CYTOGENETICS OF THE VEGETABLE CROPS.
GARDEN PEPPER, *CAPSICUM* SP.

L. F. LIPPERT, P. G. SMITH, AND B. O. BERGH
Departments of Vegetable Crops and Horticultural Science,
University of California, Riverside and Davis, California

ORIGIN

Historians agree on the new world origin of *Capsicum.* Dried pods recovered from burial tombs in Peru are believed to be more than 2,000 years old (Safford 1926). DeCandolle (1886) concluded from lack of reference to this genus in ancient languages that "no capsicum is indigenous to the old world."

The center of diversity of the common cultivated pepper, *Capsicum annuum,* is Mexico, with a secondary center in Guatemala. *C. frutescens* is widely distributed throughout the tropical and subtropical Americas, both in wild and cultivated forms, and was domesticated in Central America. The other cultivated and wild species also have their origins in Central and South America and the genus quite clearly is South American in origin (Bukasov 1930, Smith and Heiser 1957).

Capsicum was carried to the old world by the early explorers, being introduced into Spain by Columbus on his return trip in 1493 (Boswell 1949). Cultivation spread from the Mediterranean area to England by 1548 and to Central Europe by the close of the 16th century (Boswell 1949). The Portuguese brought *Capsicum* to India from Brazil prior to 1585, and cultivation was reported in China during the late 1700's (Sturtevant 1885).

TAXONOMY

The genus *Capsicum* is a member of the Solanaceae or Nightshade family. Early taxonomic treatment of the genus resulted in descriptions of nearly 100 supposedly good species and botanical varieties (Fingerhuth 1832, Irish 1898). Modern taxonomists, recognizing the extent of genetic variability, have consolidated the cultivated *Capsicum's* into five species: *C. annuum* L., *C. frutescens* L., *C. pendulum* Willd., *C. pubescens* R. & P., and *C. chinense* Jacq. (Heiser and Smith 1948, Erwin 1949, Rick 1950, Smith and Heiser 1951, Smith, Rick, and Heiser 1951, Hunziker 1961b, Eshbaugh 1964). Wild forms of all except *C. pubescens* are known (Hunziker 1961a, Eshbaugh 1964; Smith, unpublished). Eshbaugh (1964), in the most recent examination of the genus, proposes *C. pendulum* and the closely related wild species *C. microcarpum* Cav. to be botanical varieties of *C. baccatum* L.

Some 10 purely wild species are also recognized: *C. cardenasii* Heiser & Smith, *C. chacoense* Hunz., *C. cornutum* (Hiern.) Hunz., *C. eximium* Hunz., *C. galapogense* Heiser & Smith, *C. geminifolium* (Dammer) Hunz., *C. minutiflorum* (Rushby) Hunz., *C. praetermissum* Heiser & Smith, *C. schottianum* Sendt., and *C. scolnikianum* Hunz. (Hunziker 1950, 1954, 1961a; Heiser and Smith 1958). At least seven additional wild South American specimens, each deserving species rank, are now under culture and examination (Eshbaugh 1964; Smith, unpublished), and it seems reasonable to expect that more will be found.

TABLE I.

Morphological characters distinguishing *Capsicum* species.[1]

Species	Corolla color	Corolla throat spots	Corolla shape	Anther color	Calyx teeth	Flowers/ node
C. annuum	White	None	Rotate	Blue to purple	Present	1
C. frutescens	Greenish-white	None	Rotate	Blue	None	2-3 (5)
C. chinense	White to greenish-white	None	Rotate	Blue	Present	3-5
C. galapogense	White	None	Rotate	Yellow	None	1
C. chacoense	White	None	Rotate	Yellow	Present	1
C. schottianum	White	Yellow	Rotate	Yellow	None	5-7
C. microcarpum *C. pendulum*	White	Green to yellow	Rotate	Yellow	Present	1-2
C. praetermissum	White to lavender	Yellow	Rotate	Yellow	Present	1
C. eximium	White to lavender	Yellow	Rotate	Yellow	Present	2-3
C. pubescens	Purple	None	Rotate	Purple	Present	1
C. cardenasii	Blue	Greenish-yellow	Campanulate	Pale blue	Present	1-2
C. scolnikianum	Yellow	—	Campanulate	—	Present	—

[1] *C. cornutum*, *C. geminifolium*, and *C. minutiflorum* have been omitted because of lack of living material or clear drawings on which to base differences.

As has been proposed (Morton, in Standley 1938, Heiser and Smith 1958) a number of species classed as *Capsicum* but possessing soft, pulp-filled, non-pungent berries have been excluded from this list.

Principal morphological features characterizing the cultivated and wild species are presented in Table I, with compatibility reactions of those species diagrammatically summarized in Figure 1.

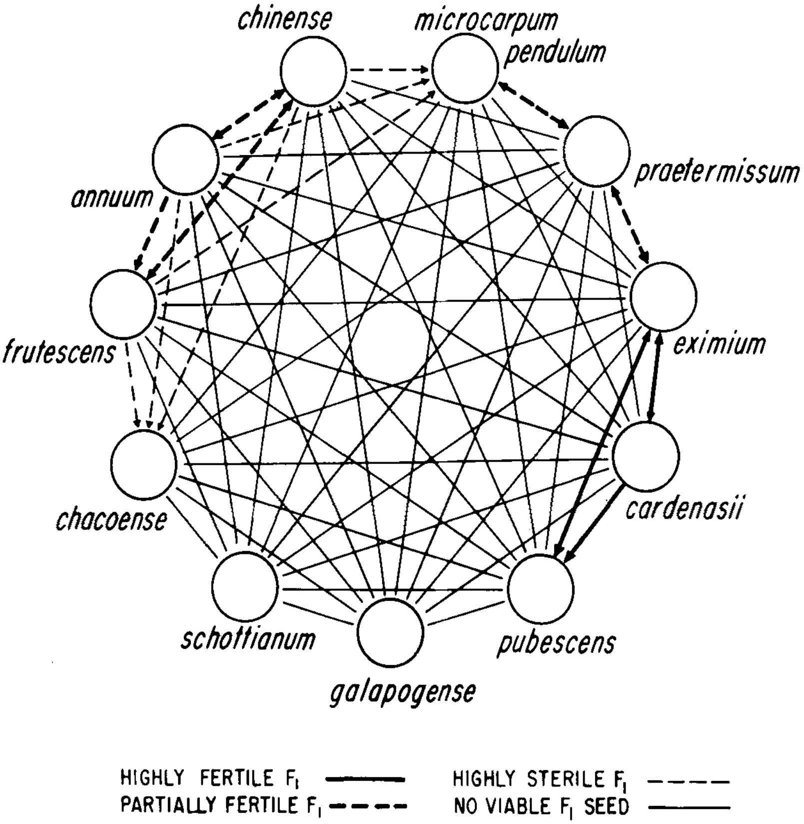

Figure 1. Cross compatibility of cultivated and some wild species of *Capsicum*.

Choice of the species nomenclature, whether *C. annuum* or *C. frutescens,* for the cultivated types in North America and Europe has stimulated considerable controversy. Around the turn of the 20th century, Kuntze (1891) proposed *C. annuum* with five botanical varieties whereas Bailey (1923) later proposed the same five varieties under *C. frutescens.* Irish (1898) listed the cultivated varieties under both species without clearly separating them. *C. annuum* and *C. frutescens* were differentiated more clearly by Smith and Heiser (1951) with the common cultivated pepper being placed under *C. annuum* without varietal subdivisions. By current rules of botanical nomenclature the terminology *C. annuum* L. is correct (Shinners 1956).

The two wild species, *C. eximium* and *C. cardenasii,* as well as at least five of the yet unnamed species, are self-incompatible (Heiser and Smith 1958, Eshbaugh 1964). Curiously, the self-incompatible species are centered in Bolivia and immediately adjoining areas.

CHROMOSOMES

NUMBER AND MORPHOLOGY

The chromosome number has been reported as $n=12$ for each of the species so far studied by either somatic or meiotic chromosome counts (Huskins and La-Cour 1930, Dixit 1931, Yamamoto and Sakai 1932, Tokunaga 1934, Raghavan and Venkatasubban 1940, Pal, Ramanujam, and Joshi 1941, Chennaveeraiah 1947, Schnack and Covas 1947, Sinha 1950, Vazart 1950b, 1951, Ohta 1962a, c, Eshbaugh 1964). A single discrepancy was reported as $n=6$ (Kostoff 1926) but was later explained as a misinterpretation of number and separation of bivalents (Huskins and La-Cour 1930, Dixit 1931).

Chromosome size has been referred to as both small (Christensen and Bamford 1943, Marks 1952) and large (Sinha 1950). In actual size, the various chromosomes at mitotic metaphase average 4.1 μ long by 0.5 μ diameter with a chromatic volume of 18 μ^3 (Vazart 1950b). By the end of prophase the chromosomes have the shape of rods, or resemble the letters "U," "V," or "J," with primary constrictions very evident (Sinha 1950, Vazart 1950b).

Certain somatic chromosomes can be distinguished by unequal length of segments, secondary constrictions, or satellites (Dixit 1931, Sinha 1950, Vazart 1950b, Ohta 1962a, c). The number of chromosomes with satellites in *C. annuum,* however, has been reported as both one (Sinha 1950, Ohta 1962a, c) and two (Dixit 1931, Vazart 1950b). Karyotypes have been presented for *C. annuum* (Vazart 1950b, Ohta 1962a, c) and for some other species (Chennaveeraiah 1947, Sinha 1950, Ohta 1962a, c). Ohta (1962a) divided six species into four karyotypic groups based on number of satellites and presence or absence of chromosomes with prominent secondary constrictions. Species grouping by karyotype corresponds closely to cross-compatibility reactions as determined by interspecific crosses (Smith and Heiser 1957, Hirose, Nishi, and Takashima 1960).

MEIOSIS

Chromosome behavior during meiosis in *C. annuum* appeared to be regular with the normal 12 bivalents observed (Huskins and La-Cour 1930, Dixit 1931, Pal, Ramanujam, and Joshi 1941, Vazart 1951). Vazart (1950a, 1951) presents a particularly detailed account of the phenomenon in this species. At the onset of meiosis in pollen mother cells, the nuclei have a diameter of 10 μ and a volume of 580 μ^3, slightly larger than meristematic nuclei which average 9 μ in diameter and 380 μ^3 in volume. The nuclei are characterized by a domed network of chromatic material and are referred to as skull-cap nuclei. Numerous diploid and triploid pollen grains were formed due to incomplete partitioning of tetrads during meiosis.

An inversion, resulting in bridges in 4 per cent of first meiotic divisions, was reported in 'Cayenne' *(C. annuum),* but was not evident in 'Chili Piquin' *(C. annuum)* or in 'Tabasco' *(C. frutescens)* (Abd-el-Maksoud Mohamed 1953). Chiasmata development appeared limited to achromatic regions of the chromosomes with a maximum of three chiasma per bivalent (Abd-el-Maksoud Mohamed 1953). Swaminathan, Ninan, and Magoon (1959) observed nearly all bivalents in *C. annuum* to be of the ring type with chiasmata in both arms.

Asynapsis or non-pairing of chromosomes in meiosis was observed in a single plant of *C. annuum,* with unequal and irregular distribution of univalents at anaphase. Of the 10 plants grown from the few seed set on the plant by open pollination, two were triploid, two trisomic, and the remainder diploid (Pal and Ramanujam 1940). Irregularities during microsporogenesis have been described in virus infected plants (Swaminathan, Ninan, and Magoon 1959).

Meiosis in pollen mother cells in *C. frutescens* is normal (Abd-el-Maksoud Mohamed 1953, Ohta 1961a) although Sinha (1950) observed disorganized reduction-division with resultant sterility in his two-plant study of this species.

POLYPLOIDY

Haploids and Polyembryony

In *C. annuum* haploids occur frequently as members of twin and triplet seedlings arising from polyembryonic seeds (Christensen and Bamford 1943, Morgan and Rappleye 1950). Three triplet and 291 twin seedlings were obtained from 78,005 germinated seeds (Christensen and Bamford 1943) and a later combined count indicated 1,619 multiple seedlings from among 300,683 germinated seeds (Morgan and Rappleye 1954). Various combinations of chromosome numbers occurred among multiple seedlings with twin seedlings observed in the following ascending order of frequency: unattached $2n$-$4n$, unattached n-n, conjoined or partially attached $2n$-$2n$, unattached n-$2n$, and unattached $2n$-$2n$. Two sets of $2n$-$2n$-$2n$ triplets each with two members conjoined and one unattached and single $2n$-$2n$-$2n$ and n-n-$2n$ triplets with unattached members were also observed. A single quadruplet seedling with unattached members (ploidy levels not indicated) was reported (Morgan and Rappleye 1950, 1954).

Frequencies of twin seedlings among *Capsicum* cultivars varied from 0.06 to 0.65 per cent, with differences statistically significant. Homozygous lines having high, intermediate, and low frequencies of polyembryony were isolated by colchicine treatment of haploid sporophytes. The high line produced 2.85 per cent multiple seedlings in comparison with 0.65 per cent for the parental cultivar, 'Goliath'. Eighty-five per cent of all twin seedlings produced by the derived line were of the unattached n-$2n$ type compared with 34 per cent of this type for the parental line (Morgan and Rappleye 1954). Characteristic and distinctive frequencies of the individual lines demonstrated a definite effect of female genotype on polyembryony (Morgan and Rappleye 1954, Campos and Morgan 1960).

Experimental evidence obtained from genetic studies to determine the origin of multiple seedlings in *Capsicum* indicates that the major portion of unattached $2n$ twin seedlings arose from a single embryo sac. However, two embryo sacs can function in the development of $2n$-$2n$ twin seedlings. All diploid members of the multiple seedlings were sexual in origin. The haploid members arose from reduced cells of the female gametophyte, presumably the synergids, and were therefore maternal in origin. The formation of a viable sexual embryo is not essential to the development of the haploid. Stimulation of the synergids followed by disintegration of the sexual embryo was proposed to account for the occurrence of maternal *n-n* twin seedlings (Morgan and Rappleye 1954).

A single haploid plant from a monoembryonic seed produced fruit and foliage characters of the male parent only, indicating it to be an androgenetic haploid deriving its inheritance entirely from a sperm cell (Campos and Morgan 1958).

Haploid seedlings are generally weak and require special handling for survival. Resulting plants are difficult to distinguish from diploids by their size, flowers, or leaves, except by critical observation. Haploids may be characterized readily, however, by smaller stomata, very poor pollen, smaller fruit, and rare seed (Christensen and Bamford 1943).

Meiosis in haploids is very erratic, with production of multinucleate pollen mother cells and high proportions of shrunken and variously sized pollen grains. The condition of the pollen indicates that these plants are nearly self-sterile and fruit set probably occurs by open pollination with diploids (Christensen and Bamford 1943).

Methods are reported for maintenance of haploids by cuttings and grafting and for chromosome doubling by colchicine to produce homozygous diploids (Toole and Bamford 1945). The value of these homozygous diploids in genetic studies and breeding programs has been discussed (Christensen and Bamford 1943, Morgan and Rappleye 1950, 1954).

Triploids

Information on triploids in *Capsicum annuum* is not extensive. A single instance of a naturally occurring triploid is reported (New Delhi 1942), although a triploid from a colchicine-treated seed lot may have arisen spontaneously (Pal and Ramanujam 1939). Attempts to produce triploids in $2n \times 4n$ and reciprocal crosses produced a high proportion of aborted seeds. Triploid and hypotriploid ($3n-1$) plants were obtained with metaphase configurations in triploids varying from $12_{II} + 12_{I}$ to 12_{III} (Nishiyama and Karasawa 1954) and a modal value of $9_{III} + 3_{II} + 3_{I}$ (Ohta 1962b). Triploids were practically sterile due to chromosome elimination at metaphase II (Nishiyama and Karasawa 1954).

Tetraploids

Spontaneous tetraploids (Greenleaf 1947) or colchicine-induced ones (Györffy 1939, Pal and Ramanujam 1939, Nishiyama 1939, 1940, Pal, Ramanujam, and Joshi 1941, Aleksic 1960, Palfi, Visnyovsky, and Tranger 1961, Siskovic 1962) show characteristically increased size of cells, leaves, stomata, flowers, and seed as compared with diploid plants. Fruit set and maturity are generally delayed and fruit are smaller, with thick flesh and few seeds (Greenleaf 1947, Geogieva 1959, Aleksic 1960), although tetraploids with maturity as early as diploids and with 50 per cent increased yields have been reported (Siskovic

1962). Seed germination is poor but has been improved by selection (Siskovic 1962). The $2n$ pollen grains are approximately double the size of haploid pollen (Pal and Ramanujam 1939). Multivalents in meiosis are rare, with the majority of cells producing 24 bivalents (Nishiyama 1939, 1940, Pal, Ramanujam, and Joshi 1941, Aleksic 1960).

Trisomics

The single report on trisomics ($2n + 1$) in *Capsicum* (Pal and Ramanujam 1940) involved two plants with 60-70 per cent fertile pollen and a good set of fruit with seed. At division I, the extra chromosome was found to be either outside the metaphase plate as a univalent or paired with its homologs forming a trivalent. The two trisomic plants differed in plant habit: one had thick foliage, clustered flowers and fruits; the other was dwarfed, with spreading branches and flowers borne singly. These two plants were believed to represent different primary trisomics, but the extra chromosome of each was not identified.

INFLORESCENCE

Flower Color

The usual or "normal" condition in *C. annuum* (Lippert, Bergh, and Smith 1965) is white petals, purple or blue anthers and nodes, and colorless filaments and styles. Such phenotypic expression is controlled by the gene al^+, whereas recessive *al* (originally *s*) prevents purple anthocyanin in any portion of the plant. An incompletely dominant gene *A* produces purple color in foliage, petals, filaments, and styles in the al^+ genotype (Deshpande 1939a, Odland 1960). As^+ (originally *W*) is reported to produce purple filaments and styles in al^+ types in the absence of *A*, but does not intensify the purple color of *A* (Odland 1960). Mo_A (originally *B*) intensified purple colorations of *AA* types, this gene being ineffective alone (Deshpande 1939a).

The segregation for flower color was 3 purple to 1 white in some crosses (Ikeno 1913, Hagiwara and Oomura 1947), and 15 purple to 1 white in another cross (Hagiwara and Oomura 1947). Genetic control of flower color was postulated as due to three factors, C, R_1, and R_2, with *C* and *R* genes complementary, and the *R* genes equally effective or polymeric in the presence of *C*. Purple style *As* (originally *P*) was independently inherited as dominant to white, As^+, but purple styles were produced in the CR_1 or CR_2 genotypes irrespective of *As* or As^+ (Hagiwara and Oomura 1947).

In another study of flower color (Kahn and Munir 1954) the F_2 ratio of 9 pink (purple?) to 7 white blossoms was observed, indicating action of two complementary genes which apparently also control filament and style color. A trigenic F_2 ratio of 57 pink (purple?) to 7 white was obtained for filament and style color, suggesting interaction of the two complementary genes with a third apparently independent and completely dominant gene for filament and style color.

Yellow anther color is controlled by the anthocyanin-less gene, *al*, but a brown anther color, with single gene inheritance recessive to blue, was also described (Murthy and Murthy 1962a). No crosses were reported between yellow and brown anther mutants to determine if these were controlled by separate genes, or were modified phenotypic expressions of the same mutant in different genetic backgrounds. Khan and Munir (1954) indicated genetic distinction between purple and blue anthers and postulated the following ideographic genotypes for anther color: AABB or AAbb = purple, aaBB = blue, and aabb = yellow.

Yellow petal spot, *Ys,* a taxonomic character of *C. pendulum,* is inherited as a simple dominant in interspecific crosses with *C. annuum, C. chacoense, C. chinense,* and *C. frutescens* (Bergh, Lippert, and Smith, in press).

PETAL LENGTH

Petal length was inherited as a quantitative character in a cross of two Indian chili varieties. Mean length in both F_1 and F_2 was nearly intermediate between the parents. Petal lengths equivalent to the longest and shortest parent were recovered in the F_2, suggesting that the parents did not differ by many factors for this character. Short petal length was associated with purple plant color (Deshpande 1933).

STERILITY

The gene *ms* causes genetic male sterility when homozygous in combination with sterile cytoplasm, S (Peterson 1958). Normal male fertility occurs in the presence of either fertile cytoplasm, N, or the restorer allele, ms^+. The ms^+ allele has been present in approximately half of the *C. annuum* types tested, and is considered a primitive condition. Pollen fertility may occur in plants with S *msms* genotypes under conditions of cool temperature, suggesting a genotype-environment interaction (Peterson 1958). The use of cytoplasmic-genetic male sterility in *Capsicum* breeding has been reviewed (Duvick 1959, Ohta 1961c).

Evidence of male sterility under field conditions was observed in 'Cayenne 69a', whereas greenhouse plants had normal fertility. 'Cayenne 4558' reversed this pattern, being male sterile in the greenhouse, but fertile in the field. In a third Cayenne type, complete sterility was found to be inherited as a single recessive (Martin and Crawford 1951).

Non-flowering individuals with three types of aberrant vegetative growth designated "normal," "rosette-like," and "elongated internodes" have been observed in Hungary. Each is monofactorily inherited and is independent of environment (Kormos and Kormos 1956c).

Kormos (1954a) observed a single recessive gene female sterile in which pollen was normal, but atropous ovules lacked an integument and failed to undergo meiosis or to form embryo sacs. A similarly inherited female sterile developed fruits with elongated, threadlike, non-functional ovules (Curtis and Scarchuk 1948).

Six recessive genes that result in partial to complete female sterility and various kinds of vegetative abnormalities have been described (Bergh and Lippert 1964) in *C. annuum* as spinach *sp,* branchless *bl,* glossy diminutive *gd,* scabrous diminutive *sd,* female sterile *fs,* and willow leaf *wl.* A similarly inherited gene termed styleless, *sl,* conditioning a high degree of female sterility due to abnormal gynoecium development, may be an atavism (Bergh and Lippert 1965).

FRUIT CHARACTERS

ORIENTATION

The gene *up* (originally designated independently as *u* and *p*) for upright or erect pedicel is recessive to its allele up^+ for pendent or drooping pedicel (Shaw and Khan 1928, Deshpande 1933, Miller and Fineman 1937, Singh and Roy 1945, Hagiwara and Oomura 1947). Earlier reports on this character indicated the heterozygotes to be intermediate, i.e., more or less horizontal in fruit orientation (Halsted 1909, Webber 1911, Ikeno 1913). Classification of segregants is complicated in many crosses by intra-plant variability and by apparent changes in dominance with pod maturity or with season (Ikeno 1928, Deshpande 1933). Heterozygous plants may exhibit pods in different stages of maturity with upright, intermediate, or pendent fruits. Classification of plants for these phenotypes is best accomplished by readings throughout the fruiting period (Ikeno 1928).

Kaiser (1935a) presented evidence that the single gene inheritance of fruit orientation operated through the genetic determination of a specific geotropic growth response.

SHAPE

Crosses of oblate by elongate fruit shapes gave a trimodal F_2 distribution as measured by length/width shape indexes, indicating the segregation of a major gene (Kaiser 1935b, Khambanonda 1948, 1950, Peterson 1959, Dempsey 1960). The gene *O* for oblate fruit shape was inherited as completely dominant in crosses with elongate fruit having a shape index of approximately 2.0 (Peterson 1959); however, where elongate types in the crosses approached a shape index of 4.0, segregation was less distinct (Khambanonda 1950). Intermediate classes in later progenies suggest either an incomplete dominance for the oblate gene (Khambanonda 1950) or the influence of additional genes operating in control of fruit length (Peterson 1959). Miyazawa (1953) estimated the number of genes controlling fruit length to be 0.79 in a cross of two cultivars of *C. annuum*.

Dale (1928) concluded from crosses involving parents with mean fruit length of 23 and 157 cm. that fruit length inheritance is based on multiple genes with proportionate rather than additive effects.

WIDTH

Fruit width in a cross of "wide" (1.60 cm.) by "narrow" (1.22 cm.) produced a heterotic F_1 (1.77 cm.) and the extremes of width in the F_2 exceeded the parental values. The number of controlling factors was not determined but was considered to be a low number (Deshpande 1933). Miyazawa (1953) calculated 9.52 genes controlling fruit width.

Khambanonda (1948, 1950) concluded that length and width of fruit were largely expressions of shape and weight factors, and it was unlikely that genes control length and width of fruit *per se.* Even if length and width genes were present, they would cause only minor deviations after shape manifestations were accounted for.

SIZE AND WEIGHT

Fruit size and weight appear to be quantitatively inherited, with number of genes listed as 20-33 (Khambanonda 1948) and 52.24 (Miyazawa 1953). Action of weight genes was theorized to be multiplicative and preponderantly dominant or epistatic for large fruit size (Khambanonda 1948, 1950). However, in a different study small fruit size has been reported partially dominant over large fruit size (Sakai 1952).

Carlsson (1962) estimated fruit size (volume or weight) in the F_1 fairly accurately from the formula $F_1 = \sqrt{P_1 \times P_2}$. Fruit size was positively correlated with leaf size, and large-fruited types could be selected from leaf readings of young seedlings. The correlation between the length/width ratio of fruit and that of the leaf was low, $r = 0.20$ (Hiyazawa 1953).

APEX

The gene *Pt* (originally *D*) for pointed fruit is incompletely dominant to its allele for blunt fruit apex (Deshpande 1933, Schmidt 1935). Difficulty of classification, reversal of dominance in crosses, and poor fit to expected ratios have been reported (Webber 1911, Miller and Fineman 1937).

BASE AND CALYX CONDITION

The fruit base may be either bulging or non-bulging, with the gene *fb* (originally *f*) designating the non-bulging character (Deshpande 1933, Miller and Fineman 1937, Odland 1948). The gene *ce* (originally *e*) conditions a non-enclosing calyx as opposed to the enclosing type (Deshpande 1933). Linkage has been reported between the two genes, *fb* and *ce,* with crossovers variously determined at 3 per cent (Deshpande 1933), 4.7 per cent (Miller and Fineman 1937), and 18 per cent (Kahn and Munir 1954). However, it has been suggested that perhaps these two characters are morphologically interdependent upon one another rather than the genes being linked (Peterson 1959).

PEDICEL LENGTH

Short pedicel appeared to be dominant over long pedicel as a quantitative character. Mean pedicel lengths of F_1 and F_2 progenies were close to that for the short pedicel-type parent. Some F_2 lines for short pedicel bred true the following generation, whereas long pedicel types gave lower mean values. Short pedicel was associated with purple color in the plant, with the recombination value calculated as 33 per cent from F_2 data (Deshpande 1933).

SOFT FLESH

S results in soft flesh in the mature pepper pod permitting easy separation of pod and calyx. The character was initially termed deciduous but was later redesignated soft flesh (Smith 1951a, b, Greenleaf 1952, Kormos and Kormos 1957). This condition is normal for the wild forms of the cultivated species as well as for nearly all purely wild species (Smith unpublished data, 1964).

WALL THICKNESS

Fruit wall thickness is reported to be controlled by eight pairs of genes with multiplicative, accumulative effects (Dempsey 1960).

LOCULE NUMBER

Multilobed (locule) fruits were obtained in F_1 plants from the cross of multilobed 'McMinnis' variety by bilobed 'Carolina No. 7' (South Carolina 1942). However, locule number may be variable in fruits from the same plant (Deshpande 1933).

IMMATURE COLOR

Color of unripe fruits varies from dark purple or nearly black through shades of green and yellow to ivory or sulfury white. Gene A controls purple fruit color as dominant to green (A^+). Various shades of purple are evident (Deshpande 1933), but the distinction between purple and non-purple is clear and non-integrating (Peterson 1959). Crosses of purple × ivory indicated two incompletely dominant genes, $A \not> A^+$ separating purple and green and $G \not> G^+$ distinguishing green and ivory. Nine phenotypic classes were reported in the F_2 population with varying shades from purple through green to ivory (Murthy and Murthy 1962a). The gene for purple immature fruit color, designated by symbol F (Hagiwara and Oomura 1947, Hagiwara, Hanagata, and Takano 1959), functions generally the same as A except expression is apparently possible only in combination with R_1 or R_2 genes for purple flower color. The gene *im* (originally *i*) has been proposed for an intermediate maturity color of purple in originally non-purple unripe fruit as found in the Japanese variety 'Goshiki' (Hagiwara *et al.,* 1959).

Green and yellow immature fruit colors were reported to segregate into 3:1 F_2 ratios (Webber 1911, Schmidt 1935). Within the green types, however, a series of dominant factors appear to be responsible for chlorophyll intensity in unripe fruit, with both cumulative and duplicative mechanisms of gene action proposed. Under the suggested cumulative mechanism, the presence of any one factor pair, designated $sw^+{}_1$, $sw^+{}_2$, $sw^+{}_3$, $sw^+{}_4$ . . . $sw^+{}_n$ (originally G_1, G_2, etc.), produces lettuce green or yellowish-green pod color, two factor pairs produce cedar green, and the very dark green color appears due to four pairs. Ivory or sulfury white pods result from the absence of all such chlorophyll factors (Odland and Porter 1938, Odland 1948, Peterson 1959). The symbols W_1W_2 have also been proposed for this color inheritance (Hagiwara, Hanagata, and Takano 1959).

The duplicate gene system was proposed (Jeswani, Deshpande, and Joshi 1956) to account for 15:1 F_2 ratios from the cross cedar green × lettuce green. Four pairs of duplicate genes would produce cedar green color, two pairs the lettuce green color, whereas the absence of all dominant pairs would result in sulfury white. The many true breeding lines of varying shades of unripe fruit colors available in *Capsicum* may be explained by either type of genetic mechanism (cumulative or duplicate), although further clarification is necessary.

Endo (1953) concluded from a cross of two cultivars of *C. annuum* ('Goshiki' and 'Takanotsume') that chlorophyll was controlled by one or two partially dominant genes (1.39 genes calculated) and anthocyanin by one gene of the same type (1.18 genes calculated). The anthocyanin of pepper was found to be the glycoside of delphinidin (Endo 1953).

MATURE COLOR

Of the many ripe color available in *Capsicum* fruits, yellow, y (originally r), was early reported as recessive to red, y^+ (Webber 1911, Atkins and Sherrard 1915, Shaw and Khan 1928), and was substantiated by later investigations (Smith 1950, Khan and Munir 1954, Kormos 1954b).

Kormos (1954b) determined by chromatographic analysis that levels of eight pigments in the red-fruited F_1 progeny of a cross of red × yellow types exactly matched the pigment content of the red-fruited parent. Similarly, pigments in the red and yellow F_2 segregants matched the respective parental types, suggesting total pigments to be controlled by the same factor. More extensive studies with various color shades from red to ivory indicated the action of three gene pairs, y and y^+, c_1 and $c_1{}^+$ (originally c and c^+), and c_2 and $c_2{}^+$ (originally c_1 and $c_1{+}$) (Kormos and Kormos 1960, Kormos 1962). The factors c_1 and c_2 reduced colors of y^+ and y by inhibition of the Beta carotene system, with c_1 causing approximately 1/10 reduction in red pigments. With c_2 present, red pigments occurred only in traces. Color development under this three gene-pair system was postulated as follows:

$y^+c_1{}^+$	red
y^+c_1	salmon red
y^+c_2	pink
$y\ c_1{}^+$	orange
$y\ \mathrm{c}_1$	lemon yellow
$y\ c_2$	ivory or white

Brauer (1962) analyzed Beta carotene in mature fruit and proposed the action of two genes, B and t, for high Beta carotene content. Both B and t^+ were incompletely dominant, with $BBtt$ producing high Beta carotene (188 mg./100 gm. dry powder), $BB\ t^+t^+$ intermediate levels (90-101 mg.), and $B^+B^+t^+t^+$ low levels (37-46 mg.). The heterozygotic condition t^+t was stated to be completely epistatic to B^+B but not to BB.

Brown and green mature fruit colors are controlled by the recessive chlorophyll retainer gene, cl, in combination with y^+ and y. With cl present, chlorophyll remains as the fruit matures. When cl combines with y^+ (red), a brown mature fruit color results, whereas with y (yellow), a yellowish- or olive-green color is produced (Smith 1948, 1950, Kormos and Kormos 1956b). The gene designation g (Brauer 1962) is undoubtedly synonymous with cl. With the anthocyanin gene A present in an $AABBclcltt$ genotype, mature pods, particularly when dried, would appear nearly black, as exemplified by Mexican chili varieties 'Pasilla' and 'Mulato' (Brauer 1962). This could account for the dominance of black fruit color noted by Halsted, Owen, and Shore (1908).

ASCORBIC ACID CONTENT

Inheritance for ascorbic acid content appeared to be multigenic with the F_1 mean value from crosses of low and high value parents corresponding closely to the geometric parental mean. Values in the F_2 were distributed between limits of parent lines (Györffy 1949).

PUNGENCY

The spicy flavor or pungency so characteristic of the *Capsicum*'s is due to the alkaloid capsaicin (Thresh 1876, Nelson 1910). Some early inheritance studies were hampered by lack of information on the site of capsaicin production (Erwin 1932, Miller and Fineman 1937), now recognized as being in secretory cells located along the placenta (Ohta 1962d). Soil conditions and climate, particularly temperature, have been considered responsible for variable levels of pungency in peppers from different localities (Erwin 1932, Miller and Fineman 1937). Ohta (1962d) considered high night temperature particularly favorable for high capsaicin content.

Plants from the same genotype may also be variable in capsaicin content (Brauer 1962). When classification is based on pungent or non-pungent criteria only, disregarding degrees of pungency, segregations indicate pungency or capsaicin to result from the presence of a single dominant gene *C* (Webber 1911, Deshpande 1935, Ramiah and Pillai 1935, Odland 1948, Greenleaf 1952). Brauer (1962) attempted to relate degrees of pungency to a three member allelic series, but exceptions to theoretical results were evident.

INTERNAL FRUIT PROLIFERATION

A rather frequent abnormality in *Capsicum* has been termed internal fruit or internal proliferation (Harris 1906, Bausor 1935). The fruitlike structures which are borne within the primary fruit assume no definite form, but vary from an irregular contorted body through an almost perfectly formed sterile fruit to linear bodies a few millimeters in length (Halsted 1891, Harris 1906, Cochran 1934, Murthy and Murthy 1962b). Some contain styles while others do not (Cochran 1935). The histological structure of the abnormality is carpel-like and resembles the ovary walls of the primary fruit, except for the absence of a several-cell layer constituting the epicarp (Cochran 1934). Cochran (1934) discusses ontogeny and Harris (1906) presents possible origins for the internal fruits. Both authors summarize and discuss earlier references to this phenomenon.

Mottareale (in Harris 1906 and Cochran 1934) attributed the abnormalities to short periods of cold weather during plant growth, but was not able to produce similar results under repeat conditions. Neither temperature nor nutrient level during growth of the plant appeared to be determining factors (Cochran 1934). The condition was evident among a wide selection of varietal types, being most common, however, in the large-fruited bell types (Harris 1906, Cochran 1934). Percentages of internal fruits in samples of various pepper types ranged from 0 to 22, with a mean value of 9 per cent in the total fruit examined (Harris 1906).

Cochran (1935) indicated that the abnormal fruit condition was generally associated with parthenocarpy and embryo abortion, which are heritable in some species, and that the same factor or interrelation of factors may be responsible for both the seedless condition and internal fruit abnormalities. A single instance is reported in which the internal fruit contained seed (Sturtevant 1890). No studies on heritability of this feature in *Capsicum* were encountered in the literature.

PLANT CHARACTERS

HEIGHT AND HABIT

A compact or bunchy mutant plant type, characterized by shortened internodes, reduced lateral and terminal branching, and production of 4-8 flowers and fruits in clusters, was described in chili varieties 'I. P. 46A' and 'Huntaka' from India and Japan (Anonymous 1940, Desphande 1944, Murthy and Murthy 1959, 1962b). This character had been determined earlier by Ikeno (1913) in *C. fasciculatum* (=*C. annuum*) as controlled by a single recessive gene, now designated *fa* for fasciculate (Lippert, Bergh, and Smith 1965). Variations of this dwarfed fasciculate habit, referred to as determinate, are reported in Hungary with main and axillary branches terminating in clustered inflorescences, and with some plants completely void of lateral shoots. Inheritance was not determined (Kormos and Kormos 1956a).

Webber (1911) crossed two medium-sized varieties, 'Golden Dawn' which had few, coarse, horizontal branches, and 'Red Chili' having many, fine, erect branches; he obtained F_2 segregants both giant and dwarf in comparison to the parents. The progeny distributed nearly equally between the two parental types within each of the three branch conditions. Analyses from the F_2 generation of the cross 'Santanka' × 'Truhart Perfection' pimiento indicated three pairs of polymeric genes involved in plant height (Dempsey 1960). Dale (1930a) reported a single recessive gene dwarf mutant in variety 'Coral Gem', with mutant types about six inches in height at maturity compared to the 12-inch height of normal types.

MATURITY

Limited information is available on inheritance of relative maturity. Odland (1948) recorded earliness in appearance of first bloom and first ripe fruit per plant. In crosses of an early variety ('Harris Early Giant') with medium-early ('Sunnybrook') and late ('Ornamental') varieties, earliness appeared due to several dominant or partially dominant factors. True breeding early lines were readily recovered in the F_3. A separate report recorded earliness in the F_1 from a cross of early 'Carolina #7' with a later variety (South Carolina 1942).

PUBESCENCE

The pubescent or hairy condition of stems, petioles, and leaves appeared as a 15:1 F_2 segregation with individuals in the dominant hairy class exhibiting different degrees of pubescence (Ikeno 1916). A conflicting note on this character refers to smooth stem as the dominant condition (Holmes 1934).

LEAF MUTANTS

Two mutant types with similar though not identical leaf-shape manifestations have been described. One, originally named "mutant-1" (Cook 1961b) but redesignated filiform, *fi* (Lippert, Bergh, and Smith 1965), had very elongated, narrow leaves, with petioles measuring approximately one-half the length of the leaf lamina. These plants were female sterile due to abnormal characteristics of the gynoecium, but were pollen fertile, permitting determination of single recessive gene inheritance. The second mutant (Joshi 1962) had narrow, lanceolate leaves which appeared sessile due to extension of the leaf lamina to the stem, thus resulting in absence of a well-defined petiole. Floral structure was normal except for shorter styles and filaments; however, flowers were both pollen and ovule sterile. Observation of 30 lanceolate-leaf types in a population of 180 plants suggested simple monogenic or digenic control.

PLANT COLOR AND VARIEGATION

Purple leaves and stems as well as other plant parts are due to incompletely dominant gene *A* (Deshpande 1939a, Odland 1960), with Mo_A intensifying purple color in *AA* genotypes (Deshpande 1939a). Purple node of the normal plant type is conditioned by al^+, whereas *al* (anthocyanin-less) prevents purple coloration in any portion of the plant (Deshpande 1939a, Odland 1960; see also under Inflorescence, Flower Color).

Several types of chlorophyll deficiencies or variegations have been observed. The gene vg^m (variegated mottled) produces a uniform yellow to light green mottle on foliage. The locus contains two additional alleles: the dominant vg^+ for normal green foliage and a recessive dwarfed type vg^v termed variegated virescent in which cotyledons and first true leaves, as well as all subsequent new growth, are initially yellow, becoming nearly normal green with maturity (Lippert, Bergh, and Cook 1964). Recessive *bv* (bushy variegated, originally Cook's "mutant-2") produces small, excessively branched plants with creamy-white and green mottled leaves (Cook 1962, Lippert *et al.* 1964). Marbled, *m,* has distinct zones of white, light green, and normal green on true leaves and immature fruits (Lippert *et al.* 1964). Imai (1938) illustrates a recessive variegation similar to the marbled phenotype, but identification of Imai's mutant was possible only after approximately 15 cm. of growth whereas marbled is easily identified in the first true leaves.

Kormos and Kormos (1955a) reported four chlorophyll deficiencies, two of which are xantha types with seedlings completely devoid of chlorophyll. Xantha$_1$, xa_1, is monofactorial and xantha$_2$ refers to a phenotype apparently under bifactorial control of complementary genes, xa_{2a} and xa_{2b}. Viridis, *vir*, has normal green cotyledons with true leaf blades turning yellowish-green. The homozygous recessive condition is lethal for these three mutants. The fourth recessive mutant is a chlorina type designated *chl,* with greenish-yellow foliage coloration.

Plastid instability, *pi* (originally *v*), was considered to be a Mendelian recessive with green and white variegation attributed to genetic "exo-mutation" of some green plastids into white (Hagiwara and Oomura 1939, 1947). Change of white plastids into green in a second series of crosses was considered caused by "auto-mutation" within the cytoplasm, independent of gene action (Hagiwara and Oomura 1939). Additional references to apparent maternal inheritance of variegation (Ikeno 1916, Dale 1930b, Kormos and Kormos 1955a) reported only variegated progeny resulting from crosses of variegated female × green male parents.

Two sectorial chimeras have been illustrated, in which approximately one-half of the plant showed chlorophyll deficiency of variable degrees, but no inheritance data were developed (Cochran 1939, Deshpande 1939b).

RESISTANCE TO DISEASE

BACTERIAL SPOT

Many varieties or accessions of pepper have been reported resistant to *Xanthomonas vesicatoria* (Doidge) Dows (Horsfall and McDonnell 1940, Martin 1948, Dempsey 1960, Greenleaf 1960, Sowell 1960, Cook and Stall 1963). Resistance in 'Plant Introduction (P.I.) 163192' (Cook and Stall 1963) and in a number of commercial varieties (Horsfall and McDonnell 1940) was presumed due to a single dominant gene, whereas resistance in 'Santanka' was controlled by a monogenic recessive (Dempsey 1960).

CERCOSPORA

Field resistance to *Cercospora* leaf spot (*C. capsici* Heald and Wolf) was high in four small-fruited strains of pepper. Genic analysis of segregating populations from a cross of *Capsicum annuum* accession 46101 from Brazil with 'Truhart' pimiento suggested that three or more genes were involved in inheritance of resistance (Hare 1957a, Mississippi 1957).

PHYTOPHTHORA

Five P.I. selections of *C. annuum,* 123469, 187331, 188476, 201232, and 210234, had relatively high resistance to *Phytophthora capsici* Leonian, the cause of root rot in the United States (Kimble and Grogan 1960). Two of these same selections, 201232 and 201234, and '631A Marinalco' from Mexico, as well as 'Rocoto' *(C. pubescens)* and 'Mishme Super Yellow' *(C. pendulum)* from Peru were resistant to the root rot organism *P. citrophthora* (R. E. & E. H. Smith) Leonian in Peru (Bazan de Segura 1962). 'California Wonder' and 'Oakview Wonder' have been noted as field resistant to *P. capsici* in California (Smith and Minges 1951).

VIRUSES

Potato Y

Two cultivars of *C. annuum*, 'P11' and 'S.C. 46252', are resistant to potato Y, tobacco mosaic, and tobacco etch viruses. Resistance to the N and C strains of PVY is conferred by the single recessive gene, y^a (Cook and Anderson 1959, 1960). Two distinct disease syndromes, severe and mild, in 'Large Bell Hot' corresponded to expected frequency of a dominant allele in the homozygous and heterozygous condition respectively, suggesting y^{a+} to be incompletely dominant for susceptibility (Cook 1960a). Resistance to PVY-N and TEV-E in 'P11' was originally postulated as a pleiotropic action of a single gene, ey^a (Cook 1960b), but later occurrence of susceptibility to PVY-N and resistance to TEV-E in breeding line YRP10 caused the gene ey^a to be withdrawn as invalid (Cook 1961a). Evidence suggests close linkage for the y^a and et^a loci (Cook 1961a).

"Single factor genetic" resistance available in 'Puerto Rico Wonder' to Puerto Rico pepper mosaic, later identified serologically as a strain of PVY, was derived initially from cultivar 'Cuaresmeno' (Riollano, Adsuar, and Rodriquez 1948, Perez and Adsuar 1955). The Puerto Rican virus strain, designated PVY-PR, infects peppers resistant to other PVY strains (Cook 1963a). Cook (1963a) has concluded from crossing studies with five resistant and susceptible cultivars of *C. annuum* inoculated with three strains of PVY (-N, -PR, and -N^{YR}) that three loci are associated with virus response. In addition to gene y^a for resistance to PVY-N, a second recessive gene controls resistance to PVY-N^{YR} in 'P.I. 264281' and 'S.C. 46252', whereas these cultivars are susceptible to PVY-PR.

Tobacco Etch

Monofactorially inherited resistance to this virus was found in both *C. annuum* ('S.C. 46252') and *C. frutescens* ('P. I. 152225') (Greenleaf 1956, McKinney 1952). The genes et^a and et^f (superscripts designating species origin) were postulated to determine a slow rate of multiplication of virus and masking of symptoms. Separation of susceptible and resistant genotypes was sharp; however, variable levels of resistance to near immunity in *C. annuum* were believed due to one or more modifying genes (Greenleaf 1956).

Tobacco Mosaic

Holmes (1934) described a dominant gene *L* for localization of necrosis of TMV in *Capsicum*. Subsequent investigation (Holmes 1937, Lutes 1954) revealed three alleles controlling four TMV symptoms. The alleles, designated $L > L^i$ (originally l^i) $\not>$ L^+ (originally l), acted as follows:

LL, LL^i, *or* LL^+	localized necrosis
L^iL^i	delayed necrosis with leaf abscission; recovery in many plants
L^iL^+	systemic necrosis
L^+L^+	systemic chlorosis

Similar localization reactions (*L* gene type) occur in *C. annuum, C. frutescens, C. pendulum,* and *C. microcarpum* but relationship of genes among species has not been established. L^i has been reported only from *C. annuum* (Holmes 1934, 1937, Greenleaf 1953).

Resistance in 'P.I. 183441' *(C. annuum)*, characterized by non-abscission of leaves, was ascribed to a dominant allele at the *L* locus, comparable but not identical to the *L* allele (Cook 1963b).

Vein-banding

Two loci, v_1 and v_2, with no evidence of linkage, control reaction to vein-banding virus in *C. annuum.* Genotypes in relation to seedling reactions were:

$v_1{}^+\text{-}v_2{}^+$	easily infected, vein necrosis, leaf abscission, and death
$v_1{}^+\text{-}v_2v_2$	resist infection but with vein-necrosis, mosaic, partial abscission, stunting
$v_1v_1v_2{}^+$	easily infected, severe mosaic, poor growth
$v_1v_1v_2v_2$	resist infection, with mild mosaic, good growth

Dominance of $v_1{}^+$ is incomplete, and this, together with resistance to infection conferred by v_2v_2, causes some difficulty in classification. Eight accessions representing four additional cultivated species, *C. pendulum, C. chinense, C. frutescens,* and *C. pubescens,* exhibited resistance typical of the $v_1v_1v_2v_2$ type (Simmonds and Harrison 1959).

RESISTANCE TO NEMATODES

Resistance to the root-knot nematodes *Meloidogyne incognita* (Kofoid & White) Chitwood and *M. incognita* var. *acrita* Chitwood in *C. annuum* ('Santanka xS' and '405B Mexico') is controlled by the gene *N.* The same gene possibly regulates resistance to *M. javanica* (Treub.) Chitwood and *M. arenaria* (Neal) Chitwood, but not to *M. hapla* Chitwood (Hare 1956a,b, 1957b).

GENES LISTED ALPHABETICALLY

The nomenclature system for *Capsicum* was proposed by Lippert, Bergh, and Smith (1965). Names and symbols were applied to the mutant genes, with dominant mutants designated by the first letter of the symbol capitalized and recessive mutants by lower case letters. The corresponding allele in the standard type in this system is designated by the mutant symbol superscribed with a plus (+). For example, the "normal" allele for mutant *A,* anthocyanin, is A^+ and the "normal" allele for *al,* anthocyanin-less, is al^+. Dominant or recessive gene action of the mutant is related to the standard type, established as *C. annuum* cultivar 'California Wonder'. The inclusion of the reference by Lippert, Bergh, and Smith (1965) in the following list of mutants indicates that the mutant has been named symbolized, or in some manner redesignated.

A	basic gene for anthocyanin color in plant, flower, and immature fruit. Incompletely dominant (Deshpande 1933, Peterson 1959, Odland 1960). *F* also used for the same character (Hagiwara, Hanagata, and Takano 1959).
al	anthocyanin-less, prevents any purple color in plant (Deshpande 1939a, Odland 1960). Redesignation of *s* (Lippert, Bergh, and Smith 1965).

As	style anthocyanin, purple in absence of *A* or *Asf* (Hagiwara and Oomura 1947). Redesignation of *P* (Lippert, Bergh, and Smith 1965).
Asf	style and filament anthocyanin, purple in absence of *A* (Odland 1960). Redesignation of *W* (Lippert, Bergh, and Smith 1965).
b	used by Cook (1961b) to symbolize yellow anther color; see *al.*
B	**high Beta-carotene content, interacts with *t* for range of levels in mature fruit** (Brauer 1962).
B	Modifier of *A* (Deshpande 1939a). See Mo_A.
bl	branchless (Bergh and Lippert 1964).
Bs	bacterial spot *(Xanthomonas vesicatoria)* resistance (Cook and Stall 1963, Lippert, Bergh, and Smith 1965).
bv	bush variegated, originally mutant-2 (Cook 1962, Lippert, Bergh, and Cook 1964).
c	carotene pigment inhibitor, redesignated c_1 (Kormos and Kormos 1960, Kormos 1962, Lippert, Bergh, and Smith 1965).
c_1	carotene pigment inhibitor, reduces red color of y^+ by approximately 1/10 (Kormos and Kormos 1960, Kormos 1962). Previously *c* (Lippert, Bergh, and Smith 1965).
c_2	carotene pigment inhibitor, permits only traces of red color to develop (Kormos 1962). Originally c_1 (Lippert, Bergh, and Smith 1965).
C	capsaicin or pungent fruit (Deshpande 1935).
C	designated by Hagiwara and Oomura (1947) as complementary of R_1R_2 for purple flower color.
ce	calyx enclosed around the fruit base, originally *e* (Deshpande 1933, Lippert, Bergh, and Smith 1965).
chl	chlorina variegation (Kormos and Kormos 1955a, Lippert, Bergh, and Smith 1965).
cl	chlorophyll retainer in mature fruit. Combines with y^+ (red) or *y* (yellow) to produce brown and olive green mature fruit color, respectively (Smith 1948, 1950). Synonymous with *g* (Brauer 1962).
D	pointed fruit apex, redesignated *Pt* (Deshpande 1933, Lippert, Bergh, and Smith 1965).
e	calyx enclosed (Deshpande 1933). (See *ce.*)
et^a, et^f	tobacco etch virus resistance in *C. annuum* and *C. frutescens*, respectively (Greenleaf 1956).
ey^a	originally proposed for pleiotropic gene action for resistance to tobacco etch and potato Y viruses (Cook and Anderson 1960). Now invalid (Cook 1961a).
f	non-bulging fruit base (Deshpande 1933). (See *fb.*)
F	used for purple immature fruit color (Hagiwara and Oomura 1947, Hagiwara, Hanagata, and Takano 1959). (See *A.*)
fa	fasciculate, shortened internodes, compact, bushy plant, and flowers and fruit borne in clusters (Deshpande 1944, Murthy and Murthy 1962b, Lippert, Bergh, and Smith 1965).
fb	fruit base non-bulging, originally *f* (Deshpande 1933, Lippert, Bergh, and Smith 1965).
fi	filiform, formerly "mutant-1" (Cook 1961b, Lippert, Bergh, and Smith 1965).
fs	female sterile (Bergh and Lippert 1964).
g	chlorophyll retainer (Brauer 1962), identical to *cl.*
G	suggested for green immature fruit with G^+ being ivory white (Murthy and Murthy 1962a).
G_1, G_2, G_3, G_4, ... G_n	originally referred to green immature fruit color (Odland and Porter 1938, Odland 1948, Jeswani, Deshpande, and Joshi 1956). Changed to sw_1, sw_2, etc., for sulfury white (Lippert, Bergh, and Smith 1965).
gd	glossy diminutive, also female sterile (Bergh and Lippert 1964).

Gi	graft incompatible with *Capsicum* and other Solanaceae (Kormos and Kormos 1955b, Lippert, Bergh, and Smith 1965).
H	symbol used by Holmes (1934) to designate non-pubescent or hairless stem. (See Pubescence under Plant Characters.)
im	intermediate maturity of purple in originally non-purple unripe fruit, mature fruit red (Hagiwara, Hanagata, and Takano 1959, Lippert, Bergh, and Smith 1965).
L	localization of tobacco-mosaic virus (Holmes 1934, 1937, Lutes 1954).
L^i	imperfect localization of tobacco-mosaic virus. A three gene allelic series with $L > L^i \ngtr L^+$ for four virus expressions (Holmes 1937, Lutes 1954). L^i denotes a change of symbol from original l^i (Lippert, Bergh, and Smith 1965).
l^i	See L^i
m	marbled, distinct green and white zonation on foliage and immature fruit (Lippert, Bergh, and Cook 1964).
m	used to denote mutant-1 (Cook 1961b). (See *fi*.)
M	used by Holmes (1934) for pungent. (See *C*.)
Mo_A	modifier of *A*, intensifies purple color with *A*, originally *B* (Deshpande 1939a; Lippert, Bergh, and Smith 1965).
ms	male sterile with sterile cytoplasm (S) in genotype S *msms* (Peterson 1958).
mutant-1, mutant-2	redesignated *fi* and *bv* respectively (Cook 1961b, 1962, Lippert, Bergh, and Cook 1964).
N	nematode resistance (Hare 1957b).
O	oblate fruit shape (Khambanonda 1950, Peterson 1959).
p	upright or erect pedicels (Deshpande 1933). (See *up*.)
P	style anthocyanin (Hagiwara and Oomura 1947). Redesignated *As* (Lippert, Bergh, and Smith 1965).
pi	plastid instability, green and white variegation (Hagiwara and Oomura 1947, Lippert, Bergh, and Smith 1965).
Pt	pointed fruit apex, not fully dominant to blunt (Deshpande 1933). Redesignation for *D* (Lippert, Bergh, and Smith, 1965).
r	yellow mature fruit color (Deshpande 1933). See *y* (Lippert, Bergh, and Smith 1965).
R_1, R_2	polymeric genes for purple flower color. Considered complementary with *C* for purple flower color and with *F* for purple immature fruit color (Hagiwara and Oomura 1947).
s	redesignated anthocyanin-less, *al* (Deshpande 1939, Odland 1960, Lippert, Bergh, and Smith, 1965).
S	soft flesh, fruit deciduous (Smith 1951b, Jeswani, Deshpande, and Joshi 1956, Kormos and Kormos 1957).
sl	styleless, incomplete female sterile (Bergh and Lippert 1965).
sd	scabrous diminutive, foliage surface rough as compared to glossy surface of *gd* (Bergh and Lippert 1964).
sp	spinach, ground level whorl of odd, limp leaves; flower buds completely lacking (Bergh and Lippert 1964).
sw_1, sw_2, sw_3, sw_4, . . . sw_n	sulfury white immature fruit color. Dominant alleles control various green shades. Number of genes and whether cumulative or duplicate in action not clearly established (Odland and Porter 1938, Odland 1948, Jeswani, Deshpande, and Joshi 1956). Originally G_1, G_2, etc. (Lippert, Bergh, and Smith 1965).
t	high Beta-carotene content, complementary with *B* (Brauer 1962).
u	upright or erect pedicel (Hagiwara and Oomura 1947). See *up* (Lippert, Bergh, and Smith 1965).
up	upright or erect pedicel. Redesignation of *p* and *u* (Lippert, Bergh, and Smith 1965).

v	See *pi*.
v_1, v_2	vein-banding virus resistance, combine to provide four virus expressions (Simmonds and Harrison 1959).
vg^m	variegated mottled, dominant allele to vg^v (Lippert, Bergh, and Cook 1964).
vg^v	variegated virescent, allelic to vg^m (Lippert *et al.* 1964).
vir	variegation of viridis type, homozygous lethal (Kormos and Kormos 1955a, Lippert, Bergh, and Smith 1965).
W	purple style and filament color in absence of *A* (Odland 1960). Redesignated *Asf* (Lippert, Bergh, and Smith 1965).
W_1, W_2	synonymous with sw_1, sw_2 as used by Hagiwara, Hanagata, and Takano (1959).
wl	willow leaf, leaves narrow but wider than *fi*, practically female sterile (Bergh and Lippert 1964).
xa_1	xantha$_1$, completely void of chlorophyll, homozygous lethal (Kormos and Kormos 1955a, Lippert, Bergh, and Smith 1965).
xa_{2a}, xa_{2b}	xantha$_2$, as xantha$_1$, but controlled by two complementary genes (Kormos and Kormos 1955a, Lippert, Bergh, and Smith 1965).
y	yellow mature fruit color, combinations of c_1, c_2, *cl*, *y*, and their alleles provide range of mature colors (Deshpande 1933, Smith 1948, 1950, Kormos and Kormos 1960, Kormos 1962). Replaces *r* as proper mutant symbol (Lippert, Bergh, and Smith 1965).
y^a	resistance to C and N strains of potato virus Y in *C. annuum* (Cook and Anderson 1960).
Ys	yellow corolla spot of *C. pendulum* acts as dominant in crosses with other species (Bergh, Lippert, and Smith in press).

LINKAGE RELATIONSHIPS

Comprehensive studies of linkage relationships between available characters in *Capsicum* have not been undertaken. Linkage of *A*, *O*, and sw_1 (Peterson 1959) represents the only definite association of three genes on a single chromosome. From combined information on linkage it can be assumed tentatively that *C*, *pi*, *up*, and short fruit length may represent a linkage series. Carrying the assumption further, if one of the factors (three factors calculated) for fruit length by Deshpande (1933) is comparable to the *O* gene, it is possible that these six genes are located on the same chromosome. Available data on linkage are summarized in Table II. Independent assortment or non-linkage has been determined for the gene combinations listed in Table III.

VEGETATIVE GRAFTS AND GRAFT HYBRIDS

Capsicum species have been successfully grafted with *Capsicum* (Kormos and Kormos 1955b, Yagishita 1961a, b, Ohta 1961b, 1962a, Pirovano 1962, Sagajdak 1963, Topornina 1963) and several other genera of the Solanaceae including *Datura* (Isbell 1944, Kormos and Kormos 1955b, Pichenot 1960), *Lycium* (Limberk 1951), *Lycopersicon* (Bailey 1890, Kuzdowicz 1954, Kormos and Kormos 1955b, Samuel 1960), *Nicotiana* (Kostoff 1929), *Physalis* (Bailey 1890), and *Solanum* (*S. capsicastrum* Link ex Schau., *latifolium* Poir., *melongena* L., and *sisymbrifolium* Lam.) (Bailey 1890, Dort 1947, Bonifacio 1951, Kormos and Kormos 1955b). Variable results have been obtained by reciprocal

TABLE II

Summary of linkage relationships among *Capsicum* genes.

Genes		Crossover %	References
A	sw_1	20.6	Peterson 1959
A O		6.5	Peterson 1959
O	sw_1	17.2	Peterson 1959
A	y^+	44.0	Deshpande 1933
A	short pedicel	33.0	Deshpande 1933
A	short petal	no data	Deshpande 1933
A	short fruit	no data	Deshpande 1933
As	R_1, R_2	20-24	Hagiwara and Oomura 1947
C	*up*	34.34 ± 3.87	Dempsey 1960
ce	*fb*	3; 4.7; 18	Deshpande 1933, Miller and Fineman 1938, Khan and Munir 1954, respectively
et^a	y^a	no data	Cook 1961a
pi	*up*	approx. 15	Hagiwara and Oomura 1947
up	short fruit	no data	Deshpande 1933

grafts, and with intergeneric grafts fruit and seed set were generally low. Vegetative growth of the cion, however, may be vigorous.

Reactions of genetically pure paprika varieties when grafted onto other paprikas, or to tomato, *Datura metel* L., or *Solanum sisymbrifolium*, indicated graft incompatibility to be inherited as a single dominant gene, *Gi* (Kormos and Kormos 1955b; name and symbol designation by Lippert, Bergh, and Smith 1965). A Hungarian tomato-shaped paprika was determined to possess the dominant allele whereas the recessive allele was present in "ceriforme 1" and "longum nigrum luteum." Graft incompatibility appears to be governed by biochemical differences at the graft contact surfaces (Kormos and Kormos 1955b).

Vegetative or graft hybrids between *Capsicum*'s have been reported with fruit modifications evident on the grafted cion or appearing later in selfed progenies after two or three generations of grafting. These modifications persisted in the selfed progeny of modified fruits. The higher frequency of transformed fruits, evident as a groove in the fruit base and characteristic of the rootstock parent, following two or three generations of grafting suggested the multiple grafting had a cumulative genetic effect (Yagishita 1961a, b).

Sagajdak (1963) reported that vegetative hybrids between two sweet pepper varieties produced heterotic seed with G_1 plants taller, leafier, and earlier in development. In the G_2, segregations also occurred for locule number, flavor, and orientation of the fruit. Topornina (1963) also observed G_1 and G_2 variations from parental forms in shape, size, orientation, and alkaloid content of

TABLE III

Independent assortment or non-linkage among *Capsicum* genes.

Genes		References
A	*L*	Holmes 1934
A	*sl*	Bergh and Lippert 1965
al	*fi*	Cook 1961b
bv	vg^m, vg^v	Lippert, Bergh, and Cook 1964
C	*ce*	Deshpande 1935, Khan and Munir 1954, Miller and Fineman 1938
C	*cl*	Smith 1950
C	*fb*	Miller and Fineman 1938
C	*L*	Holmes 1934
C	*Pt*	Miller and Fineman 1938
C	*y*	Smith 1950
ce	*Pt*	Miller and Fineman 1938
ce	*up*	Khan and Munir 1954, Miller and Fineman 1938
ce	*y*	Khan and Munir 1954
cl	*up*	Smith 1950
cl	*y*	Smith 1950
fb	*Pt*	Miller and Fineman 1938
fb	*up*	Miller and Fineman 1938
L	*Pt*	Holmes 1934
L	up^+	Holmes 1934
L	y^+	Holmes 1934
m	vg^m, vg^v	Lippert, Bergh, and Cook 1964
Pt	*up*	Miller and Fineman 1938
sl	y^+	Bergh and Lippert 1965
sw_1, sw_2	*up*	Odland 1948
up	*y*	Smith 1950
v_1	v_2	Simmonds and Harrison 1959

the fruit. Variations were greater in graft generations than in filial generations from sexual crosses of the same varieties.

Eight of 19 vegetative grafts of *C. annuum* cultivar 'Cayennense' onto *Datura stramonium* L. produced extra large fruit with a greater number of seed, of which 30 per cent were malformed and inviable. Seedlings obtained from the abnormal fruit compared to those from non-grafted plants were more vigorous with darker green foliage, flowered later, and bore larger fruit with more seed, all of which were viable. The modifications were inherited through six generations, with evidence for maternal cytoplasmic inheritance obtained by grafts of normal to abnormal and the reciprocals (Pichenot 1960).

Khazina (1949, 1956, 1961) described several varieties developed from supposedly vegetative hybrids between different *Capsicum* cultivars, with claims of higher yields and higher dry matter, sugar, and vitamin C content in the fruit as compared with standard varieties.

Ohta (1961b, 1962a) failed to modify either non-pungent or male fertile characteristics of the cion by grafts to pungent or male sterile stocks.

The reader is referred to the excellent discussion by Rick and Butler (1956) for evaluation of heritable changes claimed for vegetative grafts.

HETEROSIS

Heterosis, as measured by F_1 values exceeding the mean value of the superior parent, has been reported for such features as vigor, maturity, height of plant, productivity, both as fruit number and total fruit weight, and fruit thickness (Deshpande 1933, Pal 1945, Martin 1949, Fujii, Masabayashi, and Kuwahara 1959). Comparisons of varieties and their F_1 and F_2 hybrids indicate that F_2 progenies, though inferior to F_1 in yield, were superior to parental yields (Martin 1949, Fujii *et al.* 1959).

Hybrids and parents did not differ in photosynthetic, respiratory, transpiratory, or enzymatic (peroxidase and catalase) activity, ruling out these physiological processes as the cause of heterosis (Khristov and Genchev 1961).

LITERATURE CITED

ABD-EL-MAKSOUD MOHAMED, M. 1953. Cytogenetics of hybrids between *Capsicum annuum* and *C. frutescens*. Ph. D. Thesis, Univ. of Calif., Davis, 61 pp.

ALEKSIC, D. 1960. (The induction of tetraploidy in peppers.) Arh. Poljopr. Nauk. **13**: 106-113.

ANONYMOUS. 1940. Mutation in chilli. Indian Farming **1**: 178.

ATKINS, W. R. G., and G. O. SHERRARD. 1915. The pigments of fruits in relation to some genetic experiments of *Capsicum annuum*. Sci. Proc. Roy. Dublin Soc., N. S., **14**: 328-335.

BAILEY, L. H. 1890. Notes upon methods of herbaceous grafting. New York (Cornell) Agr. Exp. Sta. Bull. **25**: 175-177.

————. 1923. *Capsicum*. Gentes Herb. **1**: 128-129.

BAUSOR, S. C. 1935. A monstrous fruit of *Capsicum*. Amer. Jour. Bot. **22**: 826-828.

BAZAN DE SEGURA, CONSUELO. 1962. Search for sources of resistance in red pepper to the fungus *Phytophthora citrophthora*. Turrialba **12**: 16-24.

BERGH, B. O., and L. F. LIPPERT. 1964. Six new mutant genes in the pepper, *Capsicum annuum* L. Jour. Hered. **55**: 296-300.

————, and ————. 1965. A gene difference that affects female fertility in *Capsicum annuum* L. Amer. Nat. **99**: 159-166.

————, ————, and P. G. SMITH. Inheritance of the yellow petal spot of *Capsicum pendulum* Willd. Amer. Jour. Bot. (in press).

BONIFACIO, P. 1951. Grafting solanaceous plants. Riv. Ortoflorofruttic. Ital. **35**: 42-43.

BOSWELL, V. R. 1949. Garden pepper, both a vegetable and a condiment. *In* Our vegetable travelers. Natl. Geogr. **96**: 145-217 (pp. 166-167).

BRAUER, O. 1962. Untersuchungen über Qualitätseigenschaften in F_1-Hybriden von Paprika, *Capsicum annuum* L. Zeitschr. Pflanzenz. **48**: 259-276.

BUKASOV, S. M. 1930. The cultivated plants of Mexico, Guatemala and Columbia. Bull. Appl. Bot. Genet. and Plant Breed., Suppl. No. 47: 261-273.

CAMPOS, FILOMENA F., and D. T. MORGAN, JR. 1958. Haploid pepper from a sperm; an androgenetic haploid of *Capsicum frutescens.* Jour Hered. **49**: 134-137.

————, and ————. 1960. Genetic control of haploidy in *Capsicum frutescens* L. following crosses with untreated and x-rayed pollen. Cytologia **25**: 362-372.

CANDOLLE, A. DE, 1886. Origin of cultivated plants. (Reprint of 2nd ed.) Hafner Publishing Co., 1959, pp. 288-290.

CARLSSON, G. 1962. (Inheritance of fruit size and its relation to leaf size and fruit set and the significance of these characters in breeding *Capsicum annuum.*) Sverig. Utsädesfören. Tidskr. **72**: 249-255.

CHENNAVEERAIAH, M. S. 1947. A preliminary note on the karyotype in *Capsicum fastigiatum* Bl. Curr. Sci. **16**: 384-385.

CHRISTENSEN, HILDE M., and R. BAMFORD. 1943. Haploids in twin seedlings of pepper, *Capsicum annuum* L. Jour. Hered. **34**: 99-104.

COCHRAN, H. L. 1934. Abnormalities in the flower and fruit of *Capsicum frutescens.* Jour. Agr. Res. **48**: 737-748.

————. 1935. Morphology of an internal type of abnormality in the fruit of the pepper. Bot. Gaz. **97**: 408-415.

————. 1939. A chlorophyll deficient pimiento. Jour. Hered. **30**: 81-83.

COOK, A. A. 1960a. Syndrome of potato virus Y in progenies from crosses between susceptible Large Bell Hot and two resistant pepper varieties. Proc. Amer. Soc. Hort. Sci. **76**: 482-485.

————. 1960b. Genetics of resistance in *Capsicum annuum* to two virus diseases. Phytopathology **50**: 364-367.

————. 1961a. A mutation for resistance to potato virus Y in pepper. Phytopathology **51**: 550-552.

————. 1961b. Inheritance of mutant-1 phenotype in the pepper. Jour. Hered. **52**: 154-158.

————. 1962. Studies of a foliage variegation in pepper. Proc. Amer. Soc. Hort. Sci. **81**: 390-395.

————. 1963a. Genetics of response in pepper to three strains of potato virus Y. Phytopathology **53**: 720-722.

————. 1963b. Dominant resistance to tobacco mosaic virus in an exotic pepper. Plant Dis. Rep. **47**: 783-786.

————, and C. W. ANDERSON. 1959. Multiple virus disease resistance in a strain of *Capsicum annuum.* Phytopathology **49**: 198-201.

————, and ————. 1960. Inheritance of resistance to potato virus Y derived from two strains of *Capsicum annuum.* Phytopathology **50**: 73-75.

————, and R. E. STALL. 1963. Inheritance of resistance in pepper to bacterial spot. Phytopathology **53**: 1060-1062.

CURTIS, L. C., and J. SCARCHUK. 1948. Seedless peppers. A single mendelian recessive character. Jour. Hered. **39**: 159-160.

DALE, E. E. 1928. Inheritance of fruit-length in *Capsicum.* Pap. Michigan Acad. Sci. **9**: 89-110.

————. 1930a. Inheritance of dwarf in *Capsicum.* Pap. Michigan Acad. Sci. **13**: 1-4.

————. 1930b. Maternal inheritance in a chlorophyll variegation in *Capsicum.* Pap. Michigan Acad. Sci. **13**: 5-8.

DEMPSEY, A. H. 1960. Inheritance studies of certain fruit and plant characters in *Capsicum frutescens.* Diss. Abstr. **20**: 2506-2507.

DESHPANDE, R. B. 1933. Studies in Indian chillies. 3. The inheritance of some characters in *Capsicum annuum* L. Indian Jour. Agr. Sci. **3**: 219-300.

————. 1935. Studies in Indian chillies. 4. Inheritance of pungency in *Capsicum annuum* L. Indian Jour. Agr. Sci. **5**: 513-516.

————. 1939a. Studies in Indian chillies. 5. Inheritance of anther color and its relation to color in petal and node in *Capsicum annuum* L. Indian Jour. Agr. Sci. **9**: 185-192.

————. 1939b. A case of variegation in *Capsicum annuum* L. Curr. Sci. **8**: 313-314.

————. 1944. Inheritance of bunchy habit in chilli (*Capsicum annuum* L.) Indian Jour. Genet. Plant Breed. **4**: 54.

Dixit, P. D. 1931. A cytological study of *Capsicum annuum.* Indian Jour. Agr. Sci. **1**: 419-433.

Dort, H. W. Van. 1947. *Solanum capsicastrum* on *Capsicum annuum.* Bloemisterij **21**: 3-4.

Duvick, D. N. 1959. The use of cytoplasmic male-sterility in hybrid seed production. Econ. Bot. **13**: 167-195.

Endo, T. 1953. Inheritance of fruit color in *Capsicum.* Ann. Rep. Natl. Inst. Genet., Japan, **3**: 46-47.

Erwin, A. T. 1932. The peppers. Iowa Agr. Exp. Sta. Bull. **293**: 121-152.

————. 1949. An interesting Guatemalan chilli (*Capsicum guatemalense* Bitt.). Iowa Agr. Exp. Sta. Bull. **371**: 612-614.

Eshbaugh, W. H. 1964. A numerical taxonomic and cytogenetic study of certain species of the genus *Capsicum.* Ph.D. Thesis, Indiana University, Bloomington, Indiana, 112 pp.

Fingerhuth, K. A. 1832. Monographia Generis Capsici. Dusseldorpii, Arnz and Comp., 32+ pp.

Fujii, K., W. Masabayashi, and T. Kuwahara. 1959. Studies on the utilization of F_2 generations of red-pepper crosses. Agr. and Hort. **34**: 667-668.

Georgieva, P. 1959. Caractère de la mutabilité dans les poivrons autotetraploïdes obtenus par manière expérimentale. Nauc. Trud. Viss. Selskostopan. Inst. G. Dimitrov **7**: 173-194.

Greenleaf, W. H. 1947. A spontaneous tetraploid hybrid in pepper (*Capsicum frutescens*). Proc. Amer. Soc. Hort. Sci. **49**: 231-232.

————. 1952. Inheritance of pungency and of the deciduous character in peppers (*Capsicum annuum*). Proc. Assoc. South. Agr. Workers **49**: 110-111. (Abstr.)

————. 1953. Effects of tobacco-etch virus on peppers (*Capsicum* sp.). Phytopathology **43**: 564-570.

————. 1956. Inheritance of resistance to tobacco-etch virus in *Capsicum frutescens* and in *Capsicum annuum.* Phytopathology **46**: 371-375.

————. 1960. Resistance levels to the bacterial leaf spot disease in peppers. Proc. Assoc. South. Agr. Workers **57**: 238-239. (Abstr.)

Györffy, B. 1939. (Tetraploid paprika.) Acta Univ. Szeged., Acta Biol. Pars. Bot. **5**: 30-38.

————. 1949. The inheritance of the ascorbic acid content of paprika and tomato. Proc. Eighth Int. Congr. Genet. **8**: 585-586. (Abstr.)

Hagiwara, T., K. Hanagata, and T. Takano. 1959. Inheritance of fruit-colour in *Capsicum annuum.* Jap. Jour. Breed. **9**: 49-50. (Abstr.)

————, and Y. Oomura. 1939. Plastic inheritance of variegation in *Capsicum annuum.* Jap. Jour. Genet. **15**: 328-330.

————, and ————. 1947. On linkage in *Capsicum annuum* L. Jap. Jour. Genet., Suppl. **1**: 87-96.

Halsted, B. D. 1891. Botanical note. A strange thing on peppers. Bull. Torrey Bot. Club **18**: 151.

————. 1909. Experiments with peppers. New Jersey Agr. Exp. Sta. Ann. Rep. 1909, pp. 308-317.

————, E. J. Owen, and N. D. Shore. 1908. Report of the botanist. New Jersey Agr. Exp. Sta. Ann. Rep. 1908, pp. 285-290.

Hare, W. W. 1956a. Resistance in pepper to *Meloidogyne incognita acrita.* Phytopathology **46**: 98-104.

————. 1956b. Comparative resistance of seven pepper varieties to five root-knot nematodes. Phytopathology **46**: 669-672.

———. 1957a. Inheritance of *Cercospora* resistance in pepper. Phytopathology **47**: 15. (Abstr.)

———. 1957b. Inheritance of resistance to root-knot nematodes in pepper. Phytopathology **47**: 455-459.

HARRIS, J. A. 1906. Proliferation of the fruit in *Capsicum* and *Passiflora.* Missouri Bot. Gard. Ann. Rep. **17**: 133-145.

HEISER, C. B., JR., and P. G. SMITH. 1948. Observations on another species of cultivated pepper, *Capsicum pubescens* R. & P. Proc. Amer. Soc. Hort. Sci. **52**: 331-335.

———, and ———. 1958. New species of *Capsicum* from South America. Brittonia **10**: 194-201.

HIROSE, T., S. NISHI, and S. TAKASHIMA. 1960. Studies on the interspecies crossing in cultivated *Capsicum.* I. On crossability between species. Kyoto Prefectural Univ. Fac. Agr. Sci. Rep. **12**: 40-46.

HOLMES, F. O. 1934. Inheritance of ability to localize tobacco-mosaic virus. Phytopathology **24**: 984-1002.

———. 1937. Inheritance of resistance to tobacco-mosaic disease in the pepper. Phytopathology **27**: 637-642.

HORSFALL, J. G., and A. D. MCDONNELL. 1940. Varietal susceptibility of peppers to bacterial spot. Plant Dis. Rep. **24**: 34-36.

HUNZIKER, A. T. 1950. Estudios sobre Solanaceae. I. Sinopsis de las especies silvestres de *Capsicum* de Argentina y Paraguay. Darwiniana **9**: 225-247.

———. 1954 (1956). Synopsis of the genus *Capsicum.* Congr. Int. Bot., Rapp. et Comm., Deuxième Sér., **8**: 73-74.

———. 1961a. Studies on Solanaceae. III. Notes on the genera *Physalis* L. and *Capsicum* L. with the description of a new South American species. Kurtziana **1**: 207-216.

———. 1961b. Noticia sobre el cultivo de *Capsicum baccatum* L. (Solanaceae) en Argentina. Kurtziana **1**: 303.

HUSKINS, C. L., and L. LA-COUR. 1930. Chromosome numbers in *Capsicum.* Amer. Nat. **64**: 382-383.

IKENO, S. 1913. Studien über die Bastarde von Paprika *(Capsicum annuum).* Zeitschr. Ind. Abst. Vererb. **10**: 99-114.

———. 1916. Studies on the hybrids of *Capsicum annuum.* II. On some variegated races. Jour. Genet. **6**: 201-230.

———. 1928. Change of dominance in a cross of two strains of *Capsicum annuum.* Proc. Imp. Acad. (Tokyo) **4**: 400-403.

IMAI, Y. 1938. The mechanism of variegation in *Plantago* and *Capsicum.* Jour. Genet. **35**: 375-382.

IRISH, H. C. 1898. A revision of the genus *Capsicum* with especial reference to garden varieties. Rep. Missouri Bot. Gard. **9**: 53-110.

ISBELL, C. L. 1944. Pass the word to gardeners: Graft tomatoes onto weeds. Southern Seedsman **7**: 14, 42.

JESWANI, L. M., R. B. DESHPANDE, and A. B. JOSHI. 1956. Inheritance of some fruit characters in chilli. Indian Jour. Genet. Plant Breed. **16**: 138-143.

JOSHI, B. C. 1962. A long-leaved mutant in chilli (*Capsicum annuum* L.) Curr. Sci. **31**: 425-426.

KAISER, S. 1935a. The inheritance of a geotropic response in *Capsicum* fruits. Bull. Torrey Bot. Club **62**: 75-80.

———. 1935b. The factors governing shape and size in *Capsicum* fruits; a genetic and developmental analysis. Bull. Torrey Bot. Club **62**: 433-454.

KHAMBANONDA, I. 1948. Polygenic inheritance of fruit size in red pepper. Iowa State Coll. Jour. Sci. **23**: 48-49.

———. 1950. Quantitative inheritance of fruit size in red pepper (*Capsicum frutescens* L.). Genetics **35**: 322-343.

KHAN, A. R., and M. MUNIR. 1954. Inheritance studies in the common chillies (*Capsi-*

cum annuum L.). Proc. Sixth Pakistan Sci. Conf., Karachi, 1954, Part III, pp. 14-16. (Abstr.)

KHAZINA, E. P. 1949. (Change of heredity in the seed generation of a vegetative hybrid.) Agrobiologiya **1949**: 120-122.

————. 1956. (New varieties of sweet pepper obtained by vegetative hybridization.) Agrobiologiya **1956**: 47-54.

————. 1961. (New varieties of sweet pepper obtained by vegetative hybridization.) Agrobiollogiya **1961**: 617-619.

KHRISTOV, S., and S. GENCHEV. 1961. (Studies on the physiological properties of certain varieties and hybrid combinations of peppers.) Plovdiv. Nauch. Inst. po Zelenchukovite Kult. Maritsa. Izv. **1**: 29-43.

KIMBLE, K. A., and R. G. GROGAN. 1960. Resistance to *Phytophthora* root rot in pepper. Plant Dis. Rep. **44**: 872-873.

KORMOS, J. 1954a. (Investigations on sterility in paprika.) Ann. Inst. Biol. Tihany **22**: 235-252.

————. 1954b. (Inheritance of carotenoid pigment.) Ann. Inst. Biol. Tihany **22**: 253-259.

————. 1962. Einige Bermerkungen über die Karotenfarben der Paprikafrucht. Acta Bot. (Acad. Sci. Hung.) **8**: 279-281.

————., and JÓZSEFNÉ KORMOS. 1955a. (A contribution to the genetics of chlorophyll-deficiency.) Ann. Inst. Biol. Tihany **23**: 177-186.

————, and ————. 1955b. (Affinity in grafting.) Ann. Inst. Biol. Tihany **23**: 161-175.

————, and ————. 1956a. (Determinate growth in paprika.) Növenytermeles **5**: 1-10.

————, and ————. 1956b. (Variations in color and gland in green pepper fruits.) Növenytermeles **5**: 141-152.

————, and ————. 1956c. (Experimental data on the morphogenesis of flowering plants.) Comm. Sect. Bot. Soc. Biol. Hungary **1956**: 207-217.

————, and ————. 1957. (Soft green pepper.) Növenytermeles **6**: 33-44.

————, und K. KORMOS. 1960. Die genetischen Typen der Carotinoid-Systeme der Paprikafrucht. Acta Bot. (Acad. Sci. Hung.) **6**: 305-319.

KOSTOFF, D. 1926. Die Bildung der Pollenkörner bei einigen Varietäten von *Capsicum annuum*. Jahrb. Univ. Sofia **4**: 101-126.

————. 1929. Acquired immunity in plants. Genetics **14**: 37-77.

KUNTZE, O. 1891. Revisio generum plantarum. Pars. II, pp. 447-450.

KUZDOWICZ, A. 1954. (Reciprocal grafting of tomatoes *(Lycopersicum esculentum)* and red pepper *(Capsicum annuum)*.) Acta Agrobot. **2**: 97-102.

LIMBERK, J. 1951. (Grafting herbaceous plants on woody plants. II. Experiments on grafting tomato and red pepper on *Lycium barbatum*.) Sbornik Cesk. Akad. Zemedelske **24**: 335-340.

LIPPERT, L. F., B. O. BERGH, and A. A. COOK. 1964. Three variegated seedling mutants in the pepper. Multiple allelism indicated in crossing studies. Jour. Hered. **55**: 79-83.

————, ————, and P. G. SMITH. 1965. Gene list for the pepper. Jour. Hered. **56**: 30-34.

LUTES, D. D. 1954. Inheritance of resistance to systemic tobacco mosaic infection in pepper. Diss. Abstr. **14**: 1900-1901.

MARKS, G. E. 1952. A controllable carmine technique for plants with small chromosomes. Stain Tech. **27**: 333-336.

MARTIN, J. A. 1948. Bacterial spot resistance in peppers. Proc. Amer. Soc. Hort. Sci. **52**: 336-340.

————. 1949. Preliminary studies on the influence of F_1 and F_2 seed on the yield of Cayenne peppers. Proc. Assoc. South. Agr. Workers **46**: 111. (Abstr.)

————, and J. H. CRAWFORD. 1951. Several types of sterility in *Capsicum frutescens*. Proc. Amer. Soc. Hort. Sci. **57**: 335-338.

McKINNEY, H. H. 1952. Two strains of tobacco-mosaic virus, one of which is seedborne in an etch-immune pungent pepper. Plant Dis. Rep. **36**: 184-187.

MILLER, J. C., and Z. M. FINEMAN. 1937. A genetic study of some qualitative and quantitative characters of the genus *Capsicum*. Proc. Amer. Soc. Hort. Sci. **35**: 544-550.

MISSISSIPPI. 1957. Seventieth Ann. Rep. Mississippi Agr. Exp. Sta. for year ending June 30, 1957, p. 35.

MIYAZAWA, A. 1953. On genes controlling quantitative characters in *Capsicum annuum* L. Ann. Rep. Natl. Inst. Genet., Japan, **3**: 47-48.

MORGAN, D. T., JR., and R. D. RAPPLEYE. 1950. Twin and triplet pepper seedlings: A study of polyembryony in *Capsicum frutescens*. Jour. Hered. **41**: 91-95.

————, and ————. 1954. A cytogenetic study on the origin of multiple seedlings of *Capsicum frutescens*. Amer. Jour. Bot. **41**: 576-585.

MURTHY, B. S., and N. S. R. MURTHY. 1959. A cluster chilli mutant *(Capsicum annuum)*. Andhra Agr. Jour. **6**: 208-211.

MURTHY, N. S. R., and B. S. MURTHY. 1962a. Inheritance studies on chilli *(Capsicum annuum)*. Andhra Agr. Jour. **9**: 140-144.

————. 1962b. Proliferation of the central axis in *Capsicum,* a fruit abnormality in *Capsicum annuum* var. *grossum* (a preliminary note). Andhra Agr. Jour. **9**: 348-349.

NELSON, E. K. 1910. Capsaicin, the pungent principle of *Capsicum* and the detection of capsicum. Jour. Ind. Eng. Chem. **2**: 419-421.

NEW DELHI. 1942. Scientific reports of the Imperial Agricultural Research Institute, New Delhi, for the year ending June 30, 1941, 73 pp.

NISHIYAMA, I. 1939. (Studies on artificial polyploid plants. I. Production of tetraploids by treatment with colchicine.) Agr. Hort. **14**: 1411-1422.

————. 1940. (Studies on artificial polyploid plants. IV. Comparative studies on a polyploid series in red pepper.) Bot. and Zool. **8**: 905-913.

————, and H. KARASAWA. 1954. Somatoplastic sterility in reciprocal crosses between 2x- and 4x- plants in *Capsicum*. Jap. Jour. Breed. **3**: 36-40.

ODLAND, M. L. 1948. Inheritance studies in the pepper, *Capsicum frutescens*. Minnesota Agr. Exp. Sta. Tech. Bull. **179**: 1-32.

————. 1960. Inheritance of flower color in *Capsicum annuum* L. Proc. Amer. Soc. Hort. Sci. **76**: 475-481.

————, and A. M. PORTER. 1938. Inheritance of the immature fruit color of peppers. Proc. Amer. Soc. Hort. Sci. **36**: 647-651.

OHTA, Y. 1961a. Cytogenetical studies in the genus *Capsicum*. I. *C. frutescens* x *C. annuum*. Jap. Jour. Genet. **36**: 105-111.

————. 1961b. Grafting and cytoplasmic male sterility in *Capsicum*. Seiken Ziho/Rep. Kihara Inst. Biol. Res. **12**: 35-39.

————. 1961c. The use of cytoplasmic male sterility in *Capsicum* breeding. Seiken Ziho/Rep. Kihara Inst. Biol. Res. **12**: 59-60.

————. 1962a. Genetical studies in the genus *Capsicum*. Kihara Inst. Biol. Res. **1962**: 1-94.

————. 1962b. Cytogenetical studies on polyploid red pepper. Seiken Ziho/Rep. Kihara Inst. Biol. Res. **13**: 89-92.

————. 1962c. Caryotypes of *Capsicum*. Seiken Ziho/Rep. Kihara Inst. Biol. Res. **13**: 93-99.

————. 1962d. Physiological and genetical studies on the pungency of *Capsicum*. IV. Secretory organs, receptacles and distribution of capsaicin in the *Capsicum* fruit. Jap. Jour. Breed. **12**: 179-183.

PAL, B. P. 1945. Studies in hybrid vigour. 1. Notes on the manifestation of hybrid vigour in grams, sesamum, chilli and maize. Indian Jour. Genet. Plant Breed. **5**: 106-121.

————, and S. RAMANUJAM. 1939. Induction of polyploidy in chilli *(Capsicum annuum* L.) by colchicine. Nature **143**: 245-246.

————, and ————. 1940. Asynapsis in chilli (*Capsicum annuum* L.). Curr. Sci. **9**: 126-128.

————, ————, and A. B. Joshi. 1941. Colchicine-induced polyploidy in crop plants. II. Chilli (*Capsicum annuum* L.). Indian Jour. Genet. Plant Breed. **1**: 28-40.

Palfi, G., Z. Visnyovszky, and B. Tranger. 1961. (The production of polyploid red peppers.) Kiserlet. Közlem. **54/C**: 3-13.

Perez, J. E., and J. Adsuar. 1955. Antigenic relationship between Puerto Rican pepper-mosaic virus and a strain of potato virus Y. Jour. Agr. Univ. Puerto Rico **39**: 165-167.

Peterson, P. A. 1958. Cytoplasmically inherited male sterility in *Capsicum*. Amer. Nat. **92**: 111-119.

————. 1959. Linkage of fruit shape and color genes in *Capsicum*. Genetics **44**: 407-419.

Pichenot, M. 1960. Sur la nature et le devenir des modifications obtenues chez *Capsicum annuum* L. var Cayennense à la suite de greffage sur *Datura stramonium* L. Compt. Rend. Acad. Sci. Paris **250**: 214-216; Agrobiologiya **1960**: 894-895.

Pirovano, A. 1962. (Hereditary modifications produced by grafting.) Frutticoltura **24**: 665-672.

Raghavan, T. S., and K. R. Venkatasubban. 1940. Studies in the South Indian chillies. I. A description of the varieties, chromosome numbers and the cytology of some X-rayed derivatives in *Capsicum annuum* Linn. Proc. Indian Acad. Sci. **12** (Sect. B): 29-46.

Ramiah, K., and M. R. Pillai. 1935. Pungency in chillies *(Capsicum annuum)*. A mendelian character. Curr. Sci. **4**: 236-237.

Rick, C. M. 1950. *Capsicum pubescens,* a little known pungent pepper from Latin America. Bull. Missouri Bot. Gard. **38**: 36-42.

————, and L. Butler. 1956. Cytogenetics of the tomato. Adv. in Genetics **8**: 267-382.

Riollano, A., J. Adsuar, and A. Rodriquez. 1948. Breeding peppers resistant to a Puerto Rican type of mosaic. Proc. Amer. Soc. Hort. Sci. **51**: 415-416.

Safford, W. E. 1926. Our heritage from the American Indians. Ann. Rep. Smithsonian Inst. **1926**: 405-410.

Sagajdak, I. M. 1963. (Obtaining heterotic seed by supplementary root grafting.) Dopov. Akad. Nauk Ukrajin RSR (Proc. Ukrain. Acad. Sci.) **1963**: 651-655.

Sakai, K. 1952. Genetic studies on some fruit characters in *Capsicum annuum*. Ann. Rep. Natl. Inst. Genet. Japan **2**: 31.

Samuel, E. 1960. Die Ganbapflanze. Saatgut-Wirt. **12**: 35.

Schmidt, M. V. 1935. (A contribution to breeding and seed production in peppers and eggplants.) Nikita State Bot. Gard., Crimean Regional Exp. Sta. Veg. Culture, 105 pp.

Schnack, B., and G. Covas. 1947. Karyological studies in flowering plants. Haumania **1**: 32-41.

Shaw, F. J. F., and A. R. Khan. 1928. Studies in Indian chillies. I. The types of *Capsicum*. India Dep. Agr. Mem., Bot. Ser. **16**: 59-82.

Shinners, L. H. 1956. Technical names for the cultivated *Capsicum* peppers. Baileya **4**: 81-83.

Simmonds, N. W., and E. Harrison. 1959. The genetics of reaction to pepper veinbanding virus. Genetics **44**: 1281-1289.

Singh, M. P., and R. S. Roy. 1945. Inheritance of fruit position in a chillie cross. Curr. Sci. **14**: 133.

Sinha, N. P. 1950. The somatic chromosomes and meiosis in *Capsicum*. Indian Jour. Genet. Plant Breed. **10**: 36-42.

Siskovic, M. 1962. (The production of autotetraploids of red pepper *(Capsicum annuum)*.) Savremen. Poljopr., Novi Sad **10**: 227-239.

Smith, P. G. 1948. Brown, mature fruit color in pepper *(Capsicum frutescens)*. Science **107**: 345-346.

———. 1950. Inheritance of brown and green mature fruit color in peppers. Jour. Hered. **41**: 138-140.

———. 1951a. Deciduous character of pepper; tiny fruited form is crossed with non-deciduous variety to get easy-to-pick pepper for commercial use. Calif. Agr. **5**: 12.

———. 1951b. Deciduous ripe fruit character in peppers. Proc. Amer. Soc. Hort. Sci. **57**: 343-344.

———, and C. B. HEISER, JR. 1951. Taxonomic and genetic studies on the cultivated peppers, *Capsicum annuum* L. and *C. frutescens* L. Amer. Jour. Bot. **38**: 362-368.

———, and ———. 1957. Breeding behavior of cultivated peppers. Proc. Amer. Soc. Hort. Sci. **70**: 286-290.

———, and P. A. MINGES. 1951. Resistance of strains of California Wonder pepper to *Phytophthora* root rot. Plant Dis. Rep. **35**: 509.

———, C. M. RICK, and C. B. HEISER, JR. 1951. *Capsicum pendulum* Willd., another cultivated pepper from South America. Proc. Amer. Soc. Hort. Sci. **57**: 339-342.

SOUTH CAROLINA (W. C. BARNES). 1942. Paprika breeding. South Carolina Agr. Exp. Sta. Ann. Rep. **1942**: 148-150.

SOWELL, G., JR. 1960. Bacterial spot resistance in introduced peppers. Plant Dis. Rep. **44**: 587-590.

STANDLEY, P. C. 1938. Flora of Costa Rica. Field Mus. Nat. Hist. Bot. Ser., Publ. 420, **18**: 783-1133.

STURTEVANT, E. L. 1885. Kitchen garden esculents of American origin. II. Peppers Amer. Nat. **19**: 544-550.

———. 1890. Seedless fruits. Mem. Torrey Bot. Club **1**: 141-185.

SWAMINATHAN, M. S., T. NINAN, and M. L. MAGOON. 1959. Effects of virus infection on microsporogenesis and seed fertility in *Capsicum*. Genetica **30**: 63-69.

THRESH, J. C. 1876. Note on capsaicin, the active principle of Cayenne pepper. Pharm. Jour. and Trans. **7**: 473.

TOKUNAGA, K. 1934. Studies on the chromosome numbers of some species in Solanaceae. Jap. Jour. Genet. **9**: 231-238.

TOOLE, MARGUERITE G., and R. BAMFORD. 1945. Formation of diploid plants from haploid peppers. Jour. Hered. **36**: 67-70.

TOPORNINA, N. A. 1963. (Vegetative hybridization of sweet pepper.) Agrobiologiya **1963**: 58-64.

VAZART, J. 1950a. On the existence of polyploid pollen grains in *Capsicum annuum* L. Compt. Rend. Acad. Sci. Paris **231**: 1244-1245.

———. 1950b. Nouvelles observations sur les noyaux à calotte: étude caryologique comparée de *Hordeum vulgare* L., *Capsicum annuum* L., *Pastinaca urens* Req. et *Solanum ovigerum* Dun. I. Noyau interphasique et mitosis. Rev. Gén. Bot. **57**: 517-553.

———. 1951. Nouvelles observations sur les noyaux à calotte: étude caryologique comparée de *Hordeum vulgare* L., *Capsicum annuum* L., *Pastinaca urens* Req. et *Solanum ovigerum* Dun. II. La méiose et la formation du pollen chez *Capsicum annuum* L. Rev. Gén. Bot. **58**: 42-61.

WEBBER, H. J. 1911. Preliminary notes on pepper hybrids. Ann. Rep. Amer. Breed. Assoc. **7**: 188-199.

YAGISHITA, N. 1961a. Studies on graft hybrids in *Capsicum annuum* L. I. Variation in fruit shape caused by grafting and the effects in the first and second seed generations. Bot. Mag. Tokyo **74**: 122-130.

———. 1961b. Studies on graft hybrids of *Capsicum annuum* L. II. Variations in fruit shape caused by grafting for three successive generations and the effects in the progeny. Bot. Mag. Tokyo **74**: 480-489.

YAMAMOTO, K., and K. SAKAI. 1932. On the chromosome number in some Solanaceae. Jap. Jour. Genet. **8**: 27-33.