uses:* pickled yellow, vinegar sauce; red, Tabasco sauce.

Some Leading Bell Pepper Cultivars

Most of the following cultivars were chosen from among the better entries in the 1979–1981 National Pepper Cultivar Evaluation Trials (*95*). Others are superior varieties of long standing. This list is not complete and is intended to serve only as a guide and as seed sources for growers, home gardeners, and breeders: Marengo, Shamrock, Skipper, Early Calwonder, California Wonder 300 (Asgrow); Grande Rio 66 (Baxter); Hybelle, Ladybelle (Harris); Ferry Morse 6 C-X57 (F_1), 6 C-236 (OP), Big Belle; Keystone Hybrid 6700, Keystone Resistant Giant; PetoSeed 9275, 10275, 21476, California Wonder, Yolo Wonder L; Miss Belle (MSU).

Seed sources. Walter Baxter Seed Co., Weslaco, TX 78596; Joseph Harris Seed Co., Inc., Moreton Farms, Rochester NY 14624; Ferry Morse Seed Co., Box 1010, San Juan Bautista, CA 95045; Keystone Seed Co., Box 1438, Hollister, CA 95023; PetoSeed Co., Inc., Rt. 4, Box 1255, Woodland, CA 95695; Mississippi State U. Truck Crops Branch Experiment Station, Crystal Springs, MS 39059.

In 1981 Dr. Pieter Vandenberg, plant breeder for Nickerson International Plant Breeders S.A., P.O. Box 1787, Gilroy, CA 95020, wrote me this note. "In Spain, Italy, France, Greece they grow long blocky bell peppers under plastic almost the year around.

These peppers are pruned and trained. They use hybrids like Lamuyo (developed by INRA). We are currently selling Victor, Challenger, Chieftain. Sizes average 15–18 cm long and diameter of 8 cm.''

CULTURE

Production of Transplants

Greenhouse Plant Production

Various commercial ready-to-use growing media (without sand,) such as Jiffy Mix, Pro-Mix A, Pro-Mix BX, and Speedling Mix are satisfactory for growing peppers, provided they are kept sterile. Jiffy Mix, Pro-Mix BX, and Speedling Mix contain a wetting agent which is helpful. All made-up mixes should be steam pasteurized for 30 min at 82°C with free-flowing steam and only sufficient pressure to assure circulation between the spaced layers of flats. If a suitable steam sterilizer is not available, a commercial mix is preferred, because toxicity resulting from oversteaming is a common problem. Seeds will germinate in the toxic medium, but the seedlings will turn yellow and stop growing. Standard (14 × 21 × 3 in.) wood flats that have been treated with 2% copper naphthanate (never with creosote, which is highly toxic) are packed with 54 Jiffy Strip 2¼ in. square peat pots and filled with pasteurized medium. The medium is firmed carefully by hand to avoid breaking the peat pots. From 5 to 10 seeds are sown per pot. The flats are then drenched with a solution of a completely soluble fertilizer, such as NutriLeaf-60 or Peter's 20 : 20 : 20, 1 cup/55 gal. of warm water plus ½ cup $Ca(NO_3)_2$, ½ cup $MgSO_4$, and ½ cup of tribasic copper sulfate for protection against damping-off fungi. The plants are watered with the nutrient solution as needed. Fungi and insects are controlled by spraying with one of the following fungicides: Bravo 500, Manzate 200, or Dithane M45, plus one of the insecticides Lannate, Malathion, Diazinone, Cygone, Vydate, or Pyrenone. Kelthane plus Tedion will control spider mites. Vydate and pyrethroids will control leaf miners. Wettable powders are preferred to avoid toxicity from organic solvent carriers. One teaspoon (5 cc) of liquid soap or of a spreader–sticker, e.g., Ortho 77 or Volk, is added per gallon of spray. The plants should be ready for hardening off outdoors in about 4 weeks and should be ready for transplanting to the field in 5–6 weeks. Ideal greenhouse growing temperatures would be 68°F at night and 80°–85°F during the day. The seeding date should be about 6 weeks before the last average killing frost.

Speedling Plants

Many more plants can be produced per square foot of greenhouse area by the Speedling system. The plants are grown in patented, reusable styrofoam trays (21 × 13 in.) with 200 cone-shaped cavities (1 × 1 × 3 in. deep). Such plants are much smaller than bare-rooted field-grown transplants and hence are more easily handled in quantity for machine transplanting. However, they are also more delicate and take longer to become established and are not as tolerant of environmental stress. Larger, stronger seedlings can be produced in Speedling trays with larger 1½-in and 2-in. cells, holding 128 and 72 plants, respectively.

Field-Grown Transplants

Most pepper growers in the Southeast use field-grown plants produced in central Florida in early spring. The land is fumigated with Vorlex the preceding fall to control nematodes and fungi. Two thousand pounds of 8 : 8 : 8 fertilizer with minor elements is

broadcast per acre. Starting early in February the seed is drilled in rows spaced 1 ft apart, at the rate of 35 lb/acre. Seeding is customer timed for different sections of the country. The young plants are side-dressed twice with 400 lb each application of 12 : 12 : 12. They are sprayed weekly with Dithane M-45 plus Lannate, Cygone, or Vydate plus a spreader–sticker. Plants are certified free from diseases and nematodes by state inspectors. One million plants are pulled per acre, packed, and shipped 2000 per crate. A cover crop of beggarweed follows the peppers.

Field Culture

Transplanting

Freshly dug, state-inspected, Florida field-grown transplants are probably the cheapest and best plants if properly handled, shipped promptly, and not allowed to dry out or to heat in transit. The processor provides the plants. Plants should be field set as early as possible, but after the danger of frost and of cold winds is past. This is about April 20 in central Alabama. Greenhouse-grown plants must be acclimated for 1 week in the open before tranplanting, which is done either by hand or with a mechanical transplanter for larger plantings. Transplanting into dry soil is not advised, even with the use of a starter solution. The starter solution should be very dilute, containing no more than 1 lb of 20:20:20 all-soluble fertilizer per 100 gal. of water plus 2 lb of Terrachlor for southern blight control. Dry weather will concentrate the fertilizer in the soil solution and evaporation, especially following a light rain, will bring it to the soil surface, where it can kill the plants. Plants should be spaced 15 in. in rows spaced 3.5 ft.

A Treflan premerge treatment at ½ lb/acre on light soils to 1.0 lb on heavy soils should be followed with a diphenamide (Dymid) overspray at 6.0 lb/acre within 2 weeks after transplanting and before weed seedlings have emerged. A lay-by treatment of 40 lb/acre of 10% granular Amiben about 4 weeks after transplanting completes the weed control schedule. A no-tillage system of culture is recommended to avoid root pruning of the plants, save moisture, and reduce costs.

Plastic Mulch Systems

Black and Rolston reported on the repellent action on aphids of reflected light from aluminum-foil-covered pepper beds (*11*). The number of aphids trapped over aluminum foil was only 10% of the number trapped over black polyethylene or no-mulch plots during the first 3 weeks after planting; and at the first harvest, only 10% of the plants showed virus symptoms versus 85% on black plastic and 96% on no-mulch beds. Later tests were conducted with aluminum-painted black plastic, which proved to be equally effective, but was cheaper and more easily handled. A 6-year average yield from 1974 to 1979, based on 8–10 harvested acres each year was 469 bu (25 lb/bu) for aluminum-painted mulch plots, as compared to the state average of 200 bu. Another advantage of this system is that a second crop of peppers, tomatoes, squash, cucumbers, green beans, or cowpeas can be grown on the same plastic mulch with economy of cultivation, weed control, and fertilizer, and with excellent yields. Chiseling 12–16 in. deep in advance of mulching to break any hard pan and promote deeper root penetration improves yields.

Florida Gradient Mulch System

This is a plastic-mulch-covered, raised-bed system with subirrigation from shallow water tables. The fertilizer is incorporated into the bed or is variously banded for availabil-

ity to the seedlings and to avoid salt injury (*54,60*). This establishes a fertilizer gradient by diffusion downward by rain and upward from the water table, which is periodically raised by flooding to within about 3 ft from the soil surface. The roots grow into the most favorable nutrient concentrations.

Plants spaced 12 × 12 in. In double rows on 30-in. wide beds on 54-in. centers (19,360 plants/acre) have yielded 1196 bu/acre. With three rows per bed the yield was 1436 bu. Seeding is done with a machine that cuts holes in the plastic and places a compressed plug of a scientifically compounded growing medium containing fertilizer and seed into each hole. This is known as the plug mix seeding method (*73*). Because this intensive system of culture requires a high fertility level under the plastic and because all of the fertilizer is applied before planting, salt injury to the seedlings at the soil surface during dry periods and leaching of nutrients from around the planting hole by excessive rain have been major problems that have been only partially overcome by the use of controlled-release fertilizers, e.g., Osmocote, which is too costly for field culture.

Field Seeding of Pregerminated Seed in Gel

Pepper seeds have an extended germination period of 7–14 days. This results in much variation in seedling and mature plant size, fruit maturity, and yield. The use of pregerminated seed would avoid these problems by promoting quicker emergence and stand establishment. Peppers require high temperatures for rapid germination, but once germinated will grow below their minimum germination temperature. Essentials of the method are (1) germination of the seed at optimum temperature (30°C) in aerated water columns or immersion in a meshed bag with aeration, (2) separation of the germinated seed in the early radicle emergence stage by specific gravity in a sugar solution (25/75 wt/wt, specific gravity 1.105), (3) suspension in a gel, and (4) drilling or clumping the germinated seed in the field. Germinated seed must be handled with care to avoid damage to the radicle, and if not planted immediately can only be held for 2–3 days at 5°C. Seedling emergence of California Wonder (CW) was 50% in 7.5 days, whereas it took 16 days to obtain this percentage from dry seed. Gibberellic acid (GA_3) at 400 ppm promoted the germination of several cultivars to 81–90% in 3 days (*98,143*).

Campbell reported on the performance of the Gel-O-Flex Vegetable Planter, which he designed and built for the Campbell Soup Company (*20*). This self-propelled, hydraulic-pressure-operated machine will continuously drill or clump in hills, at desired rates, seeds of peppers, tomatoes, and other vegetables in Laponite or Viterra 2 gel at speeds up to 4 mph.

Disease Control in the Field

Irrigation and Blossom End Rot

Irrigation is essential for production of peppers, as drought is always a potential threat to the crop in the Southeast. Drought periods are common in May and June, triggering the onset of blossom end rot and of much fruit drop. The major cause of this disease has been shown to be insufficient availability of calcium in the soil solution, particularly during the period of maximum fruit set when the demand is greatest and when the plants are under drought stress. Blossom end rot can, to a large extent, be controlled with a uniform water supply during dry periods, and by liming the soil in advance.

Bacterial Leaf Spot

Genetic resistance is the only sure method of control. Seed treatment of susceptible cultivars is an important practice to prevent seedling infection from this source but cannot prevent infection from infested field soils. Georgia pimiento canners treat freshly harvested seeds for 15 min in a 4.2% calcium hypochlorite or a 2.6% sodium hypochlorite solution (50% Clorox), used at the rate of 3 gal./gal. of seed. The seed is then rinsed in water for 15 min and dried rapidly under a fan (*44*). Spraying with tribasic copper sulfate gives some control in the field but is ineffective in hot rainy weather.

Southern Blight

Crop rotation with corn, sorghum, or rye will reduce losses from this disease, caused by *Sclerotium rolfsii*. A transplanting solution containing 2–4 lb of 75% PCNB (Terraclor) WP/100 gal. of water has been widely used for control at the rate of about 1 cup/plant. This chemical must be kept uniformly suspended to avoid injury to the seedlings. Terraclor is also available as an emulsion containing 2 lb a.i./gal. or as 10% granules. The application rate with granules is 5–10 lb a.i./acre, broadcast. Biological control of *S. rolfsii* with the antagonistic fungus *Trichoderma harzianum* grown on molasses absorbed on diatomaceous earth granules has given equivalent control with peanuts at 50–100 lb/acre (*3*).

Viruses

Seed Disinfection Resistant cultivars are the best means of virus control. However, pepper seed disinfection is a valuable precautionary measure for preventing the spread of a surface-borne pepper strain of tobacco mosaic virus (TMV). We routinely treat freshly harvested, moist seed for 2–3 min in 1–2% H_2SO_4 in a plastic container with agitation, rinse under the tap, dip in a Captan solution, and dry rapidly with a fan without rinsing. Black uses a 2% solution of HC1 (*9*). Nakayama treats fresh seed in 10% Clorox for 10 min. Floaters are decanted in three rinses of tap water. Demski treated dry seed for 15 min in a 50% Clorox solution, followed by a 15-min tap water rinse, without any apparent harm to the seed (*45*).

Oil Sprays Tests with oil sprays in Florida have shown much promise for controlling aphid vectors of viruses on peppers. Proper equipment and method of application are essential to success. Zitter and Ozaki used a specially formulated mineral oil (JMS Stylet-Oil®) developed by Simons, in a 0.75% emulsion (3 qt/100 gal.) applied with Teejet TX-4 nozzles at 400 psi. No foliage injury appeared in any of the oil plots in spite of a cold winter season. Unsprayed Early Calwonder plants averaged 75% infection versus 15% in the oil-sprayed plants 10 weeks after virus spread began. The oil plots significantly outyielded the nonsprayed plots in both number and weight of marketable fruit. Spraying need not start until aphids are found on close inspection (*138,166*).

PAST BREEDING ACHIEVEMENTS

Truhart Perfection Pimiento

This leading pimiento cultivar, developed by Cochran by the pure-line pedigree breeding method between 1935 and 1942, originated from a single plant selection of the Perfection

Pimiento in a farmer's field in Georgia. The Perfection Pimiento itself was also derived from a single plant selection made by S. D. Riegel and Sons of Experiment, Georgia, from seed introduced into the United States from Spain in 1911. Riegel introduced the Perfection Pimiento in 1913. By 1935, growers and canners described this cultivar as having "run out," because commercial seed produced fruits of many shapes and sizes.

From the open-pollinated seed of the single superior plant Cochran grew the F_2 progeny in 1936. Six plants were selected for selfing under muslin-covered cages and six F_3 lines grown in 1937. One line proved to be superior to the others in productivity, fruit shape, and fruit wall thickness. Selections from this line were inbred twice more to produce the F_5 generation. Thereafter mass selection was practiced. Truhart Perfection, released in 1942, is still the leading commercial pimiento in the Southeast (*23*).

Truhart Perfection D Pimiento

This cultivar, released in 1963, was developed by Dempsey from a cross of Truhart with the pungent, bacterial leaf-spot-resistant cv. Santaka. The breeding procedure included backcrossing to Truhart and sibcrossing and selfing for 12 generations. Selection was for a smooth, tightly closed stylar scar that would prevent fungus entry into the fruit cavity and for resistance to bacterial leaf spot. In trials Truhart D outyielded Truhart by about 1000 lb/acre over a 3-year period. Fruit loss from internal mold was reduced from 10 to 5%. However, the monogenic recessive resistance of Santaka to bacterial spot was lost (*42*).

Carolina Hot

This cultivar was developed by Martin and Crawford between 1942 and 1954 by selection within the Cayenne cultivar grown for powder production in South Carolina. Selection was for strong plants with a deciduous calyx and for long, slender pods (6 × ¾ in.) borne well up in the plant canopy to reduce the amount of fruit rot from soil contact. Carolina Hot was believed to be the first cultivar of its type with a deciduous calyx. It was also more disease and nematode resistant than the original cultivar. The authors recommended that the fruit be allowed to ripen and dry on the plants rather than be harvested when succulent. Carolina Hot produced over 1 ton of dried pepper per acre, with a moisture content of about 10% (*92*).

Mississippi Nemaheart

This root-knot resistant pimiento pepper was developed by Hare between 1951 and 1966. It is the only pimiento with resistance to the southern root-knot nematode *Meloidogyne incognita* and its race *acrita,* the cotton root-knot nematode (*70*). The parentage involved Truhart and a woolly leaved, root-knot-resistant, erect-fruited, pungent Mexican pepper with light green foilage labeled M152B. Ten BC were made to Truhart, followed by seven generations of inbreeding. Root-knot screening tests were conducted during the winter in the greenhouse, and selections made for plant and fruit type in the field during the summer. Nemaheart lacked sufficient fruit size for commercial acceptance.

Pimsan 1, 2, 3 and Bighart Pimientos

These cultivars were developed by myself and co-workers at the Georgia and Alabama Experiment Stations between 1945 and 1969. The pedigree of Bighart involved 36 generations. This was a backcross–intercross program having as objectives the transfer to

Truhart of the *L* gene from Holmes' Bell, bacterial spot resistance from Santaka, and resistance to tobacco etch virus (TEV) from Cayenne SC 46252. Pimsan 1 and 2 both have the *L* gene and were released in 1956 and 1957, respectively. Pimsan 3 has the genes *L* and et^a and was released in 1958. Bighart, released in 1969, possesses the *L* gene. The gene for TEV and that for bacterial spot resistance were lost for lack of technical assistance and facilities needed to produce inocula and to screen large segregating populations from selfed BC to the susceptible cvs. YW, Truhart, and Keystone Resistant Giant. Natural epiphytotics of bacterial spot (*Xanthomonas campestris* pv. *vesicatoria*) cannot be depended upon for field screening.

Bighart Yield, Fruit Size, Recovery, and Seed Yield

Bighart yielded significantly more than Truhart and the fruit was larger. Recovery of cored raw fruit was increased 17% and canned recovery weight 11%.

About 25% of the raw pimiento fruit is waste (Fig. 3.7) (*24*). Recent laboratory tests at Auburn University have shown a 68.6% recovery of canned product from whole fresh Truhart fruit when steam peeled vs. 65.6% when lye peeled (*139*). In canning plants the usual lye peel process recovers only about 30%.

The seed yield of Bighart was 1.6% of the fresh fruit weight and air-dried seed was 0.8%. One ton of fruit yielded 16 lb of dry seed vs. 41 lb from Truhart. One pound of Bighart seed contained 63,000 seeds (*68*).

Greenleaf Tabasco (Tabasco G)

Tabasco, the cultivar of the Tabasco industry in Louisiana, was introduced into the United States from Mexico about 1848. This pepper responds with a lethal wilt disease when infected with TEV (*63*). I transferred the TEV resistance of *C. chinense* PI 152225 to Tabasco by the BC method (*64,69*). Progeny from this cross had golden yellow–green rather than green foliage, which prompted me to introduce a second TEV-resistant cultivar of *C. chinense* into the pedigree at the BC_3 level (Fig. 3.8). There was much sterility during the early BC generations. This was expressed in partially developed, short stubby fruits with few or no seeds. The sterility was gradually overcome by additional backcrossing, interline crossing, and selection. The recessive mode of inheritance of TEV resistance required that alternate selfed generations be screened for TEV resistance before making the next BC. Greenleaf Tabasco, introduced in 1970, has saved the Tabasco

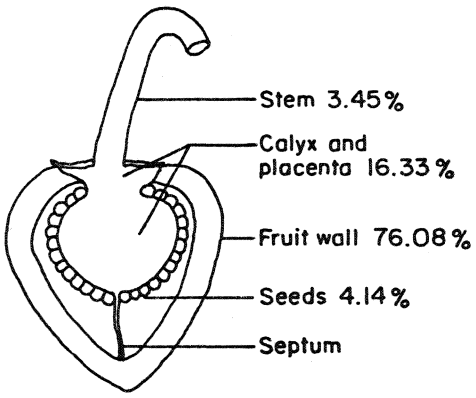

FIGURE 3.7. Truhart Perfection Pimiento fruit showing mean percentages of constituent parts. Average fresh fruit weight 0.173 lb (78.25 g).
After Cochran (*24*).

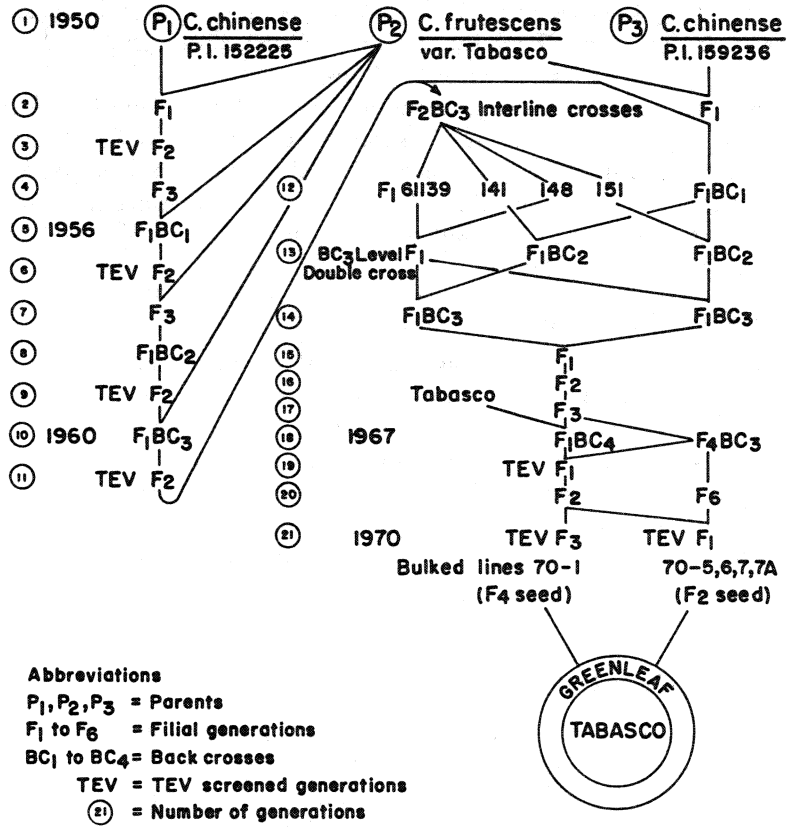

FIGURE 3.8. Pedigree of Greenleaf Tabasco.

industry in Louisiana from the aphid-transmitted etch wilt disease (*65*). Zitter reported that Tabasco G was also resistant to pepper mottle virus (PMV), an unexpected bonus (*162*).

Yolo Y, VR2, and Delray Bell

These three virus-resistant bell peppers were developed by Cook and co-workers in Florida (*29,32,35*). Yolo Y, released in 1966, originated from a single mutant plant of Yolo Wonder (YW) resistant to potato virus Y (PVY), discovered by Cook. This plant, the parent of Yolo Y, possessed a single recessive gene y^a that conferred resistance to mild strains of PVY. This cultivar also carries the gene L^1 (L^i) of YW which determines the imperfect localization response to infection with common TMV, described by Holmes (*75*). Yolo Y yielded slightly less than YW (690 vs. 668 bu/acre) in 17 trials in eight states.

Florida VR2, released in 1976, is resistant to TEV, PVY, and TMV. Sources of resistance were the small, pungent, fruited *C. annuum* PI 163192 and PI 264281, and Cayenne SC 46252. All carry the gene et^a, which confers resistance to mild strains of TEV and to mild and severe strains of PVY (*26–28*). F_1 hybrids of these cultivars with YW and California Wonder (CW) were variously backcrossed to YW, Yolo Y, CW, and Florida Giant. Four BC were made, the last one to Yolo Y, followed by two field and two

greenhouse generations. Selection was for horticultural characters, for virus resistances, and for resistance to bacterial spot race 2 (*Bs2*) from PI 163192. Florida VR2 is homozygous for et^a, L^1, and *Bs2*.

Delray Bell, released in 1977, is resistant to TEV, PVY, and PMV. These viruses have been major problems in Florida's Delray Beach pepper production area. TEV and PVY resistance came from various breeding lines with the gene et^a, and that for PMV from Avelar (et^{av}). The gene L^1 for resistance to common TMV was lost in backcrossing to susceptible parents. Delray Bell will eventually develop a mild mottle from PMV but no fruit symptoms. Its yield was superior to that of commercial cultivars in virus-infested areas and was comparable in areas with no virus problems.

Yolo Y, VR2, and Delray Bell produced flat pods with few seeds in cold weather, probably from insufficient pollination. Early Calwonder was much less affected and was preferred by buyers.

Cook Breeder Line Releases

Cook released four advanced breeding lines in 1982: Florida VR2-34, XVR3-25, Florida VR4, and USAJ15 (*31*). Florida VR2-34 was developed from a bulk of several lines reselected from Florida VR2 for larger fruits with square nondepressed blossom ends. Preliminary trials indicate that VR2-34 has larger fruits and yields better than CW or VR2. It carries the same genes for disease resistances as VR2 (et^a, L^1, *Bs2*). XVR3-25 (et^a, L^1, *Bs1, Bs2*) is similar to VR2-34, but also carries resistance to race 1 of the spot bacterium (*X. campestris* pv. *vesicatoria*) from *C. chacoense* PI 260435. Florida VR4 (et^a, et^{av}, *Bs2*) is resistant to TEV, PVY, PMV, and race 2 of pv. *vesicatoria* but susceptible to common TMV. This line derives from the cross Florida VR2 × Delray Bell. All three of the new bell lines have large fruits, averaging 10 × 8 cm, with fruit walls 5–6 mm thick. USAJ15, a medium long, slightly curved, pointed hot pepper is resistant to TEV and PVY. It derives from a cross of PI 264281 (et^a) with a PVY-resistant pepper from Ecuador ECUAJI. Fruit size averages 9.6 × 1.8 cm. The fruit wall is 1.5 mm thick and the fruit weight ranges from 5 to 12 g. Maturity is 81 days from transplanting.

Cayenne 16 through Cayenne 20

These five cayenne peppers were selected by Black and Simmons for TEV and PMV resistance in a long-fruited cayenne strain grown in Louisiana for making hot sauce. This strain is longer and larger fruited than Carolina Hot. Cayenne 16, the largest, averages 7.5 in. (19 cm) long, weighs 26.5 g, and is slightly curved and pointed (*12*).

Texas Bell 76004, Long Green Chile 76042, and TAM Mild Jalapeno-1

These three peppers were developed by Villalon and released in 1979. They are the product of an intensive interdisciplinary breeding program initiated in 1971 by Texas A&M University to assist growers with pepper disease problems, primarily viruses, in the lower Rio Grande winter production area. All three cultivars, according to Villalon, are resistant to the south Texas strains of TEV, PMV, PVY and to Samsun latent TMV (SLTMV) (*157*). He conducted the first virus disease surveys in 1971, and by means of host range studies and diagnostic serological and electron microscopic techniques, found that TEV, PMV, PVY, cucumber mosaic virus (CMV), SLTMV, and tobacco ringspot

virus (TRSV) were the most common viruses of peppers in south Texas. Over 100 commercial bell peppers were susceptible to all of these viruses. For sources of resistance, he screened 13 exotic germplasm stocks with TEV, using an artist airbrush inoculation technique at 125 psi. Resistant selections were crossed with commercial bell types and several large-fruited sweet lines developed by the BC method. Because genes for virus resistances are recessive, each F_2 generation was screened for virus resistance before making the next BC.

Villalon found that by intercrossing resistant lines of diverse origin higher levels of resistance could be obtained, indicating that modifier genes were additive in effect. Concurrently with the bell pepper BC, resistant pungent-fruited segregates were backcrossed to Long Green Chili, Red Chili, Serrano, Ancho, pimiento, cherry, yellow pickling, and paprika types, and multiple virus-resistant derivatives of these cultivars also developed. A significant feature of Villalon's breeding method was to screen first for a high level of TEV resistance. Once TEV resistance was fixed in F_3 he screened in F_4 for PMV, PVY, and SLTMV resistance. That he was able so quickly to obtain resistance to all four viruses in F_5 lines supports other evidence that multiple resistance is conferred by the stronger potyvirus resistance alleles. F_6 lines were tested in replicated statewide trials. Villalon recommends that growers test his new cultivars on a limited commercial scale for several seasons for adaptation to soils and climate and for processor and consumer acceptance before planting their entire acreage to them. He points out that the ultimate step, processor evaluation and consumer acceptance, must be taken by the industry itself.

Pepper Breeding in Brazil—Agronomico 8 and Agronomico 10

Nagai reported that strains of PVY were the most prevalent at Campinas, S.P., Brazil. By combining the PVY-resistant germplasms of several cultivars, such as Puerto Rico Wonder, Moura, Ikeda, Avelar, Casca Dura, and PI 264281 (P11), he developed the multiple-resistant cultivar Agronomico 8, released in 1967. This cultivar has shown a high level of resistance to a complex of potyviruses in the southeastern United States, in California, and in Europe. Following an outbreak of a new strain of PVY in Brazil, Nagai made additional crosses between selections within a pool of resistant germplasms and developed a new series of resistant lines designated Agronomico 10. This is now the leading cultivar in Brazil. He is currently incorporating a hypersensitive-type resistance to bacterial spot into Agronomico 10. This cultivar has shown resistance to PMV in Florida (*99*).

BREEDING FOR HORTICULTURAL CHARACTERS

Earliness

Pochard observed transgressive segregation for this trait (*114*). He determined earliness by two methods, first by ranking the cultivars by date of first bloom, starting with the earliest Antibois on June 12, as time zero. Vinedale was +2, YW +12, Quadrato Giallo +15, and Piment de Bayonne +22 days later. In the second method he used the percentage of ripe fruit harvested by August 30 as a measure of earliness. When the first method was used, 45% of the F_3 lines from the cross YW × Antibois (large, subspherical squash type) and 10% from the cross Quadrato Giallo (bell) × Antibois flowered earlier than Antibois. One of the F_3 lines of the latter cross flowered 14 days before Antibois. The second method yielded similar results, 13 of 78 F_3 lines producing 80–100% ripe fruit

weight by August 30. This improvement resulted from the selection of the earliest 4% of the F_2 plants by either method. Inheritance of earliness in these crosses was oligogenic.

Fruit Shape and Size

In certain crosses of small oblate or round-fruited cultivars of *C. annuum* and of *C. chinense* with larger elongate-fruited cultivars, the F_1 is small fruited and oblate and the F_2 segregates 3 oblate : 1 elongate. All fruits with a length/width ratio above 1.0 are classed as elongate. Elongate fruit range from short and blunt to long and pointed. Elongate fruit is determined by polygenes that are recessive to the dominant gene *O*. This gene is present in *C. chinense* Acc. 1555 (Fig. 3.1B). Early, productive, smooth, nearly round deep-fruited segregates from BC_2 to pimiento give promise that a large, nearly round fruited cultivar can be developed from this cross.

Other crosses between oblate and elongate produce an intermediate F_1 and an F_2 with a continuous range of fruit shapes and sizes, typical of quantitative inheritance. Fruit size and shape in such crosses are determined by polygenes, with the genes for small fruit being dominant. Because about 30 genes determine fruit size, large fruits cannot be recovered in F_2 (*83*). Four or more BC are required to recover the fruit size of the larger parent.

According to Pochard, extra large fruit is undesirable because it is usually associated with lower productivity, irregular fruit shape, and poor quality. The French pepper breeding program stresses improvement in fruit appearance through more uniformity in shape and size. Plants are selected for large, glossy, firm, thick-fleshed fruit that will withstand shipping and that are resistant to blossom end rot. CW possesses these characteristics.

Selection for Fruit Quality

Selection, by taste, of plants with fruit having a strong, pleasing, high sugar/acid ratio and other desirable flavors is probably the most practical method for the breeder to incorporate quality into his breeding lines. Soluble-solids measurements with a refractometer could also prove helpful. Pochard reports that fruit acidity increases with maturity in all cultivars but particularly in the YW group. Both the fresh and canned product of F_4 and more advanced lines would need to be evaluated by carefully chosen taste panels. Such tests should be designed to provide statistically unbiased probability estimates. Laboratory tests for flavor compounds, pigment content, and vitamin C levels would be valuable for selecting the better advanced lines. High pigment, according to Pochard, is a partially dominant trait of polygenic inheritance.

The vitamin C content of YW fruit was only 150 mg/100 g fresh wt. vs. 190 mg in CW and 300 mg in Doux d'Alger (*114*). Rymal has developed a quick color spot test suitable for making quantitative estimates of vitamin C in pepper fruits in the field (*126*).

Fruit Flavor and Pungency

Flavor in peppers, according to Jones and Rosa, is due to several aromatic substances present in very small quantities but not connected with pungency (*81*). Buttery *et al.* first identified the important flavor component of bell peppers as 2-isobutyl-3-methoxyprazine (*19*). This compound has an extremely potent aroma, its odor being detectable in as little as 2 ppt in water solution or 1 drop in an olympic-sized swimming pool. Huffman *et al.*

defined and quantified the flavor components of fresh jalapeno and bell peppers by means of gas chromatography and mass spectrometry (*77*). They confirmed that the above compound is the major flavor component in both bell and jalapeno peppers. Although its concentration is very low, in the ppb range, jalapeno peppers, originally from Jalapa, Mexico, have a strong flavor. The highest concentration was found in the outer wall, with lesser amounts in the cross walls and in the placenta and with none in the seed. Thermal processing destroyed most of the flavor compound. The authors concluded that this odorant is synthesized in many cells in different parts of the fruit but is concentrated in the outer wall.

Haymon and Aurand identified 23 flavor compounds in Tabasco peppers, all of which were necessary to produce the characteristic Tabasco aroma. There was no single dominant flavor compound as in bell or jalapeno peppers (*72*).

Flavor of Pimiento vs. Bell Peppers

The flavor of canned pimientos has traditionally been considered superior to that of canned bell peppers, but until recently no data were available to decide this question. Also, pimientos that were flame peeled were not comparable with bell peppers that were either unpeeled, lye peeled, or steam peeled because the superior flavor of the pimientos could well have been due to the roasting process. Rymal *et al.* used the triangle test design and statistical probability to answer this question. Six taste panelists were presented with diced samples of three canned pimiento and three canned bell pepper cultivars in 15 different comparisons and asked to identify the odd sample. The test was replicated four times for a total of 360 decisions. The results showed that there was no significant difference in flavor, color, or texture between the pimiento and bell pepper samples when they had been similarly processed (*128*).

Pungency in peppers is due to capsaicin ($C_{18}H_{27}NO_3$), a fat-soluble, flavorless, odorless, and colorless compound, the structure of which was determined by Nelson in 1920 (*100a*). Capsaicin distribution in fresh jalapeno peppers was highest in the cross walls, followed by the placenta, seeds, and outer walls. Processing increased the capsaicin content many times throughout the fruit, indicating that heating had transformed a precursor into capsaicin (Table 3.5). Huffman *et al.* found no specialized structures that produced either the flavor compound or capsaicin, but Ohta observed receptacles high in capsaicin on the fruit cross walls (Fig. 3.9) (*107*).

Pepper cultivars differ greatly in capsaicin level, with those of *C. frutescens* among the highest (Table 3.6) (*104*). Pochard uses a quick chemical color test for pungency. A bit of placenta tissue is transferred to filter paper with a spear needle and a little of the oily secretion absorbed on the paper. When a drop of a 1% solution of vanadium oxytrichloride in carbon tetrachloride (Marquis reagent) is added, a bluish color develops if capsaicin is present. A negative color test could always be verified by taste (*117*). Van Blaricom and Martin have devised permanent color standards for this test (*155*).

Total Capsaicinoids and Scoville Units

Total capsaicinoids include capsaicin plus four structurally similar, pungent compounds. The pungency stimulus of peppers is predominantly piperine. The percentage of capsaicinoids in dried red capsicum powder and in oleoresins is an important index of quality for these products, which are widely used as spices by the world food industry to provide pungency and red color.

TABLE 3.5. Mean Values of Capsaicin Content in Various Parts of Fresh and Thermally Processed Jalapeno Pepper[a]

	Capsaicin[b] (mg/100 g)	
Pod portion	**Fresh**	**Processed**
Outer wall	0.12a	128.19ab
Cross wall	18.37c	345.96c
Placenta	8.2b	194.05b
Seed	0.45a	68.24a

[a]After Huffman *et al.* (*77*).

[b]Means followed by different letters are significantly different at the 1% level according to the Student–Newman–Keuls test. Each mean represents eight determinations.

The American Spice Trade Association uses the Scoville unit (SU) measure of pungency, which is the reciprocal of the highest dilution at which pungency can still be detected by a taste panel. The method is subjective, with results varying by up to 150% (*152*). It is nonetheless the preferred method of the U.S. industry because chemical tests are lengthy and laborious and do not relate directly to pungency. Chemical tests are, however, necessary to monitor the reliability of the SU method. Rajpoot and Govindarajan (*122*) found that paper chromatography used in conjunction with a spectrophometer to measure absorbance by capsaicinoids at 615 nm gave reproducible results that correlated closely with SU values. They expressed this relationship by the least squares regression equation $y = -9.22 + 164.126x$ ($r \simeq 1$), where y is the SU (in 1000s), x the total capsaicinoids (%), and r the correlation coefficient, which is equal to or close to 1. y can therefore be calculated directly from x and vice versa. This method can also be used to estimate capsaicinoids in immature peppers that have been dried. In bell and paprika peppers that have very low concentrations of capsaicinoids (<0.1%), SU values may be overestimated due to the presence of nonpungent phenolic compounds, e.g., epigenol and lutein (Table 3.6).

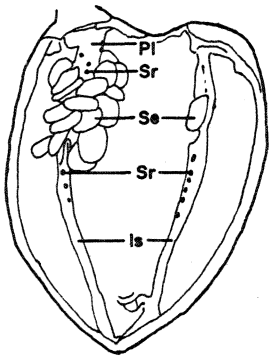

FIGURE 3.9. Secretory receptacles in the F_1 hybrid Takanotsume (pungent) × Large Bell (sweet). Pl, placenta; Sr, secretory receptacles of capsaicin; Se, seed; Is, interlocular septum.
After Ohta (*107*).

TABLE 3.6. Capsaicinoid Levels (as Percentage of Dry Matter and in Scoville Units, SU) in *Capsicum* Species, Cultivars, and Accessions[a]

Species	Variety or accession	Capsaicinoids (%)	SU (1000)
C. annuum	059-991	0.80	131
	Long Red Cayenne	0.55	90
	Fresno Chili	0.32	52
	AC 1874	0.16	26
	N58-248	0.67	110
	KUSE 132A	0.25	41
	KUSE 132B	0.26	43
	KUSE 132C	0.30	49
	KUSE 751A	0.32	52
	KUSE 751B	0.34	56
	KUSE 751C	0.35	57
	KUSE 751D	0.33	54
	Large Bell	0.06	10
	Bola	0.05	8
	Doux	0.04	7
C. frutescens	Tabasco	0.88	144
	AC 1443	0.96	157
	AC 1651	0.50	82
	AC 1585	0.46	75
	AC 1448	0.43	70
C. microcarpum	AC 1553	0.58	95
C. chacoense	AC 1256	0.35	57
	AC 1751	0.24	39
C. pendulum	AC 1941	0.41	67
	AC 1786	0.40	66
	AC 1233	0.30	49
C. pubescens	Roja	0.65	107

[a]Estimated SU pungency scale (1000): no pungency detectable (0.0–10); mildly pungent (11–30); moderately pungent (31–80); highly pungent (>80). KUSE: collected by Kyoto University Scientific Expedition to Afghanistan and Iran, 1955. [After Ohta (*104*).]

Rymal *et al.* have developed an injection–extraction method for the rapid determination of total capsaicinoids in single whole pepper fruits (*127*).

Inheritance of Pungency

Inheritance studies of pungency generally support the single dominant gene hypothesis. Webber reported a ratio of 25 hot- to 5 sweet-fruited plants in the F_2 of the cross Red Chili (hot) × Golden Dawn (sweet) (*160*). Deshpande observed an F_2 ratio of 202 pungent to 70 nonpungent plants, $\chi^2(3:1) = .078$, $P = .90$, in a cross of a cayenne with a sweet bell type. He assigned the symbol *C* for capsaicin to this gene (*46*).

However, Ohta, using a quantitative method for determining pungency, namely, a combination chromatography–taste threshold method, found varying degrees of pungency in F_1 and bimodal distributions in F_2 and in BC populations. His results clearly showed polygenic inheritance of pungency. A major gene determined pungency, but the poly-

genes acting in a cumulative manner, both positive and negative, determined various degrees of pungency (*106*). Ohta also found that high nighttime and daytime temperatures increased the capsaicin content.

Inheritance of Mature Fruit Color

Smith reported the mode of inheritance of red, brown, and green mature fruit colors in peppers (*140*). Chocolate brown fruit is common in Mexican cultivars of *C. annuum*. The cross Mexico Acc. 406 (red) × Mexico Acc. 401 (brown) produced a red F_1 and an F_2 ratio of 3 red : 1 brown. The BC to Acc. 401 produced 18 red : 19 brown, and the BC to Acc. 406 produced only red. The cross Oshkosh (yellow mature fruit) × Acc. 401 (brown) produced a new green mature fruit color in the F_2, the double-recessive genotype. The digenic ratio was 132 red : 46 brown : 44 yellow : 11 green, a good fit to a 9 : 3 : 3 : 1 ratio (P = .50–.70). Smith ascribed brown fruit color to the presence of a recessive chlorophyll retainer gene *cl*, which prevents the complete degradation of chlorophyll. The presence of chlorophyll with the red pigment lycopene (gene y^+) produces the brown fruit color. Hence, the mature fruit colors and their genotypes are Oshkosh (yellow) y/y, cl^+/cl^+; Acc. 406 (red) y^+/y^+, cl^+/cl^+; Acc. 401 (brown) y^+/y^+, cl/cl; and mature green y/y, cl/cl. The latter fruit color may prove valuable for breeding green peppers with a longer harvesting period and a longer fresh market life, since mature red bell peppers are not acceptable to the fresh market.

Inheritance of Immature Fruit Color

Odland and Porter studied the inheritance of immature fruit color in crosses between several cultivars of *C. annuum* (*102*). The cultivars, their immature fruit colors, and deduced genotypes were Ornamental, sulfury white, *sw1/sw1, sw2/sw2, . . . , swn/swn;* Hungarian Yellow Wax, yellow green or lettuce green, $sw1^+/sw1^+$, *sw2/sw2, . . . , swn;* Oshkosh and Red Cherry, both dark green or cedar green, $sw1^+/sw1^+$, $sw2^+/sw2^+$, . . . , *swn*. The cross Ornamental × Oshkosh produced a medium-green F_1 and an F_2 ratio of 15 green : 1 sulfury white. Because of incomplete dominance, the 15 green F_2 plants include four shades of green, corresponding to the number of sw^+ genes present in their genotype. The BC to Ornamental produced a ratio of 1 medium green : 2 yellow green : 1 sulfury white. Similarly, the cross Oshkosh × Hungarian Yellow Wax produced a medium-green F_1 and an F_2 ratio of 1 dark green : 2 medium green : 1 yellow green. Subsequently, Odland confirmed the duplicate-factor hypothesis with additional crosses of Harris Earliest, Harris Early Giant, and Cayenne, all cedar green, with Ornamental (sulfury white). However, certain F_2 families of the crosses with Harris Early Giant and with Cayenne segregated 63 green : 1 sulfury white. Other F_2 families from the same crosses produced 15 : 1 ratios, indicating that some plants of these two cultivars carried three sw^+ gene pairs (*101*).

Inheritance of Pedicel Length

A long, slender pedicel is desirable to allow for expansion of the developing fruit, especially of large-fruited bell peppers. A short pedicel on a determinate plant results in many deformed fruits. Subramanya and Ozaki reported that long pedicel was partially dominant over short and polygenic in inheritance. F_2 populations exhibited a continuous range of phenotypes. Estimated additive gene heritability was 88% and the genetic ad-

vance based on the selection of 5% of the F_2 plants with the longest pedicels was 42%. At least three loci determined this trait (*151*).

Inheritance of Multiple Fruitedness

C. annuum typically sets one fruit per axil, whereas *C. chinense* sets from one to four. The transfer of this trait to *C. annuum* promises potentially higher yields. Subramanya reported on the inheritance of multiple flowers in the cross Delray Bell × PI 159236. He concluded that probably three major dominant genes control double flowers but that more genes are required to produce three to four flowers per node (*150*). J. E. Watson and W. H. Greenleaf (unpublished) concluded that seven semirecessive additive genes determined multiple fruitedness in *C. chinense* Acc. 1555. Both studies indicated that the transfer of double fruitedness to *C. annuum* was possible by the BC method. Our results indicate that genes for this trait would need to be concentrated in selections made in alternate selfed generations before each BC.

Breeding New Ideotypes

Genetic restructuring of the plant habit of large fruited bell and pimento cultivars from indeterminate to determinate promises to increase the yield per plant.

Hoyle (*76a*) described four variations in the indeterminate habit of chili peppers, and concluded that the ideal chili plant is 18–24 in. tall, erect and compact, and produces up to 15 fruits. For this type plant to develop, the fruit must be set early so that all the branches on both sides of the main fork develop equally. Unbalanced plants produce fewer fruits.

Subramanya defined two promising determinate ideotypes (*148a*). The first has a single unbranched stem with one or two fruits per node and a single unbranched terminal cluster of four fruits for a total of 13 fruits. The second type, also with a single stem bears all of its fruits (up to 12) in a single, branched compact terminal cluster. The first plant type lacks foliage cover and may be subject to sunscald, whereas the second is bushy and compact and protects the fruit well. Both plant types are structured for resistance to breakage from a heavy fruit load and also to permit close spacing. No cultivars of these two new ideotypes have yet been released.

Among potential parents for breeding determinate plant types of *C. annuum* are Truhart Pimento (for fruit size and long fruit pedicel), *C. chinense* Acc. 1555, PI 159236, and Rocotillo (for multiple fruited nodes and disease resistance), and Santaka and Frommage (with the gene *fa* for compact determinate fruit clusters).

Selection for Seedling Emergence Free from the Seed Coat

Failure of pepper seedlings to emerge free from the seed coat (sticky seed) has been observed in otherwise promising lines. This major weakness prevents the separation of the cotyledons and retards the growth of affected seedlings. It can be avoided by rigorous selection.

Internal Fruit Proliferation

This undesirable genetic trait is common in a wide variety of large-fruited pepper cultivars, ranging from 0 to 25% of affected fruit (*89*). The fruitlike outgrowths from the base of the placenta or fruit wall should be avoided when making selections.

BREEDING FOR DISEASE RESISTANCE

Fruit Rots, Cercospora Leaf Spot, and Powdery Mildew

Most pepper cultivars are susceptible to fruit rots of several kinds. Morgan-Jones, mycologist at Auburn University, identified the following from infected field-grown fruit: (1) *Alternaria tenuissima,* (2) *Colletotrichum dematium,* (3) *Colletotrichum gloeosporium,* (4) *Curvularia lunata,* and (5) *Phoma destructiva.* I observed high field resistance to fruit rot, including soft rot caused by *Erwinia carotovora,* in *C. chinense* Accs. 1555, 1554, 906 (Uvilla Grande), and others. Resistance appears to be dominant and dependent on few genes. The mode of inheritance to specific organisms would need to be determined by controlled inoculation. Bartz and Stall found that Jalapeno was the most resistant to *E. carotovora* of some 26 cultivars tested by puncture inoculations of stem, calyx, and fruit wall (*6*).

Among other cultivars the following have been reported from India as resistant to anthracnose (*Colletotrichum capsici*) fruit rot: *C. annuum* cvs. Chinese Giant, Yolo Y, Hungarian Yellow Wax, Spartan Emerald, and Paprika; to cercospora leaf spot (*C. capsici*): California Wonder, Canape (F1), Merrimack Wonder, and *C. microcarpum;* to powdery mildew (*Leveillula taurica*): *C. microcarpum, C. pendulum,* and *C. pubescens;* moderately resistant cultivars of *C. annuum* were World Beater, Florida 1063-2, Bull Nose, Midway, Spanish Long, PI 159252, PI 288982, and Chilli Long (*154*). From the F_1, F_2, and the BC to Pimiento of the cross *C. annuum* Acc. 46101 (Brazil, res.) × Pimiento (susc.), Hare concluded that resistance was semidominant and its inheritance trigenic.

Bacterial Leaf Spot

This disease, caused by the bacterium *X. campestris* pv. *vesicatoria,* can quickly defoliate pepper plants in hot humid weather, resulting in sun-scalded fruit, heavy crop loss, and even crop failure. Fieldhouse and Sasser have developed a selective culture medium that will support growth of pv. *vesicatoria* but essentially prevent the growth of all other species of *Xanthomonas,* contaminant bacteria, and fungi (*57*). Two races of this bacterium occur in Florida, of which race 2 is the more common. PI 163192, a cayenne type from India, and *C. chacoense* PI 260435 possess single dominant gene resistance to race 2 and 1, respectively, when the plants are inoculated by infusion into the leaves (*33,34*).

Sowell, and Sowell and Dempsey reported that *C. annuum* PIs 163189, 163192, 271322, and 322719 were resistant to both races when inoculated by spraying the plants. Of these, PI 322719 was perhaps the more valuable to breeders because of its larger, nonpungent fruits (*144,145*). Dempsey transferred the resistance of PI 163192 to pimiento. This resistance has held up at Experiment, Georgia, for over 20 years. Adamson and Sowell confirmed the monogenic dominant resistance in PI 163192 and showed further that PI 322719 carried a different single dominant gene and that PI 163189 possessed two or more additive genes, at least one of which was linked with the dominant gene in PI 163192 (*1*). Cook incorporated resistance to race 2 into VR2 and to both races into XVR3-25 (*31*).

Stall, however, reported a breakdown of race 2 resistance from PI 163192 in Florida due to a high mutation rate in pv. *vesicatoria* for a change in race, namely, one cell in 40,000. This high rate of mutation according to Stall would prevent the use of this single dominant gene (vertical resistance). By the use of the leaf infusion technique with a

sufficiently low concentration of bacteria (2.5×10^3 cfu ml^{-1}), whereby separate lesions were produced on the leaves rather than a confluent necrosis, Stall could differentiate resistant plants in the F_2 of the cross PI 271322 × Early Calwonder by their lower lesion counts. The F_2 ratio of 140 susceptible : 10 resistant plants indicated that two recessive genes determine this horizontal resistance, which the bacterium would presumably be less likely to overcome (*147*).

Phytophthora Root Rot

This soilborne disease, caused by the fungus *Phytophthora capsici,* is common in the furrow-irrigated Southwest and California. Kimble and Grogan reported that of 613 Acc. of *C. annuum* only 13 exhibited various degrees of resistance, determined by survival counts of seedlings 30 days after inoculation. PIs 188376, 201232, and especially 201234, a cayenne type from Central America, proved resistant with only 7–15% of dead plants (*84*). Smith *et al.* found resistance dominant in F_1 hybrids with YW. F_2 and F_3 progeny gave 3 : 1 and 15 : 1 ratios, with acceptable χ^2 probabilities, indicating that one or two independent dominant genes (duplicate factors) conferred resistance. However, there was much heterogeneity among the ratios. The authors nevertheless concluded that a high level of resistance could be transferred to desirable cultivars (*142*).

In Brazil, Matsuoka conducts tests with *P. capsici* in the greenhouse at 20°–30°C. He sows 20–30 seeds per row and inoculates seedlings 40 days later by pouring 30–40 ml per row of a suspension containing about 4.8×10^4 zoospores per milliliter. Young pathogenic cultures are grown on V-8 juice agar under continuous fluorescent light of 2000 lux. To induce sporulation, 20 ml of distilled water are added per petri dish culture and the surface is rubbed gently to collect the sporangia. Most of the young sporangia discharge zoospores within 2 hr at room temperature. Cold treatment was not necessary for the release of zoospores (*93*).

Pochard and Chambonnet devised a quantitative method, suitable for making resistant individual plant selections (*120*). Young potted plants in the early flower bud stage are decapitated above the seventh or eighth leaf with a razor blade. The cut stem surface is inoculated with a 4-mm-diameter disk from a mycelial culture in a petri dish and protected from desiccation with aluminum foil. The plants are usually transferred to a growth chamber maintained at 22°C and 12 hr of fluorescent light of 900 lux at plant level. Measurements of the length of the stem necrosis were made to ±1 mm every third day. The rate of fungus advance is usually negatively correlated with the survival rate of seedlings by the root inoculation method. The authors demonstrated transgressive segregation in a cross of the moderately resistant cv. Phyo 636 with a susceptible cultivar. The hybrid possessed both a higher level and a more stable resistance than Phyo 636. The latter is similar to YW; it derives from the cross PI 201234 × YW, followed by three BC to YW and five selfed generations. Resistance determined by the above method must be confirmed by the seedling root inoculation method.

Pochard concluded that PI 201234 remains the best source of resistance so far identified. It has been used extensively to incorporate resistance into several French cultivars. He described resistance in F_2 as plurimodal, determined by at least two complementary dominant genes, their expression depending on the genetic background. Significant variety–isolate interaction showed that resistance was variety–isolate specific, not general. Mulato proved highly resistant in Bulgaria, both in the field and when artificially inoculated.

Southern Blight

This important disease of peppers caused by *Sclerotium rolfsii* is common in the tropics and subtropics. This organism usually exists as a saprophyte in the soil and expresses its pathogenic potential only under favorable conditions of nutrition, moisture, and temperature (30°–35°C). Typically the stem is invaded at the soil surface, where the fungus can be identified by its cottony mycelium and by its white and later dark brown sclerotia. Success in breeding for resistance is dubious because there are no well-defined levels of genetic resistance and the fungus is an omnivorous, facultative parasite. However, significant differences in survival of pepper cultivars have been reported (*43*), but the genetic basis and nature of this resistance remains obscure. In the currant tomato (*Lycopersicon pimpinellifolium*) PI 126932 resistance is associated with a thick cork periderm that develops when the plants are about 6 weeks old (*96*).

Southern Bacterial Wilt

This is an important disease of peppers and tomatoes in the tropics and subtropics as well as in parts of the southern United States. It is caused by the bacterium *Pseudomonas solanacearum*. In field tests on Guadeloupe, Kaan and Anais screened 35 pepper cultivars of diverse types for resistance (*82*). Of these, 18 were highly susceptible, including Florida Giant, Florida VR2, Puerto Rico Wonder, Titan, Yolo Wonder, Allbig, World Beater, Aconcagua, Agronomico 8, Avelar, Truhart Perfection Pimiento, Vinedale, Sunnybrook, and Sweet Cherry. Moderately resistant were Bastidon, Doux d'Espagne, Doux de Valence, Chinese Giant, Saint-Remy, Narval, and Largo Valenciano B209. These cultivars have large, elongated, thick-walled fruits. Cubanelle, Hungarian Sweet Wax, and Sweet Banana were also moderately resistant. Highly resistant were the more primitive cvs. Antibois, Chay 3, Conic, and two Cook lines derived from a cross of the Philippine cv. Bontoc with Pimiento. Local cultivars of *C. chinense* and *C. frutescens* on Guadeloupe appear unaffected by *P. solanacearum* and unlike most cultivars of *C. annuum* will set fruit at high night temperatures.

Root Knot

Hare reported that Santaka and a pepper labeled 405 B Mexico (both *C. annuum*) each carry a single dominant gene that confers resistance to the southern root-knot nematode *Meloidogyne incognita* and to its race *acrita,* the cotton root-knot nematode. He assigned the symbol *N* to both genes. From Hare's data it appears probable that this resistance was also effective against *M. arenaria* and *M. javanica*. He selected six homozygous resistant lines in F_3, three from crosses of Santaka with Ruby King and California Wonder Special, and three from crosses of 405 B Mexico with Burlington and Truhart Pimiento. The six lines were also highly resistant to the above two species. Early California Wonder, used as the check, was susceptible to all four nematodes, but Ruby King, Burlington, and California Wonder Special were only slightly susceptible to *M. arenaria* and resistant to *M. javanica*. All of the above-mentioned cultivars are susceptible to *M. hapla,* the northern root-knot nematode (*70*).

Screening for Root-Knot Resistance

Chopped Galled Roots Method

A simple method is to chop galled roots, preferably of okra, tomatoes, or squash, into small pieces with a hatchet on a wood block. Mix thoroughly 1 vol chopped roots with 4

vol moist field soil. (This is important to prevent decomposition of the roots by fermentation.) Place a sheet of newspaper in the bottom of a standard wood flat (21 × 14 × 3 in.) and cover with a 1-in. layer of moist sand or of a peat–sand mixture (unsterilized) for drainage. Level and tamp. Cover with a 1-in. layer of the root-knot inoculum; level and tamp.

Finish with a 1-in. layer of moist, sterile medium. Sow seeds into the sterile medium in five rows and cover with more sterile medium. Drench flats with a tribasic copper sulfate plus NutriLeaf-60 solution (1 tsp of each per gallon) to control damping-off. Thin seedlings in cotyledon stage to 20–24 per row. Duration of the test should be about 40 days from emergence. The temperature of the root medium must not exceed 85°C at any time because higher temperatures cause a breakdown of resistance (*76*). Seedlings are classified visually into five classes: 1, heavily knotted; 2, moderately knotted; 3, slightly knotted; 4, very few knots; 5, no knots. Classes 4 and 5 seedlings are resistant. True breeding resistant F_3 lines are easily recognized. With 16 F_3 seedlings all resistant, $P = 0.99$ that the population is homozygous (*159*).

Egg Inoculation Method

Hussey and Barker tested several methods of egg preparation of *Meloidogyne* species (*78*). Probably the best method, which gave a 70% egg hatch and 58% larval penetration, was to treat the chopped galled roots in ⅕ strength Clorox for 4 min with agitation. Shepherd drains the Clorox solution through a 200-mesh screen into a 500-mesh screen to catch the eggs and then rinses off the digested roots under the tap (*131*). The eggs are left standing in 1–2 liters of water for about 1 hr to free them of Clorox, and then rescreened. One-milliliter aliquots are counted under the binocular microscope, and the egg suspension is diluted to 1000 eggs/ml. Pepper seedlings are inoculated in the cotyledon stage with 10 cc each of the inoculum. Duration of the test is about 40 days from emergence.

VIRUSES

Viruses are among the more serious agents of disease in peppers, sometimes causing whole fields to be abandoned prior to harvest. Virus RNA in the nucleus interferes with the normal synthesis of chlorophyll, causing chlorosis and a mottling of the foliage known as mosaic. Symptoms vary greatly in severity from a mild mottle to severe mottling, leaf puckering, leaf distortion, shoe stringing, and extreme plant stunting (rosetting). Some viruses cause systemic necrosis, which may be lethal. Only rarely is a lethal wilt induced, as by TEV in Tabasco.

Resistance to Common TMV

Holmes' research with viruses laid the foundation for breeding TMV-resistant peppers (*74,75*). He discovered the necrotic local lesion reaction to TMV infection in *C. frutescens* cv. *Tabasco* and in *C. annuum* cv. Minimum Blanco. Localized necrotic lesions develop on the inoculated leaves in 3–4 days (Fig. 3.10). The lesions are interpreted as a hypersensitive reaction to infection. The invaded cells promptly die, thus localizing the virus in the lesions and preventing systemic spread. In 5–7 days the inoculated leaves turn yellow and abscise, leaving the plant free of virus. In contrast, most cultivars of *C. annuum* produce a systemic mottle disease known as mosaic. Holmes found that the local necrotic lesion reaction was dominant in crosses with mottling reaction plants and inher-

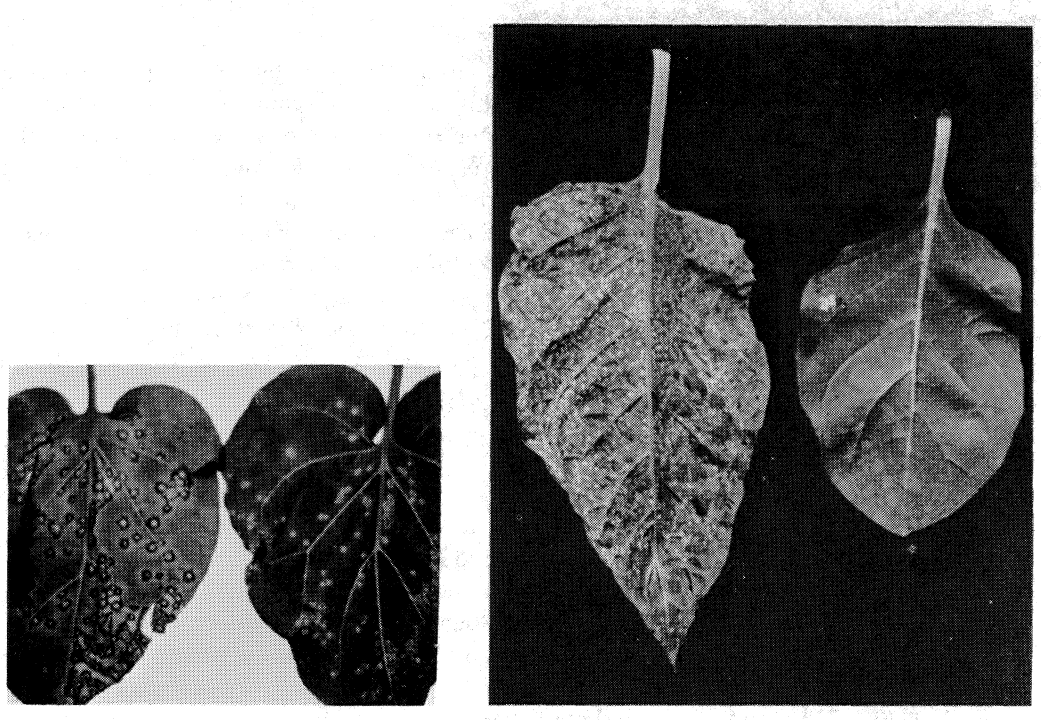

FIGURE 3.10. Virus symptoms on tobacco. (A) Larger lesions induced by common TMV vs. (B) smaller lesions produced by SLTMV on *Nicotiana glutinosa;* (C) TEV-infected leaf and (D) healthy leaf of *Nicotiana tabacum.*

ited as a monogenic dominant trait. He assigned the symbol *L* to this gene and *l* to the recessive allele and transferred it from Tabasco to bell peppers. This important gene prevents systemic infection in the greenhouse and field by common strains of TMV.

Holmes found an additional gene at the *L* locus in Long Red Cayenne, in Sunnybrook, and in a selection from cv. Sweet Meat Glory. Plants with this gene produced yellowish primary lesions that tended to become necrotic, the necrosis spreading along the leaf veins. Leaf abscission would usually occur with recovery and freedom from virus, but a few plants would develop scattered secondary (systemic) lesions in noninoculated leaves. Holmes designated this gene l^i to denote the imperfect localization of the virus. The gene *L* was completely dominant over l^i and *l*, but l^i/l genotypes would respond with systemic necrosis, especially at higher temperatures (approx. 30°C), and all of the plants would die. Pochard reports that l^i acts as a completely dominant gene with most European tomato strains of TMV (Aucuba type) at 20°–25°C. The inoculated cotyledons abscise, thus freeing the plants of virus (*119*).

Several important commercial pepper cultivars have the l^i/l^i genotype, among them Keystone Resistant Giant, YW, Yolo Y, Florida VR2, VR2-34, XVR3-25, and the Dutch greenhouse cv. Verbeterde Glas. These cultivars are not infected by common strains of TMV under normal greenhouse and field environments. The allelic series of Holmes $L>l^i>l$ has been redesignated $L^3 > L^2 > l^1 > L^+$ by Boukema (Table 3.7) to include recent data and to conform to present rules for gene symbols (*15*).

Pepper Strains of TMV

McKinney isolated a pepper strain of TMV from a TEV-resistant pungent cultivar from South Carolina, Cayenne SC 46252 (*94*). This strain, unlike common TMV, produced no local lesions on this cultivar, but a systemic mottle disease. A second distinguishing feature was its failure to infect tomato (*Lycopersicon esculentum*). A third was that it appeared to be latent (symptomless) in Turkish Samsun tobacco. This virus has since been reported from Alabama, Florida, Louisiana, and south Texas. Greenleaf *et al.* designated it the Samsun latent strain of TMV (SLTMV) (*67*). Several strains of this virus have been identified by Rast in Holland (*123*) where it poses a threat to the considerable greenhouse production of bell peppers, which was 22,000 tons from 435 acres in 1977. SLTMV continued to spread despite soil steaming, seed and tool disinfection, and hand dips in skim milk (*150*). SLTMV stunts the plants, roughens the fruit, and reduces yield.

Resistance to SLTMV

An intensive search has been made to discover local lesion-type resistance to SLTMV similar to that so effectively provided by the L^2 gene (*L* gene of Holmes) against strains of common TMV. Greenleaf *et al.* screened 125 PIs of several species (*67*), and Simmons tested 1105 Accs., mostly of *C. annuum,* but including a few of *C. chinense* and *C. pendulum.* No local lesion response was found, but differences in susceptibility were noted. Simmons listed 28 PIs, of which some plants remained apparently symptomless after repeated inoculation (*137*). The progeny of 10 selected plants from PIs 297486, 179870, 174809, and 174111 showed intermediate levels of resistance expressed in a lower virus titer and mild symptoms (*10*).

Boukema (*15*) screened 524 PIs of 10 species with Rast's strains P8 and P11 and discovered 10 PIs of *C. chinense* that produced local necrotic lesions with strain P8. These PIs possessed a third gene L^3, allelic with Holmes *L* series. Breeding for L^3 resistance appeared promising until Rast isolated strain P14 in 1979, which overcame L^3 resistance (Table 3.7). It was concluded that oligogenic or polygenic sources of resistance were needed to control this mutable virus.

Additional TMV Strains in Peppers

A pepper strain of TMV that produces local lesions on *L* gene peppers that are followed by systemic infection but that will not infect tomato (*L. esculentum*) has been reported from Argentina (*56*); and a tomato strain that reacts similarly on peppers has been reported from Hungary (*38*). Of some 20 cultivars of several species tested, only *C. chinense* PI 159236 proved resistant. This PI responded with small necrotic local lesions that eventually resulted in leaf abscission and freedom from virus.

Other Pepper Viruses

In surveys of viruses in pepper fields in Louisiana, Sciumbato and Whitam found that cucumber mosaic virus (CMV), potato virus Y (PVY) and tobacco etch virus (TEV) accounted for over 90% of infected plants. Tomato spotted wilt virus (TSWV) and the pepper strain of TMV (SLTMV) made up most of the remainder. Common TMV was rare, and surprisingly, pepper mottle virus (PMV) was absent from pepper fields in Louisiana (*130,161*).

Villalon identified the same viruses in peppers in south Texas, plus PMV and tobacco

TABLE 3.7. Relation between Genotypes for Resistance in *Capsicum* and Strains of TMV[a]

Accession	Genotype symbols		TMV strains			
				Pepper strains		
	Original (Lippert *et al.*)	Proposed (Boukema)	Tomato (P_0)	P_{11} (P_1)	P_8 ($P_{1.2}$)	P_{14} ($P_{1.2.3}$)
C. annuum cv. Early Calwonder	L^+L^+	L^+L^+	+	+	+	+
C. annuum cv. Verbeterde Glas	L^iL^i	L^1L^1	−	+	+	+
C. chinense Ru 72-292	L^iL^i	L^1L^1	−	+	+	+
C. frutescens cv. Tabasco	$L\ L$	L^2L^2	−	−	+	+
C. chinense PIs[b]		L^3L^3	−	−	−	+

[a]After Boukema (*15*).
[b]PIs 152225, 159233, 159236, 213917, 215024, 224424, 257117, 257284, 315008, 315023.

ring spot virus (TRSV) (*157*). PMV was first identified by Zitter in Florida (*162,163*). PVY, TEV, and PMV are long flexuous rods, classified as potyviruses, named after the type virus PVY. The various strains of TMV are long straight pods, classed as tobamoviruses. CMV, the type virus of the cucumovirus group, is isohedral (*25*).

Sources of Virus Infection

Weed Hosts

Mechanical transmission of viruses from weeds to peppers is generally difficult. Whitam transferred CMV, PVY, TEV, and TSWV to pepper from 18 species of weeds (*161*). The largest number of successful transmissions were from *Solanum nigrum* (black nightshade) 26/42; *Medicago anabica* (spotted bur clover) 15/85; *Rudbeckia amplexicaulis* (Blackeyed Susan) 12/54; *Melilotus officinalis* (yellow sweet clover) 10/51; *Geranium carolinianum* (cranesbill) 8/40; and *Senecio glabellus* (butterweed) 5/69. Of 615 attempted inoculations, 47 yielded CMV, 45 PVY, 21 TEV, and 7 TSWV.

Crop Plant Hosts

Sciumbato assayed cultivated crop plants growing near pepper fields and mechanically transferred the following viruses to peppers: CMV, TEV, TMV, and potato virus X (PVX) from tomato; CMV from cantaloupe; CMV and TEV from eggplant; TMV, TEV, and PVX from tobacco and PVX from mustard.

Virus Transmission by Aphids

CMV, PVY, TEV, and PMV are transmitted from diseased weeds or crop plants to peppers by aphids, in a nonpersistent stylet-borne manner. Common vectors of CMV in Louisiana were *Myzus persicae* (green peach aphid) and *Aphis gossypii,* and of PVY and TEV, *M. persicae* and *Aphis craccivora.* CMV is reported to be transmitted by over 60 species of aphids (*25*). TSWV is transmitted by thrips.

Seed Transmission of Viruses

Transmission of common TMV in tomatoes and of SLTMV in peppers through the endosperm of the seed is rare, and the embryos of both species appear to be immune.

Seedling infection may occur from surface-contaminated seed during seedling emergence (*36,45,153*). However, Sciumbato found that only 1–2% of Tabasco seedlings became infected by SLTMV during germination when left undisturbed, but that handling during transplanting and especially pruning the plants to make them bushy, resulted in nearly 100% infection. Seed treatment removes this source of infection. CMV, PVY, TEV, and PMV are not seed transmitted.

Yield Reduction from Viruses

Sciumbato reported yield reductions from SLTMV-inoculated Tabasco of 38 and 22% in two tests, and from TEV in bell peppers and Cayenne of 23 and 21%, respectively. CMV reduced the yield of bell pepper by 97% and of Cayenne 61% (*130*).

Villalon reported similar yield reductions in bell peppers inoculated with four viruses prior to field planting (Table 3.8). Field losses were similar for jalapeno and chili peppers (*157*).

TABLE 3.8. Yield Reduction in Six Bell Pepper Cultivars Caused by Four Viruses[a]

Variety	Virus	Tons/acre[b]	Yield reduction (%)
Tamu Bell 7506	Check	9.6a	—
	TEV	8.1b	15.6
	SLTMV	7.0c	27.1
	PMV	5.7d	40.6
	PVY	4.8d	50.0
Lucky Green Giant	Check	8.4a	—
	TEV	5.2a	38.1
	SLTMV	4.2bc	50.0
	PVY	3.7c	56.0
	PMV	2.0d	76.2
VR-2	Check	6.4a	—
	TEV	5.8a	9.4
	PMV	3.3b	48.4
	PVY	3.2b	50.0
	SLTMV	2.9b	54.7
Keystone Resistant Giant #3	Check	7.7a	—
	TEV	6.5ab	15.6
	PMV	5.8bc	24.7
	PVY	5.1bc	33.8
	SLTMV	4.5c	41.6
Delray Bell	PVY	6.7a	+1.5
	Check	6.6a	—
	TEV	6.3a	4.5
	PMV	6.0a	9.1
	SLTMV	3.5b	47.0
Pip	Check	4.9a	—
	PVY	3.6b	26.5
	SLTMV	3.3b	32.7
	TEV	3.3b	32.7

[a]After Villalon (*157*).

[b]Figures not followed by the same letter differ significantly at $P = .05$ according to Duncan's multiple-range test.

Virus Inoculation Methods

Carborundum Leaf-Wiping Method

This is the standard inoculation method for mechanically transmissible viruses, e.g., TMV, TEV, PVY, PMV, and CMV. The procedure outlined is to serve only as a guide. Virus experiments require careful planning in advance. Young, vigorously growing test plants are needed, e.g., peppers 5–6 weeks and tobaccos 7–8 weeks from seed. The plants are spaced out on the greenhouse bench and labeled in advance. The leaves to be inoculated are marked and dusted with 400- to 600-mesh carborundum. Avoidance of chance virus contamination by contact or by aphids is critical, and the hands need to be washed with soap and water between operations.

Water checks are always inoculated first. Inoculum is prepared by grinding leaves or whole shoots of infected source plants in a mortar or blender. A weighed sample is ground in a measured volume of water or phosphate buffer (KH_2PO_4, 0.01–0.1 *M*, pH 7.0–7.5) to facilitate grinding and to determine the dilution factor. The crude extract is filtered through cheesecloth. TMV extracts are used at 1/100 and TEV, PVY, PMV, and CMV at 1/10 to 1/20 dilution w/v.

Transmission difficulties with CMV due to virus inhibitors in pepper sap were overcome by Pochard by the use of an extraction solution containing 0.025 *M* phosphate buffer, pH 7.0, 5% sodium bisulfite, 1.7 g/liter sodium diethyldithiocarbamate, 0.5% caffeine, and 100 mg of activated vegetable charcoal per cubic centimeter of inoculum.

Test plants are each inoculated in three to four leaves. A wad of cotton or a cloth pad saturated in the inoculum serves as a wiper. The leaf is supported with one hand and is wiped gently three or four times. The plants are rinsed off promptly with tap water when the inoculations are completed. Symptoms develop in 3–10 days, depending on the virus, and maximum virus titer is reached in about 14 days.

Spray Gun Method of Inoculation

This method works well with highly infectious viruses like TMV or SLTMV, but is not as reliable with the less infectious viruses TEV, PVY, PMV, and CMV. Carborundum must be added to the inoculum, about 5% by volume. The plants are sprayed forcefully from a distance of 3–4 in. at 60–100 psi. With this method hundreds of 5- to 6-week-old seedlings in flats can be inoculated in a few minutes. Villalon uses an artist's airbrush at 125 psi. He considers this method only 90% as reliable as the leaf-wiping method but satisfactory for large-scale screening (*158*).

Frozen Storage of Viruses

Cook maintains CMV at a high titer in tobacco by making transfers every 5–7 days. For prolonged storage he freezes finely cut leaves in small test tubes loosely plugged with cotton and placed over $CaCl_2$ within larger rubber-stoppered tubes. In such storage he estimates the longevity of CMV to be 6 months, the potyviruses 1 year, and TMV 10 years (*30*). Crude extracts of TMV diluted 1/10 to 1/50 can also be stored frozen for several years.

Virus Identification

Identification and maintenance of a virus on a suitable host is essential before screening tests for resistance can begin. Identification can be difficult and may involve the cooper-

ative efforts of the breeder, a virologist, an electron microscopist, an entomologist, and an immunologist (to produce antiserum), as well as the help of technicians. For such a team to function properly would require the development and formal approval of a cooperative research project, so that all the scientists can officially justify their involvement.

Differential Host Reactions

This is an important method of virus identification. The unknown virus is inoculated into several tester hosts. Symptoms are compared with those induced by known viruses on the same hosts. Characteristic symptoms on one or more hosts matching those of a known virus can be diagnostic for the unknown virus, e.g., Tabasco wilt for TEV. To identify a new virus requires additional tests.

The identification by Zitter of the new potyvirus PMV in south Florida by this method, supplemented by immunodiffusion tests, is shown in Table 3.9. He separated the virus isolates from peppers into four basic types: TEV-C, a common mild strain; TEV-S, a severe strain; PVY-C, a common mild strain; and PMV (*9,162*).

Cross Protection

This is a sensitive biological test of relationship between strains of the same virus. One strain must be of a known virus that produces local lesions on a tester host in which the unknown virus is systemic. If the two viruses are closely related, the presence of the one systemic in the host will *protect* against entry by the challenge virus, and no local lesions will appear. Examples are common TMV vs. SLTMV on Pimiento Bighart (*69*), and

TABLE 3.9. Reaction of Pepper Cultivars to Florida Potyviruses[a]

	Datura stramonium positive		*Datura stramonium* negative	
Cultivars	**TEV-C**	**TEV-S**	**PVY-C**	**PMV**
Early Calwonder	M	M	M	M
PI 264281	R	M	I	M
SC 46252	R	M	I	M
23-1-7	R	M	I	M
Yolo Y	M	M	I	M
23-1-7 × Yolo Y	R	M	I	M
Avelar	R	MM	I	MM
Agronomico 9	R	MM	I	MM
Ambato Immune	R	MM	I	MM
PI 342947	R	M	I	M
PI 152225	R	R	I	I
PI 159236	R	MM	I	I
Serrano Acc. 2207	R	M	I	M
PI 281367	R	M	I	M
Tabasco	MW	MW	MM	LM
Greenleaf Tabasco	R	R	I	I

[a]Susceptible reaction as determined visually, by indexing on California Wonder or serological tests. TEV-C and TEV-S are, respectively, mild and severe strains of TEV. R, Resistant; I, probably immune; M, chlorotic mottle; MM, mild mottle; MW, mottle and wilt; LM, local lesions on inoculated leaves and occasionally on systemically infected leaves; systemic mottle, with leaf and stem necrosis on young plants, followed by death or regrowth from below the necrotic stem region. [Adapted from Zitter (*162, 164*) and Black (*9*).]

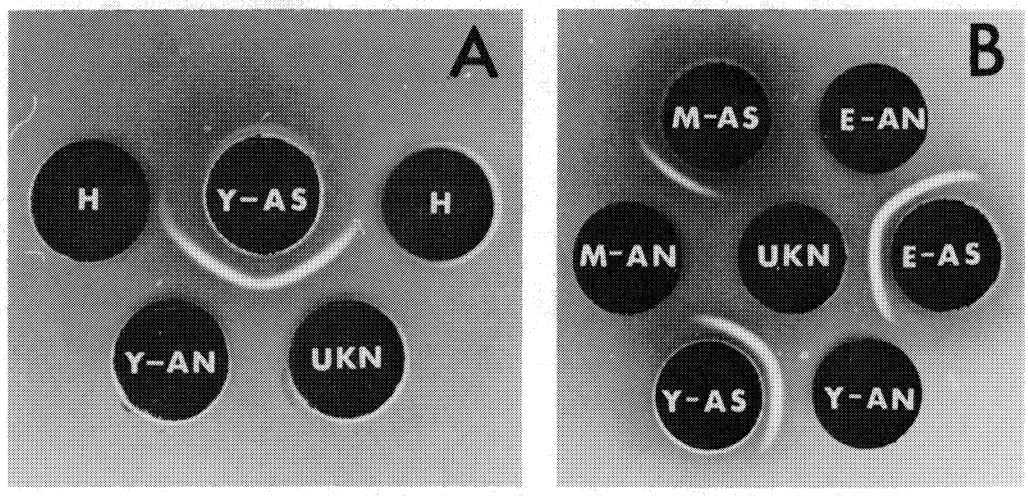

FIGURE 3.11. Immunodiffusion patterns and techniques for the identification of tobacco viruses. (A) Identification of a known virus as PVY. Y-AS, Antiserum to PVY; H, juice from a healthy plant; Y-AN, juice from a PVY-infected plant; and UKN, juice from a plant infected with the unknown virus: (B) Identification of viruses in a doubly infected plant. UKN, Juice from a plant suspected to be infected with PVY, TEV, TVMV, or a combination of these; Y-AS, antiserum to PVY; Y-AN, juice from a plant infected with PVY; E-AS, antiserum to TEV; E-AN, juice from a plant infected with TEV; M-AS, antiserum to tobacco vein mottling virus (TVMV), M-AN = juice from a plant infected with TVMV. AN = antigen (virus); AS = antiserum.
After Gooding (*61*).

Fulton's local lesion *Vinca* strain of CMV vs. virulent systemic strains of CMV on peppers (*59*).

Serology

Definitive identification of a virus may require serological methods as well as electron microscopy. For serological tests, antisera to known viruses are prepared against which the unknown virus (antigen) is tested. Antisera are produced by injecting partially purified virus into rabbits, taking blood samples after a suitable time interval and separating the serum as described by Ball (*4*). (Virus antisera can be obtained from American Type Culture, Rockville, Maryland.) Some viruses are more strongly immunogenic than others, meaning that they produce stronger precipitin reactions and hence a more reliable test. Among the available methods of identification, namely, particle morphology, physical–chemical properties, inclusion bodies, host range, symptomatology, cross protection, and antigenic homology, Gooding considers the last mentioned *the most reliable parameter currently known that can be used alone for identification* (*61*). The main advantage of the agar-gel double-diffusion technique is that *the known virus, the unknown, and control extracts from healthy plants are tested in the same system* (Fig. 3.11).

Enzyme-Linked Immunosorbent Assay (ELISA)

This sensitive immunological technique for plant virus identification was originally developed for human and animal virus diseases, but has also been shown to have wide applicability to plant viruses. In this test, antigen (virus), antiserum, and a serum or antigen-specific enzyme are successively adsorbed to a special plastic microplate. When

the enzyme substrate is added, a color develops, the intensity of which is proportional to the degree of homology of virus and antigen (*52*).

Inheritance of Virus Resistance

Potyvirus Resistance Alleles

TEV resistance in *C. annuum* Cayenne SC 46252 is recessive and monogenic. A few plants remained symptomless after repeated inoculation and gave negative recovery tests on Tabasco, indicating that modifier genes increased the resistance level to near immunity. Resistance in *C. chinense* PI 152225 (identical with PIs 152233 and 159241) was likewise recessive and monogenic. Resistance in both species was expressed in a reduced rate of virus multiplication in plant tissues as compared with susceptible hosts, rather than immunity. The symbols et^a and et^c were assigned to the respective resistance genes to denote their species origin (*64*). Cook subsequently demonstrated monogenic recessive resistance in *C. annuum* PI 264281 (P11) and in SC 46252 (P34) to a common strain of etch (TEV-C) and apparent immunity of both cultivars to PVY-N^{YR}, a more virulent mutant of PVY-N.

The genes in P11 and P34 were allelic and apparently identical with et^a (Cook's invalid gene ey^a) (*26*). Cook later discovered a single PVY-N immune plant in YW, which was the progenitor of Yolo Y. This plant possessed a single recessive gene, which he designated y^a. This gene proved to be allelic with et^a (*27*). Strain PVY-N^{YR} subsequently appeared in Yolo Y (*28*). Cook had thus shown that et^a was allelic with y^a, but did not distinguish clearly between et^a, ey^a, and y^a.

Zitter and Cook reported a third gene that conferred resistance to PMV in *C. annuum* cv. Avelar from Brazil. This gene was allelic with and dominant over et^a. Because Avelar progeny that were tolerant to PMV were also resistant to TEV and PVY, a single gene in Avelar must confer resistance to all three viruses (*165*). This allele, here designated et^{av}, has a higher potency than et^a, which protects only against TEV-C (common strain) and PVY-N^{YR}. Zitter reported similar reactions to TEV-C and PMV in PI 159236 and Avelar but observed a higher level of resistance to PMV in this PI (*162,163*). Subramanya elucidated the genetics of this difference in the cross Delray Bell (et^{av}) × PI. Surprisingly, the F_1 was susceptible to PMV and the F_2 and both BC segregated 1 resistant : 1 susceptible (*149*). The interaction of the resistance alleles of these two cultivars resulted in susceptibility, similar to that observed in the heterozygotes L^1/L^+ (l^i/l of Holmes) in peppers and $TM2^a/TM2^+$ in tomatoes when inoculated with TMV. The published data therefore support the existence of an allelic series of resistance genes to the Florida potyviruses. Only the dominance relationship and allelism of the genes in PI 159236 and PI 152225 remain to be determined (Table 3.10). The symbols et^{c1} and et^{c2} (formerly et^c of Greenleaf) are tentatively assigned to these two genes. The reason for the choice of the etch symbol *et* for these alleles (except for Cook's gene y^a) is that the inheritance data show that genes for resistance to TEV also confer resistance to PVY. An earlier report by Bawden and Kassanis that TEV replaces PVY in mixed infections supports this conclusion (*7*). Resistance conferred by the gene et^a was effective against the Guadeloupe strain but not the Puerto Rico strain of PVY (*28,82*).

Barrios *et al.* (*5*) reported a dominant gene with resistance to TEV in LP-1, a *C. frutescens* cv. LP-1 remained symptomless when inoculated with TEV. The F_1 hybrid LP-1 × Tabasco also remained symptomless when inoculated, showing neither mottle nor wilt symptoms. The F_2 segregated 98 mosaic and wilt resistant to 42 wilted plants (χ^2 =

TABLE 3.10. Resistance Alleles to Florida Potyviruses[a]

Virus strains of increasing virulence (left to right)			
PVY-C PVY-N	TEV-C PVY-N^{YR}	PMV	TEV-S
Sources of resistance			
Yolo Y	PI 264281 SC 46252 VR2	Avelar Delray Bell PI 159236	PI 152225 Tabasco G
Increasing potency and dominance of resistance alleles (left to right)			
y^a <	et^a <	$et^{aw} \nless et^{c1}$ <	et^{c2}

[a]PVY-N, mild strain from tomato, Yolo Y is immune; PVY-N^{YR}, mutant strain of PVY-N that infects Yolo Y; PVY-C, mild strain from Early Calwonder, Yolo Y is immune; TEV-C, common mild strain from Early Calwonder, Avelar is immune; TEV-S, severe strain from Avelar that induces a mild mottle in this variety as does PMV. PI 159236 is rated resistant to PMV, whereas Avelar is only tolerant. The symbol $\nless$ means "not dominant," the heterozygote et^{av}/et^{c1} being susceptible to PMV. Allelism and dominance relationship of et^{c1} and et^{c2} with respect to TEV-S are not established.

1.86, $P = .10–.20$ for a 3:1 ratio). The F_1 hybrid LP-1 × Almeda (*C. frutescens*, exhibits a TEV susceptible mottling response) also remained symptomless. The F_2 segregated 160 mosaic mottle resistant to 65 mottled plants ($\chi^2 = 1.81$, $P = .10–.20$ for a 3:1 ratio). The nature of LP-1 resistance, immunity vs. a low titer symptomless tolerance, was not investigated.

Cucumber Mosaic Virus Resistance

Rusko and Csillery report that CMV is the most common and destructive virus in Hungary and commented that, despite serious losses worldwide, few breeding programs have focused primarily on this virus (*125*). The reason is that the task is difficult because inheritance of resistance is polygenic and varies with plant age and strains of the virus. For example, young Tabasco plants up to 8 weeks old are invaded systemically and develop leaf and stem necrosis and, if they survive, produce distorted, mottled new growth. In contrast, plants 10 weeks or older are able to localize the virus in the older inoculated leaves or in young lateral shoots. In mature plants the virus is not a serious problem.

According to Pochard, no complete resistance to CMV has been discovered in peppers, not even to particular strains of the virus (*116*). He believes that a higher, more durable resistance will require a combination in a single genotype of three kinds of resistance, which he designates Ra, Rb, and Rc. Ra confers ability to escape infection if the inoculum dose is low. Its detection employs Fulton's avirulent *Vinca* strain of CMV, which produces only local necrotic lesions on peppers in numbers presumably proportional to their susceptibility to more virulent systemic strains (Table 3.11). In this, the NF (necrotic Fulton strain) test, young pepper plants are decapitated above the seventh leaf, inoculated in the sixth or seventh leaf, and the number of local lesions produced counted.

Rb is a hypersensitive-type resistance that localizes the virus through necrosis of the invaded tissue. It is detected in plants decapitated above the fourth leaf and inoculated in the third leaf with a virulent local strain of CMV. In susceptible lines the third inoculated leaf becomes necrotic and abscises. Both the third and fourth axillary shoots that develop within a month become necrotic, whereas in hypersensitive lines the fourth axillary shoot

TABLE 3.11. Resistance Levels to CMV in *Capsicum* Species and Cultivars Determined by the Local Lesion Test with Fulton's *Vinca rosea* Strain[a]

Accession	Average number of lesions/leaf
C. chacoense	85
C. chinense Acc. 2	71
C. frutescens Acc. 10	50
C. pubescens Acc. 2	43
C. annuum cv. Bighart Pimiento	42
C. baccatum Acc. 5	31
C. annuum cv. Hatvani	31
C. annuum cv. Yolo Y	31
C. praetermissum Acc. 1	27
C. annuum cv. Javitott Cecei	6.3
C. frutescens Acc. 11	1.7
C. baccatum Acc. 2	1.1
C. frutescens Acc. LP1	0.8
C. annuum Acc. Perennial (Singh)	0.03

[a]After Rusko and Csillery (*125*).

usually remains symptomless and virus free. The absence of virus can be checked by necrotic local lesion tests on *Vigna sinensis* (NV tests).

Rc resistance is non-necrotic and is expressed in a slow rate of virus multiplication in the inoculated sixth or seventh leaf. The degree of resistance is indicated by the number of local lesions produced in periodic subinoculations to *Vigna sinensis*. Decapitation above the seventh leaf is advantageous for this test, as abscission of the inoculated leaf is then delayed for over a month as compared with 7–8 days when decapitated above the fourth leaf.

Field selection for CMV resistance is not reliable, because the amount of inoculum is variable and other viruses may also be present. Cultivars classified by type of resistance were *C. baccatum* (Rb), Moura (Ra, Rc), Ikeda (Rc), Val (Rb), and LP1 (Ra, Rb). The field tolerance of the Brazilian cvs. Moura, Ikeda, and Avelar and of other small-fruited introductions is difficult to assess by the above tests. Rb test symptoms on them were severe. One hope resides in the possible association of resistance in these peppers with the unique, large, unpigmented lesions they produce with the Fulton strain. Pochard observed transgressive segregation for CMV resistance in the cross Val × Babas, both of Rb type. Val derives from Antibois and Babas from the cross *C. baccatum* × Bastidon. The breeding objective is to combine the genes that determine the different identifiable mechanisms of resistance.

SOURCES OF GERMPLASM FOR BREEDING

The largest collection of *Capsicum* species in the United States is maintained at the Southern Region Plant Introduction Station, Experiment, Georgia. Professional breeders around the world have access to this collection of about 2500 PIs. Many have been screened for disease resistances and horticultural characteristics (*109*).

BREEDING METHODS

A survey of the methods by which pepper cultivars have been developed reveals that the following were used: (1) pedigree breeding with selections from superior cultivars; (2) pedigree breeding following hybridization between superior cultivars; (3) transfer of single genes from primitive cultivars or wild forms to leading cultivars by the BC pedigree method; (4) intercrosses between different BC families with different recurrent parents and with different target genes from diverse germplasms to combine several disease resistances and new horticultural traits.

Backcross–Intercross Scheme for Breeding PMV- and CMV-Resistant Bell Peppers

Assume that *C. chinense* Acc. 1555 proved immune to PMV in preliminary screening tests and carries either the gene et^{c1} or et^{c2} that we wish to transfer to Cook's large-fruited, multiple-disease-resistant bell pepper XVR3-25. Additional desirable traits that could be transferred from Acc. 1555 are a round fruit shape (gene *O*), earliness, ripe-fruit rot resistance, and multiple fruitedness. We also wish to transfer the resistance to CMV from Perennial. If preliminary Ra, Rb, and Rc tests were to show that Acc. 1555 also has a high level of CMV resistance, the cross with Perennial would not be needed. A breeding procedure designed to combine the resistance genes for PMV and CMV is shown in Fig. 3.12.

Diallel Crosses and Pepper Improvement[1]

Conventional plant breeding may involve selection of superior individuals from a variable population, hybridization among selected parents followed by pedigree selection, or character introduction into a population by BC breeding. Quantitative plant breeding generally involves crosses among a number of selected parents to initiate a program of general population improvement. Pepper traits that are inherited quantitatively, or whose expression depends upon the accumulation of many genes each contributing small increments to the total expression, include fruit size, fruit yield, carotenoid content, and adaptation to environmental conditions.

Problems to be considered by the quantitative plant breeder are (1) which parents and how many parents to include in matings to provide desirable genetic input, and (2) how to handle the combined population throughout the breeding program to increase the expression of the desired traits.

The diallel cross offers one approach to the evaluation and selection of parents to be combined to form a genetically variable population. It also provides information on genetic control of quantitative traits, which is useful in choosing the breeding procedures that will accomplish the desired improvements. Additionally, the diallel mating scheme provides valuable information on heritability and heterosis, and the results may be used in predicting performance of synthetic populations that may be formed from various combinations of parents.

Simply stated, a diallel cross involves the mating of selected parents (p) in all possible two-parent combinations, with evaluations made on the resulting hybrids. A complete diallel square consists of p^2 crosses, including selfs and reciprocals. A more commonly

[1]This section was written by Dr. L. F. Lippert, University of California, Riverside, and is presented with his permission.

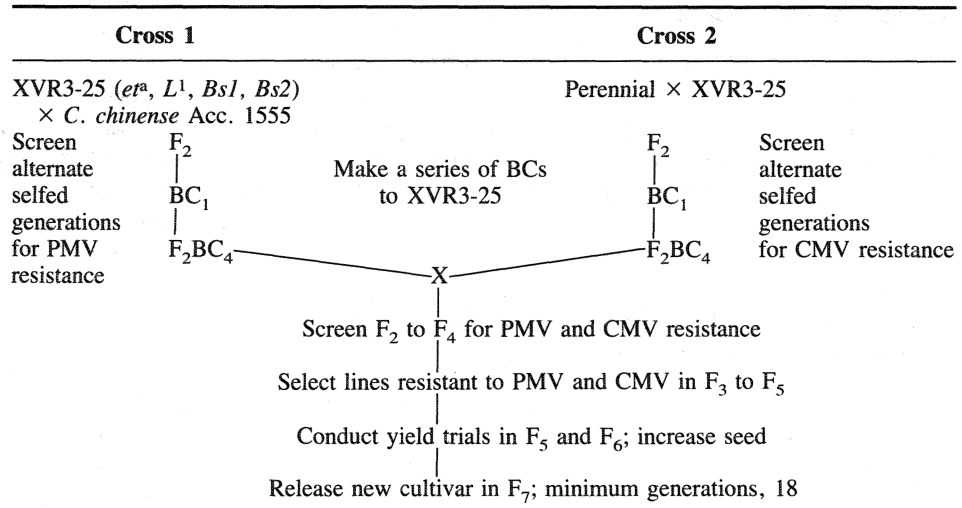

FIGURE 3.12. Backcross–intercross scheme for breeding PMV- and CMV-resistant bell peppers.

used diallel scheme eliminates selfs and reciprocals and evaluates $p(p\text{-}1)/2$ hybrid combinations.

Results from a nine-parent diallel cross in chili pepper were reported by Lippert (*87*) and Marin and Lippert (*90*). Parents were selected pepper cultivars and breeding lines representing mainly Anaheim chili types, but including one high-color Mexican chili type (60M4) and one small-fruited chili (Red Chili) with high fruit number per plant. The purpose of the diallel was to determine types of gene action controlling characters of importance in chili production and to evaluate the nine parents for combining ability, with eventual selection of parents for incorporation into a synthetic population with broad genetic base.

Biparental hybrids and parental selfs were made in the greenhouse and the diallels of 36 hybrids and nine parents were tested during two seasons in southern California. Records included fruit number per plant, dry weight yield per fruit and per plant, percentage of mature fruit at harvest, fruit length and width, and total carotenoid content of the dry fruits. Fruits from this study were also analyzed for pod component percentages by separation into endocarp, exocarp, stem, septa, and seed. The goal of a breeding program would be to maximize the percentage of endocarp, which contains the valuable carotenoid pigments, without reduction of total dry-fruit yields.

The evaluation of parents was accomplished by comparing the performance of each parent in hybrid combination with all other parents. This evaluation is termed general combining ability (GCA) and relates to the additive gene effects within the population. The performance of individual F_1 hybrids compared to average performance of the parent lines involved is specific combining ability (SCA) and relates to nonadditive gene effects. The combining ability effects have the following association in the performance of a particular hybrid:

$$x_{ij} = \mu + g_i + g_j + s_{ij},$$

where x_{ij} is the hybrid performance for a given trait, μ the overall population mean, g_i and g_j the GCA effects for parents i and j, and s_{ij} the SCA effect for hybrid x_{ij}.

Analyses of variance of the diallel data provided significant differences among hybrids for fruit number per plant, dry weight per fruit, fruit length and width, and total carotenoids, as well as for all components for the total dry pod. Separation of the among-crosses variation into GCA and SCA indicated that additive gene effects (GCA) were more important than nonadditive effects (SCA), both in magnitude of variances and significance levels. GCA effects of each parent for four characteristics evaluated in this study are presented in Table 3.12. High positive values for dry-fruit weight and carotenoid levels relate to desirable parental performance. High positive values for endocarp component coupled with negative values for seed indicate desirable parents for those pod components.

Selection of parents for inclusion in a mating program to improve characteristics can be assisted by predicting the performance in synthetic populations from the combination of various parents. The formula for these predictions is

$$\text{performance of synthetic} = \overline{F}_1 - (\overline{F}_1 - \overline{P})/n,$$

where $\overline{P}$ and $\overline{F}_1$ are mean values of selected parents and hybrids between these parents, and n is the number of parents incorporated into the synthetic.

Performance was calculated for a synthetic population based on the mating of three parents, Sweet Pickles, Gentry 456, and 60M4, each selected for high carotenoid content in the dry fruits and for high GCA for this trait. Performance of a four-parent synthetic was predicted with the addition of 57M75, a fairly large-fruited type, but with low GCA for carotenoids, to estimate increase in fruit size and dry-fruit yields. Values of seven characters predicted for these two synthetics are shown in Table 3.13.

Several mating designs and selection schemes may be used to improve the expression of quantitative traits in genetically variable populations. Recurrent selection is effective for traits under additive gene control. Superior individuals identified from an original population are intermated to form a population for the next cycle of selection. Reciprocal

TABLE 3.12. General Combining Ability Effects for Parental Entries for Characters Measured on the Two-Season Performance of F_1 Hybrids in a Nine-Parent Chili Pepper Diallel Experiment[a]

Parent	Dry-fruit wt./plant	Carotenoid content	Pod components	
			Endocarp	Seed
Sweet Pickles	0.53	749	−0.70	0.75
College 6-4	−5.41	− 41	1.30	−2.57
Oxnard Chili	−4.37	−315	0.21	−0.19
Red Chili	5.27	26	−7.14	7.83
Lark	−1.60	−827	−0.71	−0.05
Gentry 456	3.41	711	0.77	1.11
60M4	2.96	567	2.22	0.05
57M30	−2.65	−488	1.64	−3.99
57M75	1.86	−383	2.39	−2.95

[a]Adapted from Lippert (*87*) and Marin and Lippert (*90*).

TABLE 3.13. Predicted Performance for Synthetic Populations Formed from Three and Four Parents Selected for Total Carotenoids[a]

Character	Predicted synthetic performance	
	Three-parent[b]	Four-parent
Total fruit/plant	31.8	31.0
Mature fruit (%)	76.5	79.6
Dry wt/plant (g)	96.2	99.6
Dry wt/fruit (g)	3.95	4.04
Fruit length (mm)	102	110
Fruit width (mm)	29.5	28.6
Total carotenoids (μg/g)	6415	5945

[a]After Lippert (*87*).
[b]Sweet Pickles, Gentry 456, and 60M4 comprise the three-plant synthetic, with 57M75 added into the four-parent synthetic.

recurrent selection or reciprocal full-sib selection provides simultaneous evaluation and selection within two populations, with one population tested against the other in each cycle of selection. These schemes have the advantage of improving populations for traits responding to both additive and nonadditive gene action, that is, improvement for both GCA and SCA. Each of these breeding programs has application to a self-pollinated crop such as pepper.

Genic Male Sterility

Genic male sterility is useful for making F_1 hybrids because tedious and costly hand emasculation of individual flowers is avoided. Also, F_1 hybrid peppers are generally more vigorous and more uniformly productive than open-pollinated cultivars. Male-sterile plants are found as mutants in about 0.01% of the plants in large fields. Shifriss found one completely pollen-sterile plant among 24 unfruitful mutants of various types selected from a field of 10,000 plants of the squash pepper cv. Gambo. Earlier, Shifriss and co-workers found one male-sterile plant each in the bell peppers Allbig and California Wonder. Meiosis in the male steriles appeared to be normal, but the microspores degenerated soon after the tetrad stage, and no fertile pollen was present at anthesis when examined under the microscope in 1% acetocarmine or acetoorcein (*132*).

The three *ms* genes mentioned proved to be nonallelic. The practical value of male-sterile mutants depends on the economic importance of the parent cultivar, on the degree of sterility and its stability, and on the combining ability with other cultivars in F_1 hybrids.

Because male steriles constitute only 50% of the plants ($ms/ms \times ms^+/ms$), one half must be eliminated in the seedling stage, before transplanting to the field. This has not been feasible because closely linked marker genes have not been found and the *ms* genes have no obvious phenotypic effect prior to flowering. However, male-sterile plants are easily identified at anthesis and hand pollinated in an insect-screened greenhouse.

Use of Genic Male Sterility

Pochard reports only limited use of genic male sterility to produce F_1 hybrids in Bulgaria, France, and Yugoslavia. The limited use is due to abnormal anther development

in *ms*/*ms*$^+$ hybrids at low temperatures and consequently poor pollination (*118*). On the positive side, however, Breuils and Pochard produced the popular F_1 hybrid Lamuyo–INRA by the use of the gene *ms* 509. Further, Shifriss writes that the Dutch seed company Bruinsma released a true *ms*/*ms*$^+$ hybrid in 1980, which carried an *ms* gene allelic with one of his *ms* mutants (*17,133*). Bruinsma Wonder, an F_1 hybrid greenhouse cultivar, is a cross of CW (*ms*/*ms*) × Sweet Westland, released earlier. Shifriss did not observe the anther abnormality in Israel and stated that they would use this technique in the future.

Cytoplasmic–Genic Male Sterility

Cytoplasmic male sterility (CMS) in peppers was first discovered by Peterson in *C. annuum* PI 164835 from India (*110*). Its modus operandi proved to be similar to that found in onions by Jones and Clarke (*80*). This type of male sterility is due to the interaction of sterility inducing S-type cytoplasm with a recessive nuclear male sterility inducing *ms* gene. The *ms* gene is only expressed in S cytoplasm. The only plasmon–genome combination that induces male sterility is S*ms*/*ms*. The other combinations S*ms*$^+$/*ms*, S*ms*$^+$/*ms*$^+$, N*ms*/*ms*, N*ms*$^+$/*ms*, and N*ms*$^+$/*ms*$^+$ all produce fertile pollen. The CMS system for producing F_1 hybrids has an advantage over the genic system for mass hybridization, because all of the female parent plants are male sterile as compared with only 50% with the *ms*-gene method. Three parent lines are required to produce F_1 hybrid seed by the CMS system: the male-sterile or A line S*ms*/*ms*, the maintainer line N*ms*/*ms*, and a fertility restorer or C line N*ms*$^+$/*ms*$^+$ or S*ms*$^+$/*ms*$^+$. The male-sterile line is maintained by hybridization, in isolation, with a maintainer line of the same cultivar. In the field, crossing would need to be by bees, supplemented by hand pollination during periods of maximum flowering. The commercial hybrid would be produced by crossing the S*ms*/*ms* line with a good combiner line or cultivar of similar type to generate heterosis. Unfortunately, Peterson's S*ms*/*ms* lines were unstable in fluctuating environments, producing pollen at lower temperatures, and hence could not be relied upon to produce F_1 hybrids.

Synthesis of Additional Cytoplasmic Male Steriles

Peterson grouped pepper cultivars according to the presence of restorer genes (*ms*$^+$) or of non-restorer genes (*ms*) (*110*). Shifriss and Frankel expanded this list (Table 3.14) (*134*). Duvick suggested that CMS could probably be found or induced in most crop species (*51*). On this premise and with a need for more stable CMS genotypes, Shifriss and Frankel searched for and discovered two additional sources of S-type cytoplasm in two hot peppers from India, PI 154-1 and PI 164682 (*134*). When crossed onto the bell pepper Yolo Y (N*ms*/*ms*), both F_1 hybrids were pollen fertile, but two F_2 populations, one from each cross, segregated ¼ male-sterile plants. Proof of CMS vs. genic sterility were the 1:1 and 1:0 ratios of male-fertile to male-sterile plants obtained from reciprocal crosses of the two types of cytoplasm (S*ms*$^+$/*ms* × N*ms*/*ms*). Peterson's S cytoplasm appears to be identical with the two new S cytoplasms because cultivars known to be restorers or non-restorers reacted similarly in crosses with all three cytoplasms. Ohta obtained similar results with the S cytoplasms of Fresno Chili, Delaware Bell, and Liberty Bell (*108*).

Shifriss and Guri incorporated the two new cytoplasms into the sweet pepper cvs Bikura, Yellow Yolo Y, and Zohar with six to eight BC and tested the stability of their pollen sterility in the field under conditions of natural cross-pollination. Recessive marker genes in the female parents permitted determination of the percentage of plants produced

TABLE 3.14. Male-Sterile and Restorer Genes in Pepper Cultivars[a]

Male-sterile gene (*ms*)		Restorer gene (*ms*$^+$)	
Yolo Wonder	Fresno Chili	Floral Gem	PI A-J
Yolo Y	Long Red Cayenne	Anaheim Chili	PI A-8
California Wonder	PI 206421	California Chili	PI 154-1
Delaware Bell	PI 164835	Mexican Chili	PI 164682
Liberty Bell		Fushimiamanaga	PI 164738
Naharia		Takanotsume	PI 164847
Vinedale		Jalapeno	PI 195557
Ojishi		Puri Red	PI 201228
Pimiento		Serrano	PI 201231

[a]Adapted from Peterson (*110*), Shifriss and Frankel (*134*), and Ohta (*108*).

by self-pollination. The crosses and the percentages of selfed plants were Bikura (*Sms*/*ms*) × Yolo Y (*Sms*$^+$/*ms*$^+$), <1%; Zohar × Yolo Y, 28%; Zohar × Maor, 28%; Yellow Yolo Y × Maor, 18.5%. These results show that the degree of pollen sterility and stability of different CMS lines depends not only on the *Sms*/*ms* component but also on the rest of the genotype. The authors concluded that cultivars with the high pollen sterility and stability of Bikura, with <1% selfing, can serve as A lines in the production of F_1 hybrid seed by natural cross-pollination. Further improvement of CMS lines, now variable in pollen sterility, should be sought by (1) the use of genetically different maintainer lines, (2) the incorporation of recessive marker genes to permit elimination of selfed plants in the seedling stage, and (3) the production of F_1 hybrid seed under more constant high-temperature environments (*135*).

Breeding Success with the CMS System

This breeding method has only been occasionally successful. Shifriss produced YW-type *Sms*$^+$/*ms* hybrids that exhibited incomplete pollen fertility restoration and set a considerable amount of flat, seedless fruit. In contrast, he found the method promising for the production of hot-pepper hybrids (*133*):

> From my experience one can plant the A line (*Smsms*) towards anthesis under temperatures optimal for male sterility (July in Israel). In my cytoplasmic male sterile lines there is a lag period of 1–2 hr between flower and anther opening. If pollen from C-line (N*ms*$^+$*ms*$^+$) is available and bees are active, such lag period is advantageous if the Smsms plants are partially pollen fertile. In our studies we obtained 100% hybrids when A and C lines were exposed to natural crossing. This technique is now being tried in Israel by the Hazera Seed Company. Since most of the hot cultivars contain restorer genes this technique is more promising with this group [*136*].

Pochard reports similar problems with the CMS system: viz. that "the sterility in the Peterson system is not always complete," and that "cytoplasmic systems are linked to deleterious effects on growth and fruit setting" (*118*).

HAPLOIDY

It has long been thought that haploidy offered the breeder a short-cut method for obtaining homozygous diploid lines in one step, by doubling the chromosomes of haploids with colchicine. This would save several years of inbreeding hybrids to the desired uniformity

of the F_7 generation (*22*). All haploids originate by parthenogenesis from haploid female or male nuclei in the embryo sac (Fig. 3.13) (*21,97,121*). Experimentally they have been produced as a result of interspecific hybridization, by irradiation of buds and pollen, chemical treatments of pollen, N_2O gas treatment of the embryo sac, and by in vitro pollen culture (*22,47,48*).

Most *Capsicum* haploids have occurred naturally from *n–2n* twin seedlings of polyembryonic seeds. Haploidy, according to Pochard, is the most frequent mutation in *Capsicum,* occurring in 1 per 1000 to 1 per 10,000 plants. This frequency has been increased 6–10 times by selection in crosses between haploid-derived autodiploid lines. It was also shown that field-grown seed produced significantly more haploids than greenhouse-grown seed, namely, 2.0 vs. 0.4 per 1000 plants (*121*).

Cultivars differed significantly in the frequency of polyembryony, Goliath producing 0.65%, CW 0.28%, and Perfection Pimiento 0.06% vs. 2.8% in a haploid-derived autodiploid of Goliath. Although polyembryony is only occasionally higher in haploid-derived autodiploids than in the original population, it can be increased by selection (*121*).

Cytological evidence indicates that *n–2n* twins originate from a synergid and a fertilized egg nucleus. The *n–n* type of twins originate from a synergid and an unfertilized egg nucleus, or from a synergid nucleus by division. The other synergid disintegrates after passage through it of the pollen tube (*47*). The antipodal nuclei in peppers disintegrate before fertilization. The chromosome numbers of multiple seedlings were, in ascending order of frequency, *2n–4n*(1), *n–n*(2), *2n–2n* conjoined (19), *n–2n* (41), *2n–2n* unattached (76), three sets of triplets *2n–2n–2n,* and one set of quadruplets, probably also diploids. Rarely *n–n–2n* triplets occur with the haploids conjoined. These are interpreted as arising by cleavage from a haploid proembryo developed from a synergid plus a zygote nucleus.

Several androgenic haploids have been documented. One appeared among 652 F_1 plants from the cross of an autodiploid of Perfection Pimiento with Floral Gem and had the yellow fruit color of Floral Gem (*21*). A pair of conjoined androgenic haploids of identical genotype has also been reported (*121*).

Diploidization of Haploids

Pochard decapitates young plants in the 8–10 leaf stage above the eighth leaf, to eliminate apical dominance, removes the axillary buds with a scalpel, and applies a drop of 0.5%

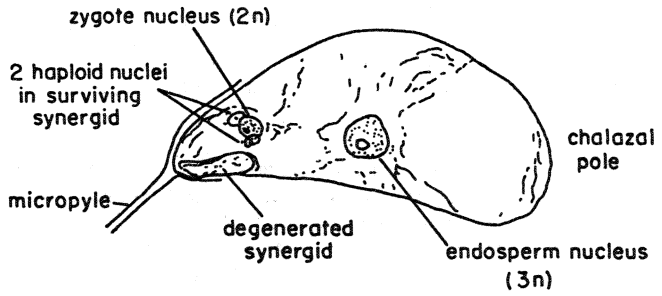

FIGURE 3.13. Postulated synergid origin of haploids in *Capsicum.* Embryo sac in a high haploid producer line of Doux Long des Landes, showing two haploid nuclei near the zygote nucleus in the surviving synergid, 4 days after pollination. After Dumas De Vaulx (*47*).

colchicine containing 1% of a pest oil (e.g., DuPont No. 7) to the wound for better penetration. New buds grow out within a month. The diploid sectors, generally fairly large, can be recognized by their darker green and smoother leaves and by the production of normal flowers with abundant pollen (*118*).

Haploidy as a Breeding Method for Peppers

Extensive research with haploid-derived autodiploids by Pochard and co-workers has cast serious doubt on the value of haploidy as a pepper breeding method. Autodiploid lines have proved inferior in fertility and stability as compared with standard inbred lines. From 20 to 30% of the plants of the first selfed generation (H_1) of an autodiploid from the F_1 hybrid YW × L107 were partially sterile, and in H_2 the mean seed yield per fruit of the best 14 lines was less than that of the standard F_9 parent lines. The sterility was transmitted through successive generations. Instability in plant height of a new cultivar candidate line, i.e., an increase in height between H_1 and H_5, rendered it useless. There was also excessive variation in plant and fruit characters of sib lines from the same autodiploid parent during successive selfed generations. Repeated haploid–diploid cycling increased the degree of instability. Such disturbing phenomena had not been observed previously in conventional inbred lines (*121*). Absolute homozygosity is obviously undesirable in *Capsicum*. In contrast, Thevenin produced superior F_1 asparagus hybrids of great uniformity by the use of haploids (*22*).

TRISOMICS AND CHROMOSOME MAPPING

Pochard identified 65 primary trisomics among 3500 F_2 progeny of the unusually self-fertile DL haploid, which averaged 2.3 seeds per fruit, more than five times the frequency of haploids from other pepper cultivars (Table 3.15). The primary trisomics could be distinguished from secondary and tertiary trisomics by their phenotype, frequency, and fertility and by their chromosome configurations in meiosis. Eleven of the 12 possible trisomics could be identified by plant, flower, and fruit characteristics and were given code names of flower colors (Table 3.16).

Pochard determined the mean lengths (μm) of the 12 chromosomes of DL and YW from six mitotic root tip plates of each and calculated the standard error of the mean chromosome length of each cultivar. Only three of the 12 chromosomes differed significantly in length. The same three chromosomes were also distinguished by Ohta (Fig. 3.3). The other nine, being metacentric and with their lengths intergrading too closely, did not permit identification.

Eleven trisomic phenotypes could be distinguished and associated with the genes they

TABLE 3.15. Chromosome Numbers of the Selfed Progeny from a Haploid Plant of Doux Long des Landes Propagated by Cuttings and Isolated in a Greenhouse from Other Pepper Genotypes[a]

Chromosome number	12	24	25	26–28	35–37	Total
Frequency of plants	3[b]	634	13	11	19	680
Percentage of population	0.44	93.2	1.91	1.62	2.79	100

[a]After Pochard and Dumas De Vaulx (*121*).
[b]Haploids from twin seedlings.

TABLE 3.16. Eleven Primary Trisomics of Doux Long des Landes[a]

Trisomic name	Trisomic[b] symbol	Chromosome no.	Description[c]	No. of trisomic plants[d]	Transmission (%)[e]	
					Selfed	× cv. Nigrum
Violet	VI	I	Anthers violet	11	4	none observed
Indigo	IN		Anthers bluish	9	47	47
Blue	BL		Foliage bluish green	13	24	17
Green	VE		Foliage intense green	9	32	32
Yellow	JA	XI	Foliage yellowish	6	21	28
Orange	OR		Mature fruit orange–red	5	14	12
Red	RO		Mature fruit dull dark red	4	43	51
Purple	PO	XII	Arbitrary name (Pourpre)	1	6	10
Black	NO		Immature fruit dull dark green	3	21	33
Brown	BR		Stamens yellowish brown	3	34	22
Dusky	BI		Arbitrary name (Bistre)	1	4	15

[a]After Pochard (*115*).
[b]First two letters in capitals of French color names.
[c]The diploid check DL has yellow anthers bordered with blue, medium-green leaves, and bright red fruits.
[d]Number of primary trisomics obtained from 3500 progeny of the selfed haploid of DL.
[e]Transmission percentage of each of the 11 trisomics when selfed (including some confounded tetrasomics), and when crossed with the cv. Nigrum.

carry. The procedure is to cross them with diploid cultivars with marker genes. From three to six F_1 trisomic plants are selected from each cross, selfed, and the F_2 segregation ratios determined. If a gene is located on a trisome, a 2:1 rather than a 3:1 ratio is obtained. The ratios will vary with the transmission frequency of the extra chromosome and the distance of the gene from the centromere (*117*). The 3:1 ratio from the diploid check serves as the control (Table 3.17).

FIELD TRIALS

Field trials are an essential part of the work of plant breeders, who wish to compare the yields of their best lines with the leading commercial cultivars. Field trials involve the concept of randomization and replication in an experimental design that permits statistical analysis of the data. If properly conducted, such trials will provide an unbiased, objective evaluation based on probability theory.

REGIONAL TRIALS

Regional trials, such as the National Pepper Cultivar Evaluation Trials, are intended to test potential new cultivars for adaptation over a wider area and also to speed up the evaluation (*95*). Superior performance in regional trials enhances the chances of commercial acceptance of a new cultivar.

TABLE 3.17. Locating the Gene L^1 for TMV Resistance by Analysis of Trisomics of Doux Long des Landes (L^+) × PM 165 (L^1 Cook Bell Line)[a]

F_2	L^+	Total	χ^2D	P	χ^2H	$P\chi^2$H	K
Normal							
Diploid	33	151	.80	.30–.50	.10	.30–.50	2
VI I	—	—	—	—	—	—	—
IN	46	187	.016	>.50	.01	>.50	2
BL	20	82	.016	>.50	—	—	1
VE	28	109	.027	>.50	—	—	1
JA XI	58	206	1.09	.10–.20	1.76	.10–.20	2
OR	31	151	1.61	.20–.30	.03	>.50	2
RO	35	145	.058	.30–.50	1.97	.10–.20	2
PO XII	45	190	.175	>.50	.46	.50	2
NO	33	151	.80	.30–.50	.10	>.50	2
BR	S	S	S	S	3.57	.30–.50	4
BI	26	76	3.44	.05–.10	—	—	1
Total or average	355	1448	.181	>.50	7.85	>.50	10
BR							
a	39	75	29.2	<.001			
b	20	39	14.4	<.001			
c	21	40	16.1	<.001			
d	29	44	39.3	<.001			
Total or average	109	198	95.4	<.001	3.57	.30–.50	4

[a] L^+, Number of TMV susceptible plants; χ^2D, χ^2 deviations from 3:1 ratios; χ^2H, χ^2 for homogeneity of K ratios; P, probability of χ^2 for 3:1 ratios; $P\chi^2$H, probability of homogeneity χ^2; S, significant deviation from a 3:1 ratio (note separate analysis); K, number of progenies originating from the same source; VI, IN, etc., are abbreviations of the French color names assigned to the 11 trisomics. [After Pochard (*117*).]

Observational Trials

Breeding lines in F_4 or F_5 are compared in single- or double-row plots of 12–24 plants per plot row. Inferior lines are discarded and the evaluation effort concentrated on the better lines. Numerical scores from 1 to 5 (5 the best) are assigned for plant vigor, plant uniformity, foliage cover (for protection of fruit from sunscald), earliness, productivity, fruit size, fruit shape, stylar closure (to prevent entry of molds and bacteria), fruit rot, and plant disease resistances. Measurements of the best lines for plant height × width, fruit length (depth) × width, and fruit wall thickness (mm) are desirable. Yield and average fruit weight estimates (lb) of the best lines are obtained by harvesting single-row plots and weighing and counting the fruits.

Yield Trials and Procedures

Yield trials are intended to compare the better breeding lines in F_5 or later generations, with leading commercial cultivars as checks.

There are many possible causes of variation in yield that can affect the accuracy and reliability of yield trial data, e.g., herbicide or spray damage, incomplete harvesting, or inconsistent fruit grading. These can be kept to a minimum, but others such as variation in soil fertility or unknown causes must be controlled by randomization and replication in standard experimental designs, which permit a variance analysis of the data.

One or two days prior to the first harvest, the yield trial entries are visually scored for

plant and fruit characteristics and overall desirability. Stand counts are made prior to each harvest so that plot yields can be corrected separately for each harvest and added to obtain the total yield per plot per block at the end of the season. Complete and uniform harvesting for fruit size and maturity and standardized fruit grading supervised by the breeder are important to reduce variance in the data. Harvesting must not exceed the capacity to grade, count, and weigh completed blocks within 1–2 days of harvest. Harvesting must not stop partway in a block because of rain or time of day, if results are to be reliable. Fruits are graded as marketable or culls. Cull fruit are further classified by causes such as fruit rots, blossom end rot, sunscald, malformation, virus puckering, fruit worms, stink bugs, harvest injury, soil abrasion, and smallness. All fruit categories are counted and weighed quickly on direct-reading (net weight) spring scales to the nearest 0.1 lb. Greater accuracy is not warranted for such data. Data are recorded on a form with the various fruit classes shown. When completed, the marketable fruit of each entry, four plots from four blocks, are bulked and the entries ranked in order of yield. The entries are then scored visually on a scale from 1 to 5 for yield, appearance, earliness, fruit size, shape, color, stylar closure, fruit firmness, wall thickness (mm), and overall desirability.

Fruit Quality Determinations

Fruit quality determinations such as objective color measurements, pH, soluble solids, total solids, vitamin C, pigment content, flavor, pungency, yield, and appearance of canned product are best done by food scientists in the laboratory. Their cooperation and assistance should be sought in advance. Valuable assistance of this nature warrants coauthorship with the breeder in any cultivar release.

EXPERIMENTAL DESIGNS

The Randomized Complete Block

This is the simplest and most commonly used design with up to 12 entries and usually four replications. The entries are first numbered consecutively and then randomized in each block by the use of a table of random numbers. The pencil is pointed randomly at the page and two-digit numbers are drawn from the table in any direction. These are mentally divided by the number of entries and the remainders written as they occur. If a number has occurred before, it is ignored. Exact multiples of the number of entries, say 10, would be entry number 10. All four blocks are thus randomized and a field plan is drawn up. The individual plot rows should be long and narrow with 12–24 plants each. Individual blocks would ideally be square to minimize soil heterogeneity. The blocks can be separate or laterally contiguous, thus requiring only two border rows.

Usually no border rows are planted at the open ends of the blocks on the assumption that all plots there are equally favored. If spray alleys are needed, they should run between the blocks. Additional border rows will then be required. In the field, the entries in each block are identified by entry and block number. A duplicate record and plot of the yield trial layout is kept for insurance against loss.

The Latin Square

The Latin square is a more efficient design than the randomized block. The reason is that in the Latin square variance due to rows, columns, and entries is subtracted from the total

variance, leaving a smaller residual error variance for testing mean differences between entries; whereas in the randomized block only two variances for blocks and entries can be accounted for. This design accommodates up to eight entries. For more complex designs, it is advisable to consult a statistician when planning the experiment.

Variance Analysis

For a detailed calculation of variance analysis for the randomized block and the Latin square, the reader is referred to Briggs and Knowles (*18*).

Duncan's Multiple Range Test

This is a test for significance between the means of all entries in a yield trial, in all possible combinations. First, a standard variance analysis is made of the data. To make the test, the variety means, the standard error with its degrees of freedom, and a table of Duncan's *significant studentized ranges* (r_p) at the 5% or 1% level of significance are required. The appropriate values from the table are multiplied by the standard error of the mean to give Duncan's *shortest significant ranges* (r_p). Duncan, Harter, and LeClerg *et al.* present the method of calculation in detail (*50,71,86*).

VARIETY RELEASE PROCEDURES

A new cultivar developed at the Alabama Agricultural Experiment Station is officially released and named by a variety release committee in consultation with the breeder. The breeder presents 2 years' yield trial data with leading commercial cultivars as checks. To be released, the new cultivar has to be superior in yield or have some compensatory advantage not present in other cultivars. A foundation seed increase requires 10–20 lb of seed.

Seed Increase and Marketing

It may prove difficult to find a reliable seed company that will take the financial risk to increase and market the seed of a new pepper cultivar. The market for the seed may be limited because canners save their own seed and guard it from their competitors. As an inducement to take the risk it may be necessary to make an exclusive release to a seed company. This involves a written agreement between the director of the agricultural experiment station and the company, with the responsibilities of both parties spelled out. Another possibility is for the station or the seed company to patent the cultivar. In this case, a royalty would be paid to the station per pound of seed sold. This money is needed to support additional plant breeding research. In the University of Florida system, seed of new cultivars is produced by the Florida Foundation Seed Producers Association or contracted for increase with private seed companies and paid for by Florida Foundation Seed (*58*).

PLANT VARIETY PROTECTION ACT

In 1930, plant patent legislation was enacted by the U.S. Congress for clonally propagated plants such as fruit trees and potatoes. In 1970 the *Plant Variety Protection Act* was passed to cover seed-reproduced cultivars of crop plants, but the following six vegetables were not included: peppers, okra, tomatoes, carrots, celery, and cucumbers. In 1980, the Congress passed an amendment that removed these exemptions. Today all crops are

covered and the developer has the exclusive right to sell the seed of a cultivar for 17 years. A cultivar that has once been released cannot later be patented. Under the *Plant Variety Protection Act,* a seed sample is deposited with the National Seed Storage Laboratory at Fort Collins, Colorado. This seed is periodically renewed. Many nonpatented cultivars are also stored there.

The Netherlands Plant Breeder's Decree enacted in 1941 championed plant breeder's rights and set the example for other countries to follow. In 1962 DeHaan wrote, "The protection of the plant breeder's ownership and the allocation of bonuses have had a favorable influence on the improvement of crop plants in the Netherlands. More efficiently organized establishments, additional personnel, more technical collaborators, better equipment and increase of the number of plant breeders have resulted" (*41*,p. 4).

Capsicum GENES[2]

The preservation of genes is the key to future crop improvement. The availability and usefulness of the national and regional germplasm banks is currently being improved by the establishment of a series of descriptors for each crop that will permit a search for and identification by computer of specific germplasms needed by breeders, from among the thousands of seed stocks of crops in the gene banks. The needed information on which PIs carry genes for specific disease resistances or horticultural traits must first be determined by a host of researchers, including geneticists, plant pathologists, and plant breeders. Several European nations have also established national gene banks. Germplasm preservation is a worldwide concern and requires international cooperation. The same is true for gene identification and gene mapping.

Lippert *et al.* have proposed that the University of California at Davis and Riverside serve as depositories of *Capsicum* germplasm in the United States.

Rules of Gene Nomenclature

Lippert *et al.* and Robinson *et al.* have established rules for designating genes (*88,124*). A gene is named for the main diagnostic feature of its phenotype. Gene symbols are formed from the first letter or not more than the first three letters of the name. Dominant genes are assigned capital letters and recessive genes lowercase letters. Normal or wild-type genes are identified with the superscript +. Thus, the normal allele of the dominant gene *A* is A^+ and of the recessive gene *y* is y^+. Multiple-recessive alleles are distinguished by lowercase superscripts and dominant alleles by capital letter or arabic numeral superscripts. Polymeric or nonallelic mimic genes are distinguished thus: *sw1, sw2, . . . , swn* and their dominant alleles by $sw1^+$, $sw2^+$, . . . , swn^+, with the numerals printed on line with the symbol. Allelism tests are required before a new symbol is assigned to a mimic, e.g., to an *ms* gene, and "a gene symbol shall not be assigned to a character unless supported by statistically valid segregation data for the gene" (*124*). Genes from different species affecting the same trait may or may not be allelic. They can be distinguished by a superscript indicating species origin, e.g., et^a and et^c from *C. annuum* and *C. chinense,* respectively. Lippert *et al.* chose California Wonder as the standard on which to base dominance or recessiveness of genetic traits. European breeders prefer the sweet cayenne pepper Doux Long des Landes as the standard because it is early, prolific, non-pungent, and better tolerates low light intensity, plus the availability of trisomics for chromosome mapping.

[2]Table 3.18 gives a list of the *Capsicum* genes considered important to breeders.

TABLE 3.18. *Capsicum* Genes[a]

Symbol	Character	Reference
Color genes		
A	*Anthocyanin*: basic gene for purple color in foliage, stem, flower, and fruit; incompletely dominant; fully effective only in presence of *MoA*; located on chromosome of trisomic RO; *A*-6.5–*O*-18.8–*sw1 are linked in C. annuum*	*88,89,110, 117*
al-1 to *al-5*	*Anthocyaninless*: nodes green, anthers yellow; *al-5* shows slight purple along line of dehiscence; epistatic to *A*, *As*, and *Asf*; nonallelic	*37,88,89*
As(P)	*Style anthocyanin*: purple in absence of *A* or *Asf*	*88,89*
Asf(W)	*Style* and *filament anthocyanin*; purple in absence of *A*	*88,89*
B	β-*Carotene*: high in mature fruit; interacts with *t* for higher level in mature fruit	*16,88,89*
c1(c)	*Carotenoid* pigment inhibitor: 1/10 reduction in red color of mature fruit	*88,89*
c2(c1)	*Carotenoid* pigment inhibitor: red color reduction much stronger than *c1*; these two independent gene pairs interact with *y* and y^+ (red) to produce a range of mature fruit colors from red to ivory	*88,89*
cl(g)	*Chlorophyll* retainer in mature fruit: combines with y^+ or *y* to produce brown or olive green mature fruit color, respectively	*16,88,89, 140*
im	*Intermediate maturity* of purple in originally nonpurple unripe fruit	*88,89*
MoA(B)	*Modifier of A*: intensifies purple color in presence of *A*; incompletely dominant; located on chromosome of trisomic BR	*88,89,117*
sw1–swn	*Sulfury white* immature fruit color: dominant alleles control various green shades; duplicate or cumulative in action; in linkage group *A*–6.5—*O*—18.8—*sw1*	*79,88,89 101,102,111*
t	High β-carotene content: complementary with *B*	*16,89*
y(r)	*Yellow* or orange mature fruit color: located on chromosome of trisomic IN	*88,89,117*
Ys	*Yellow spot*: on corolla of *C. pendulum*, monogenic dominant in interspecific cross with *C. annuum*, *C. chacoense*, *C. chinense*, and *C. frutescens*	*88,89*
yt1, *yt2*	*Yellow top*: young expanding leaves are yellow and gradually turn green	*37*
Disease and nematode resistance genes		
**Bs1*	*Bacterial spot* resistance to *X. campestris* pv. *vesicatoria* race 1 in *C. chacoense* PI 260435	*30,33,34*
Bs2(Bs)	*Bacterial spot* resistance to race 2 of pv. *vesicatoria* in *C. annuum* PI 163192	
et^a	*Tobacco etch* virus (TEV) resistance in *C. annuum* Cayenne SC 46252 and PI 264281: allelic with and dominant over y^a	*26,27,64*
$*et^{av}$	Resistance in Avelar to TEV and PVY, tolerance to PMV and to TEV-S; allelic with and dominant over et^a and y^a	*157,158*

TABLE 3.18. (*cont.*)

Symbol	Character	Reference
*et^{c1}	Resistance to PMV and TEV-C in *C. chinense* PI 159236: allelic with et^{av}; interaction of et^{av}/et^{c1} results in susceptibility to PMV	*149*
et^{c2} (et^{c},et^{f})	Resistance in *C. chinense* PI 152225 to PVY, PMV, and TEV-S: probable top allele of the series $et^{c2}>et^{c1}\gtrless et^{av}>et^{a}>y^{a}$, but allelism and dominance relationship with et^{c1} not established	*64*
L^3	*Localization* of pepper strains of TMV in *C. chinense*: member of the allelic series $L^3>L^2>L^1>L^+$	*15*
$L^2(L)$	*Localization* of common strains of TMV in *C. frutescens* (cv. Tabasco) and in certain cvs. of *C. annuum*: similar reaction found in *C. baccatum* vars. *pendulum* and *microcarpum*, but allelism with the latter not established	*74,75*
L^1 (L^i,l^i)	Imperfect *localization* of TMV: reported only in *C. annuum*; incomplete dominance of L^1/L^+ with some strains of TMV results in systemic necrosis especially at high temperature; located on chromosome of trisomic BR	*75,117*
N	Root-knot *nematode* resistance to *M. incognita* and *M. incognita* race *acrita*	*70*
v1, v2	*Veinbanding* virus resistance: combination of these two genes determines four reactions to virus infection of which only *v1/v1,v2/v2* confers resistance; similar expression of resistance observed in some accessions of *C. chinense, C. frutescens, C. pendulum,* and *C. pubescens*	*89*
y^a	Resistance in Yolo Y to a mild strain of PVY: bottom allele of series $et^{c1}\gtrless et^{av}>et^{a}>y^{a}$	*27*
Plant morphology genes		
ca	*Canoe*: margins of cotyledons and leaves are rolled up, exposing only the abaxial surface	*37*
**dw1*	*Dwarf* plant about 6 in. tall reported by Dale in Floral Gem: reduced female fertility	*88,89*
dw2(*dw*)	*Dwarf* plant 4–6 in. tall: normal number of nodes (8–10); from cross of *C. baccatum* var. *pendulum* × *C. annuum*	*37*
fa	*Fasciculate*: flowers and fruits borne in clusters on bunched, compounded nodes; bushy plants with determinate tendency	*88,89*
fil (*fi* mutant 1)	*Filiform* threadlike leaves: blossom irregularities; female sterile	*88,89*
fi2	Similar to *fil*: narrow cotyledons and leaves; threadlike petals; carpels usually not fused to pistil; incompetely female sterile; allelism with *fil* not tested	*37*
fr	*Frilly*: leaf margins undulated	*37*
Hl(*H*)	*Hairless* (smooth) stem in *C. annuum* var. *minimum* (Blanco): dominant over hairy stem in cv. Golden	*74,89*

(*continued*)

TABLE 3.18. (*cont.*)

Symbol	Character	Reference
	Dawn; Ikeno reported dominant digenic inheritance (15:1) in *C. annuum* of hairy over smooth, with stems, petioles, and leaves exhibiting various degrees of pubescence	
O	*Oblate* or round fruit shape in *C. annuum* and *C. chinense*: dominant over elongate; allelism not tested; in linkage group *A*–6.5—*O*—18.8—*sw1*	*83,111*
P(D)	*Pointed* fruit apex: incompletely dominant over blunt	*89*
pc1,pc2,pc3	*Polycotyledon*: seedlings with three to four cotyledons and fasciated stem; pseudodichotomous branching with unequally developing shoots; nonallelic	*37*
rl	*Roundleaf*: length but not width of leaves is reduced, changing the length/width ratio from 1.50 to 1.24	*66*
ru	*Rugose* or savoyed mature leaves: appeared in *C. chinense* × *C. annuum* derivative; mature leaves darker green than normal; readily classified by fleshy cotyledons with down-curved margins; good seedling vigor and survival; homogeneous 3:1 F_2 and 1 : 1 BC ratios (W. H. Greenleaf, unpublished)	
tu	Cotyledons and leaves are rolled up like a *tube*, with only the abaxial surface exposed: relationship to *ca* not tested	*37*
up (*p, u*)	*Upright* or erect pedicel and fruit orientation: intermediate expression in some genetic backgrounds; located on the chromosome of trisomic NO	*89,100,117*
wl	Willow leaf: leaves narrowed, similar to *fi*, but wider; nonallelic; highly female sterile; male fertile; sets parthenocarpic, seedless fruits	*88,89*
Sterility genes		
**fs1*	*Female-sterile* mutant in *C. annuum*: mature plants larger, otherwise normal; male fertile; sets parthenocarpic, seedless fruits	*39*
fs2(fs)	*Female-sterile* mutant in *C. annuum* PI 159276 reported by Bergh and Lippert: similar to *fs1*; male fertile; allelism with *fs1* not tested	*88,89*
ms	*Male-sterile* nuclear gene induces male sterility in S cytoplasm in genotype *Sms/ms*: three different sources of S cytoplasm produced similar reactions with different *ms* and restorer genes, indicating identity	*108,110,134*
ms1,ms2,ms3	Spontaneous *male-sterile* mutants from *C. annuum* cvs. Allbig, California Wonder, and Gambo, respectively: nonallelic; many additional male-sterile mutants have been reported	*132*
ms9, ms509, ms705	γ-Irradiation-(*ms9*) and chemical (EMS)-induced (*ms509, ms705*) *male-sterile* mutants: *ms509* is used to produce the French F_1 hybrid bell pepper Lamuyo-INRA	*17*
Genes determining physiological traits		
C	*Capsaicin* or pungent fruit: modifiers increase or decrease capsaicin to produce a bimodal distribu-	*46,88,89 104,117*

TABLE 3.18. (*cont.*)

Symbol	Character	Reference
	tion of pungency in F_2; located on chromosome 11 of trisomic JA	
Gi	*Graft incompatible*: reaction of *C. annuum* vegetatively grafted with other Solanaceae	*88,89*
Ps(S)	*Pod separates* easily from calyx: distinct from soft flesh *S*; expression improves with fruit maturity; subject to modifiers and background genotype	*62,79,146*
S(Ps)	*Soft* juicy fruit in Paprika, distinct from *Ps*: observed also in a *C. chinense* PI 152225 × Tabasco (*Ps, S*) derivative (W. H. Greenleaf, unpublished)	*85*

[a]Adapted from the gene lists of Lippert *et al.* (*88,89*). Reproduced by permission. Only genes considered important to breeders are listed. Redesignated symbols are given in parentheses. Trisomic tests are with Doux Long des Landes. Asterisks indicate proposed new symbols.

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