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The Inheritance of Resistance to Tobacco Etch and Cucumber Mosaic Viruses and Some Other Characters in Several Capsicum Species.

Hamed Ibrahim Mosokar
Louisiana State University and Agricultural & Mechanical College

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THE INHERITANCE OF RESISTANCE TO TOBACCO ETCH AND CUCUMBER MOSAIC VIRUSES AND SOME OTHER CHARACTERS IN SEVERAL CAPSICUM SPECIES.

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Horticulture

by

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B.S., Eine Shams University, Cairo 1961
M.S., Michigan State University, 1966
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ABSTRACT

Several hundred P.I. Capsicum spp. accessions, and the pepper cultivars, LP-1, Tabasco, and Almeda (all C. frutescens L.) were evaluated for resistance to Tobacco Etch Virus (TEV) and Cucumber Mosaic Virus (CMV). The P.I. group included 341 C. annuum L., 43 C. frutescens L., and 36 C. sinense.

Seedlings of P.I. 152225 and LP-1 were resistant to TEV, while those of the other accessions, Tabasco and Almeda, showed leaf-mottling, curling, or wilting symptoms of TEV.

A genetic study was made with cultivars of several Capsicum species. The purposes of the investigations were to determine the segregation and inheritance of resistance to TEV and CMV, immature fruit color, pod-bearing habit, and the associations between the last two characters.

Four parental lines of peppers, P.I. 152225, Tabasco, LP-1, and Almeda were used in this research. The crosses P.I. 152225 X Tabasco, LP-1 X Tabasco, and Almeda X LP-1 were chosen to study the inheritance of resistance to TEV. The cross Almeda X LP-1 was used to determine the inheritance of resistance to CMV, immature pod color, fruit-bearing habit, and the associations between the last two characters.
CROSSES WERE MADE ARTIFICIALLY. THE F₁ HYBRIDS WERE SELF-POLLINATED EITHER BY HAND OR BY PLACING INDIVIDUAL F₁ PLANTS UNDER INSECT-PROOF SCREEN CAGES IN THE GREENHOUSE.

PLANTS OF THE PARENTS, F₁, AND THE F₂ GENERATIONS WERE CLASSIFIED ACCORDING TO THE MODE OF SEGREGATION OF EACH CONTRASTING CHARACTER. THE CHI-SQUARE TEST WAS USED TO ANALYZE THE INHERITANCE OF EACH CHARACTER BY COMPARING THE RATIOS WHICH WERE OBTAINED FROM THE F₂ GENERATIONS WITH THE EXPECTED VALUES.

RESISTANCE TO TEV IN THE CROSS P.I.152225 X TABASCO APPEARED TO BE DUE TO A SINGLE RECESSIVE GENE, WITH ALL THE F₁ PLANTS BEING SUSCEPTIBLE, AS REPORTED BY GREENLEAF (21). HOWEVER, IN THE CROSSES LP-1 X TABASCO, AND ALMEDA X LP-1, RESISTANCE TO TEV WAS DOMINANT OVER SUSCEPTIBILITY. THE F₂ POPULATION SEGREGATED IN A 3:1 RATIO.

RESISTANCE TO CMV WAS STUDIED IN THE CROSS ALMEDA X LP-1. SUSCEPTIBILITY TO CMV WAS DOMINANT, AS THE F₁ HYBRID WAS SUSCEPTIBLE TO THE VIRUS. A PROBABILITY VALUE OF .10-.05 WAS OBTAINED FROM THE CHI-SQUARE TEST, INDICATING GOOD AGREEMENT WITH A 3:1 RATIO.

NON-CLUSTER VS. CLUSTER POD-BEARING HABIT WAS INVESTIGATED IN THE CROSS ALMEDA (CLUSTER) X LP-1 (NON-CLUSTER). THE F₁ PLANTS WERE ALL OF THE NON-CLUSTER HABIT. THE F₂ SEGREGATION WAS IN A RATIO OF 3 NON-CLUSTER TO 1 CLUSTER TYPE, INDICATING THAT THE CLUSTER HABIT WAS CONTROLLED BY A SINGLE RECESSIVE GENE.
Immature pod color was studied in the cross Almeda (greenish-yellow) X LP-1 (sulfur-yellow). The F₁ plants of the cross had greenish-yellow pod and segregated in a ratio of 3 greenish-yellow : 1 sulfur-yellow.

Pod color and fruit bearing habit associations were also investigated in the cross Almeda X LP-1. The F₁ plants were all of the non-cluster, greenish-yellow type. The F₂ segregated in a ratio of 9 non-cluster, greenish-yellow : 3 non-cluster, sulfur-yellow : 3 cluster, greenish-yellow : 1 cluster, sulfur-yellow. This confirmed that the non-cluster character was completely dominant over the cluster type, and the greenish-yellow immature pod color was dominant over sulfur-yellow. Each of these characters was monogenically inherited, and segregated independently in the F₂ generation.
INTRODUCTION

Large fruited Bell (sweet) peppers are grown in most areas of the United States; the mild to very pungent Chili peppers are grown extensively in California, Arizona and Louisiana for dehydration, pickling and canning; pungent Cayenne cultivars are widely grown in Louisiana for dehydration and sauce manufacture (9, 22); Pimiento, a mild sweet type, is produced in Georgia and South Carolina, for canning and olive stuffing; Paprika, ranging from pungent to nearly sweet, is not extensively grown in the United States, and it is very popular in Europe for dehydration as finely ground "red pepper" (23), while Jalapeno, which is very pungent, is produced in California and Mexico for pickling and fresh use. All of the above are types of *Capsicum annuum* L.

Tabasco is the only cultivar of *Capsicum frutescens* L. grown commercially in the United States, mostly in Louisiana. Tabasco is believed to have been introduced from Mexico about 100 years ago (9), where it was grown in the areas of Avery Island, Louisiana, and New Iberia, Louisiana, for processing into hot pepper sauce. Since that time, a disease problem, Tobacco Etch Virus (TEV), has resulted in localizing all production of this variety on Avery Island, isolated from other pepper areas. It is considered to be the most pungent member of the genus *Capsicum* grown in this country.

Two virus diseases which are now widespread in all commercial pepper varieties in south Louisiana have been identified as TEV and
Cucumber Mosaic Virus (CMV). Plants infected with either one, or a combination of both are stunted, unproductive, and may wilt and die. The Tabasco variety is particularly susceptible to these viruses, which are transmitted mechanically and by aphids. The source of primary infection is not known in all cases, but they are not believed to be carried in or on pepper seed (8).

Meanwhile, an intensive pepper breeding program is being conducted by the Horticulture Department. As a part of the program this study was initiated, in which locally grown parents were inoculated with TEV and CMV, then grown in the greenhouse and field to evaluate them for disease resistance. In addition, hundreds of Plant Introduction pepper accessions and other cultivars were inoculated and tested in the greenhouse and field for resistance to these diseases and possible use as parental material in the breeding program.

Since these two diseases are of considerable importance to the Louisiana hot pepper industry, the LSU breeding program was expanded in efforts to develop new disease resistant types which contain the pungency and yielding (horticultural characteristics), ability of the present commercially-produced Cayenne and Tabasco varieties.

The objects of these investigations were first, to screen and evaluate several hundred new Plant introduction accessions for TEV and CMV resistance. Also included were LP-1, a cultivar of peppers grown in Louisiana, and Almeda, a selection from Hawaii (both believed to be \textit{C. frutescens} L.).

The second objective was to study the genetic behavior of the
following characters, in order to utilize one or more of them, if possible, in the breeding program:

(A) Resistance to Tobacco Etch Virus, in the crosses LP-1 X Tabasco, Almeda X LP-1, and PI152225 X Tabasco (PI152225 reported by Greenleaf as resistant to this disease) (21).

(B) The resistance to Cucumber Mosaic Virus in the cross Almeda X LP-1.

(C) Color of the immature fruit in the cross Almeda X LP-1.

(D) Fruit bearing habit in the cross Almeda X LP-1.

(E) Associations between pedicels per node and fruit color.
REVIEW OF LITERATURE

Taxonomy and History of the Pepper

Peppers are classified in the family Solanaceae and the genus Capsicum, with a basic chromosome number of N=12 (23,31,48,58). There are believed to be 5 cultivated species in this genus; Capsicum frutescens L. (Tabasco variety), C. annuum L. (most other cultivated varieties); C. pendulum, C. pubescens, and C. sinense (chinense) (23,59). Considerable confusion exists regarding the taxonomy of the cultivated peppers; since it contains many diverse types of plants and fruits, classification is difficult (9,23,59). Cross-pollination is common, which results in the frequent appearance of new forms (18, 6).

Heiser and Smith (23) and Smith and Heiser (59) reported that 5 species of Capsicum are known to have been cultivated in the Americas in pre-Columbian times, and are still grown in various areas of the world. Most peppers commercially grown, in the United States and other principal areas are of two species, C. annuum L. and C. frutescens L. with the former by far the largest in total number of varieties. In the United States, only Louisiana produces commercial quantities of C. frutescens L. (Tabasco).

Capsicum annuum L.: Nearly all of the larger-fruited varieties grown in the temperate and other zones of the world belong to this
species (23,49). These include: Bell or sweet pepper, Cayenne, Paprika, Chili, Pimiento, Banana, and many other horticultural varieties. Fruit size, shape, and color are extremely variable, more so than any other species, ranging from 1 to 30 cm. in length, from small conical to thick-fleshed, blocky, or flat in shape. Yellow and green immature, and red, yellow, brown, and purple mature fruits are common (23,49,59). Pungency varies from sweet to very pungent. With the exception of Tabasco, all of the principal varieties in the United States belong to this species.

However, *Capsicum annuum* L. normally has white corollas and single pedicels (fruit bearing stems), while *Capsicum frutescens* L. has waxy, greenish, white corollas and frequently paired, or even three to six, pedicels at a node (23,49,59), Heiser and Smith). These characters can be used to separate these peppers from one another and from other species (23,59).

*Capsicum pubescens* was originally described from Peru in 1790, from Columbia, Mexico, Guatemala, and Honduras, and is still cultivated in those areas, but not in the United States. The greatest diversity of forms is in the Andes section; fruits are variable in size and shape and mildly-to strongly-pungent (60).

*Capsicum pendulum* is one of the most popular cultivated peppers in coastal sections of Peru, being widely distributed in South America, but unknown in Central America. Fruit size and shape are quite variable; immature fruit colors range from almost ivory-white to yellow or green; color of mature fruit from orange to red. This species is not known to be cultivated in the United States, but it has been of some value in breeding programs through the PI(S-9) program.
Capsicum sinense has been reported to be cultivated to a limited extent in the St. Augustine section of Florida; most forms of this species are found in Peru. Many P.I. accessions of *C. sinense* have been screened as sources for disease resistance to be used in breeding programs in the South, and one (P.I.152225) has been used as a parent to develop a Tabasco-type variety at Auburn University for release to commercial producers. Fruit types of this species are variable, ranging from Chili to Cayenne pods, varying immature and mature colors, but mostly green to purple when immature, and mostly red when mature (59).

**Morphology**

The plants are erect, compact in form, and dichotomously branched, with angular, herbaceous stems, which become woody with maturity. Although peppers are perennial in the tropics, they are cultivated as annuals in temperate zones. The leaves are flat and glabrous, simple, and entire, varying in shape from ovate to long and narrow (45,49,62).

Flowers (perfect) occur singly (except in *C. frutescens* L. as described above), in the axils of the branches and are formed continuously throughout the season. The corolla (except for *C. frutescens* L.) is either white or purple, rotate, and 5-parted. There are 5 stamens, not united as in the tomato; anthers dehisce by longitudinal splitting. Self-pollination occurs, in general, but there appears to be a considerable percentage of cross-pollination; much hybridization will result if different varieties are grown near each other (45,49,62).

Fruit is a pod-like berry, borne on a short, stout peduncle,
erect at first, but in some varieties becoming pendant as maturity progresses. There are generally prominent longitudinal ribs on some fruit (mostly C. annuum L., Bell, Pimiento, and Chili varieties), marking the position of the interlocular septae; in many others, however, no ribs or interlocular septae are present, and fruit is smooth, with one locule, as Cayenne, Tabasco and Sport (45).

Fruit of the Bell or Pimiento varieties have 2 to 4 locules, although more may occur in some types, which do not unite in the center except in the basal third of the fruit. The central part of the pod is occupied by a hard, white placenta (45).

The outer wall, pericarp, is fleshy and of varying thickness; it consists of: (1) a very thin cuticle, (2) 5 to 8 compact layers of small collenchyma cells, which become cutinized during maturation and provide a tough, colorless, epidermal layer, (3) several layers of large parenchyma cells traversed by the vascular tissue, and (4) a single layer of very large cells bordering on the seed cavity.

The growth of the fruit in the early stages consists of rapid cell multiplication; in the latter stages, growth is chiefly by enlargement of the cells already formed. Table I gives a summary of distinctive morphological characters of the cultivated pepper species.

In some cases sterility in peppers, as a result of interspecific hybridization, is a handicap in a breeding program. According to Heiser (23) and Smith and Heiser (60) crosses between C. pubescens and any other species appeared impossible. Smith and Heiser (60)
Table 1. Distinctive morphological characters of the cultivated pepper species

<table>
<thead>
<tr>
<th><em>SPECIES</em></th>
<th>C. annuum</th>
<th>C. frutescens</th>
<th>C. sinense</th>
<th>C. pendulum</th>
<th>C. pubescens</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flower color</td>
<td>White</td>
<td>waxy pale</td>
<td>white to pale</td>
<td>white with yellow</td>
<td>purple with white corolla base</td>
</tr>
<tr>
<td></td>
<td></td>
<td>yellowish-white</td>
<td>waxy, yellowish-white</td>
<td>throat markings</td>
<td>base</td>
</tr>
<tr>
<td>Anther color</td>
<td>blue to purple</td>
<td>blue to purple</td>
<td>blue to purple</td>
<td>yellow</td>
<td>purple</td>
</tr>
<tr>
<td>Pedicels per node</td>
<td>1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1-5, usually 2</td>
<td>2-5, usually 3-5</td>
<td>1, rarely 2</td>
<td>1, rarely 2</td>
</tr>
<tr>
<td>Flower position</td>
<td>erect to pendant</td>
<td>stiffly erect&lt;sup&gt;b&lt;/sup&gt;</td>
<td>curved to pendant&lt;sup&gt;c&lt;/sup&gt;</td>
<td>erect to pendant</td>
<td>erect or pendant</td>
</tr>
<tr>
<td>Seed color</td>
<td>yellow</td>
<td>yellow</td>
<td>yellow</td>
<td>yellow</td>
<td>purplish black</td>
</tr>
<tr>
<td>Seed margin</td>
<td>smooth</td>
<td>smooth, rarely</td>
<td>wrinkled, rarely nearly smooth</td>
<td>smooth</td>
<td>wrinkled</td>
</tr>
<tr>
<td>Constriction at base of calyx</td>
<td>variable</td>
<td>none</td>
<td>constricted</td>
<td>constricted</td>
<td>constricted</td>
</tr>
</tbody>
</table>

<sup>a</sup>Paired pedicels occasionally occur on the first flowering node.

<sup>b</sup>Pedicels at anther is very slender, about 20 times as long as thick.

<sup>c</sup>Very rarely erect. Pedicels at anthesis about 10 times as long as thick.

*<sup>N</sup> = 12 for all above species

<sup>1/</sup>Heiser and Smith (23)
Smith and Heiser (59)
indicated that crosses of *C. annuum* L. with *C. frutescens* L. and *C. sinense*, were made with the F<sub>1</sub> plants were completely to moderately self-sterile. They also reported that *C. frutescens* L. would cross with *C. sinense* and *C. pendulum*.

**Tobacco Etch Virus (TEV)**

TEV and several other viruses were recovered by Johnson (34) from naturally infected Solanaceous weeds in 1930. Holmes (27) (1941) found that TEV produced necrotic lesions on leaves of *Physalis perunian*.

In the same year Bawden (5) showed that certain varieties of tomato, *Datura*, and tobacco, were also susceptible to TEV. Anderson and Corbett (1) recovered TEV from *Solanum nigrum*, *Solanum gracile* and *Physalis angulata*. McKinney (43) reported that a variety of peppers (South Carolina line No.46252) (*C. annuum* L.) was immune to TEV when inoculated with the virus obtained from infected pepper plants.

Wilt of Tabasco pepper, *C. frutescens* L. was caused by a virulent strain of TEV, according to Greenleaf (20) (1953). The first visible symptoms of TEV on Tabasco appeared within 4 to 21 days from inoculation as a vein clearing and a general etching of the inoculated leaves, followed by wilting within a few days. He stated that wilting was usually followed by death, but occasionally a few of the young plants, about eight weeks from seeding, showed partial recovery from the disease. Such seedlings became severely defoliated, but maintained an apical tuft of leaves (20).

Greenleaf also found that resistance to TEV was inherited as a single gene (21). The symbols, *et<sup>f</sup>* and *et<sup>a</sup>* were assigned to represent the genes for resistance in *C. frutescens* L., and *C. annuum* L.,
respectively, since it was not known if the 2 recessive genes were alleles. These data were based on 5 classes of disease reactions: (1) symptomless; (2) slight mottling; (3) medium to severe mottling, with or without wilting; (4) wilting and defoliation, followed by limited recovery, and (5) wilting and dying. Classes 1 and 2 were considered as indicating resistance. Cook (10,11) reported that resistance to TEV in P11 and P34 (S.C. 4625) (C. annuum L.) pepper was controlled by a single recessive factor.

The effect of TEV on several hosts was described by Horn and Sinclair (50). They found that the virus caused wilt in Tabasco, mottling and dwarfing in Cayenne pepper, local lesions in pigweed, and leaf mottling with vein clearing in Nicotiana glutinosa. TEV was further confirmed as the cause of wilt in Tabasco pepper in Louisiana by Sinclair et al. (56)

According to White and Horn (66), there was no apparent difference in the leaves and stems of healthy and diseased plants. In the diseased roots, however, there was necrosis of the phloem and cambium tissues and collapse of epidermal and cortical cells. In no instance were xylem cells clogged. Ghabrial and Pirone (21), confirmed White's data in 1964, showing that roots of plants infected with TEV showed disruption of cambium and phloem tissue on the first day of wilt. In 1965, White and Horn (60), made histopathological studies of infected plants after the first day of wilt which revealed necrosis of phloem and cambium in stem, petiole, and leaf tissue.

Laird and Dickson (40) (1963) listed the following insects as vectors of TEV: Myzus persicae, Aphis gossipii, Aphis spiroceola,
Macrosyphum solanifolii, and M. pisi. Kuhn and Dempsey (39) reported that TEV in Pimiento pepper plants was also transmitted by aphids. TEV symptoms observed in naturally infected Pimiento fields were divided into 5 classes: (1) mild to severe mottle; (2) an upward curling of leaves; (3) various degrees of stunting of the whole plant; (4) decreased fruit set; and (5) misshapen fruit.

CUCUMBER-MOSAIC VIRUS (CMV)

A mosaic of Cucurbit plants was reported in Ohio, Massachusetts, and Connecticut during the first decade of the current century, but delineation of a distinct infectious disease was not recorded until 1916. The relatively rapid increase of the virus in many areas of the United States after the latter date brought it into the position of major importance on cucumbers where it has remained up to the present (63).

There are many strains of CMV which differ in severity of symptoms they induce in host plants. The host range is very wide, representing at least 34 plant families, including Cucurbit, spinach, banana, celery, tomato, tobacco, bean, lima bean, Crucifers, pear, beet, gladiolus, and pepper (12,63). The disease symptoms are more distinguishable on young leaves, but in some cases the mosaic pattern turns into an indistinguishable diffuse mottle as the leaves grow larger (15,63). Infected pepper plants are generally somewhat chlorotic and show mottling, local necrotic lesions, and marked vein-banding symptoms (12,52). The foliage of infected tobacco exhibits mottling, malformation, and
distortion of the plant growth (35).

The virus is transmitted mechanically, disseminated in cucumber by pickers, occurring when immature fruits are harvested frequently during the growing season (63). Doolittle and Jagger (15,32) indicated the importance of insects in transmission and spread of CMV. The green-peach aphid, *M. persicae*, was shown to be a good vector of CMV, not only among members of the Cucurbits, but also in spinach (63); gladiolus (50), tobacco (25), and pepper (61).

Electron microscopic studies by Bauden and Nixon (6) showed that CMV is approximately 15 μm wide and appeared to be rigid.

Doolittle and Zaumeyer (16) reported that lesions were produced on Turkish tobacco after inoculation with two strains of CMV also caused systemic infection of sweet pea. They further found that peppers grown in Maryland, Delaware, New Jersey and adjacent States were susceptible to CMV and the disease was characterized by symptoms of ring-marking on the leaves and fruits.

Certain strains of CMV were observed by Sinclair and Walker (55) to produce local leaf lesions on some varieties of cowpea (*Vigna sinensis*). In a genetic study, crosses were made between certain resistant cowpea varieties [Black (B11), Blackeye, and Dixie Queen], and a susceptible variety (Black), they concluded that resistance was dominant and the parents differed in a single pair of genes. This conclusion was based on the genetic behavior of the *F*₁, *F*₂, *F*₃, and the two parents.

Three strains of CMV were isolated by Simons (52), from the sap of California Wonder pepper (*Capsicum annuum* L.) grown in south Florida.
He concluded that the disease was transmitted in a non-persistent manner and found two insects, *Aphis gossipii*, and *Myzus persicae*, as carriers of the virus disease. In later work Simons (53) obtained a high correlation between mechanical inoculation and aphid transmission of CMV in peppers. The green peach aphid, *Myzus persicae*, was used as the insect vector.

Cook (10,11) reported in 1959 that CMV was one of the five viruses isolated from Bell pepper in Florida.

Four isolates of CMV were found by Webb and Smith (65) to induce systemic infection in seedlings of P.I.250771 (*Capsicum frutescens* L.) in the 3-4 leaf stage, and they concluded that selected progenies of this accession were highly resistant to systemic infection with certain isolates of CMV.

**NON-CLUSTER VS. CLUSTER BEARING HABIT**

Pepper fruits are borne singly, in pairs, or in clusters (three or more pedicels per node) (23). The number of pedicels per node is a very important taxonomic character in separating *C. annuum* L. from *C. frutescens* L. and other species, (58). However, *C. annuum* L. normally has white corollas and a single pedicel per node, while *C. frutescens* L. has waxy, greenish-white corollas and frequently paired, or even occasionally three to six pedicels per node.

Murthy and Murthy (44) and Angeli (3) reported that solitary pedicels were dominant over clusters, and that cluster bearing habit was controlled by a single recessive gene. Deshpande (13) found that normal fruit bearing habit was dominant over the economically valuable
"bunch" habit.

FRUIT COLOR

Immature fruit ranges from ivory-white to orange, purple, yellow and green in color, depending on the pigment present in the outer layers of the pericarp. The flavanols are responsible for whites and ivory, carotene for yellow and orange, anthocyanin for purple, and chlorophyll and xanthophyll for greens and yellow-green (12,47).

Mature fruit colors are red, yellow, or orange, varying with species and variety. The pigments causing red color are a mixture of lycopene, xanthophyll and carotene, while yellow and orange are due to carotene alone (47). Some green peppers can be ripened artificially, as tomatoes. Green pods of the Sport variety (C. annuum L.) dipped for 45 minutes into 3000 ppm of Ethrel, caused ripening of pods to a red color (42) in three days. This treatment did not give similar results with other varieties, (Tabasco, Cayenne).

Halsted (22), found that red color (Capsicum species, varieties unspecified), of mature fruit was due to a dominant gene, (red over orange). Deshpande (12) reported that the red color in the mature fruit of Chili pepper (C. annuum L.) is dominant over yellow. He further stated that pods of the F$_1$ plants had a red color, while those in the F$_2$ generation segregated in a 3:1 ratio of red to yellow, respectively. In later work, Jeswani et al (33) found that the cedar-green color in unripe fruit was dominant over yellowish-green, with a 15:1 ratio in the F$_2$ generation.
According to Smith (57), brown and yellow mature fruit colors were inherited as a simple recessive factor to red. The $F_2$ progenies from the cross between Oshkosh (yellow-green) and AC.401 (brown), gave 4 red, 3 brown, 3 yellow, and 1 green. El Hassan and Smith (17) stated that red and yellow mature fruit colors in SA265, and SA359 (varieties of C. pubescens) were controlled by a single gene with yellow ($y$) being recessive to red ($y^+$). Baldini (4) found that red mature fruit was dominant over yellow, and the $F_1$ hybrid was intermediate between the parents. Kormos and Kormos (37) reported that the carotenoid color was dominant over brown color. Khan and Munir (36) suggested that red color of mature fruit and yellow were simply inherited with red being dominant over yellow. In later work, Kormos and Kormos (38) concluded from their results that the genetic constitutions for carotenoid pigment production in peppers were: red $r+c+$; salmon-pink $r+c$; orange-yellow, $rc+$; lemon-yellow, $rc$; and white $r+c$ or $rc$. They suggested that red pigment formation was determined by $r+$ and yellow by $r$. Both alleles could only be fully expressed in the presence of the precursor gene $c+$, and the pigments were formed in its absence from the polygenes which accompanied chlorophyll. In the absence of both $c+$ and chlorophyll, only traces of the pigments were found.
MATERIALS AND METHODS

TOBACCO ETCH VIRUS (TEV)

In the summer of 1967, 25 seeds from each of 2 hot pepper cultivars, LP-1 and Tabasco (both Capsicum frutescens L.) were planted in steam-sterilized soil in the greenhouse. Fifteen seedlings from each of the 2 cultivars were artificially inoculated with TEV.

The inoculum was taken from a TEV susceptible variety of Bell pepper (Capsicum annuum L.) obtained from T. P. Pirone, Department of Plant Pathology, Louisiana State University. Leaves from infected plants were macerated, using a mortar and pestle with water being added to dilute the concentrated virus. The carborundum-leaf-wiping method was used to inoculate the plants of the two cultivars of peppers (20, 21, 26). The carborundum was sprinkled over 2 or 3 leaves, and the TEV was applied to these leaves by dipping a cotton pad in the inoculum and then rubbing them. Subsequently, the leaves were rubbed by hand 2 or 3 times. Following the inoculations, observations of disease symptoms were made weekly for a period of 10 weeks.

In 1968 the same 2 cultivars were again screened for TEV resistance, along with the cultivar Almeda (C. frutescens L.) and several hundred P.I. Capsicum accessions. The P.I. group included 341 accessions of C. annuum L., 43 of C. frutescens L., and 36 of C. sinense. The seeds were sown about 1/4 inch apart in rows 2 inches apart in a greenhouse bench (one row for each cultivar) with about fifty seeds
per row.

Six weeks after sowing of the seeds, plants of each cultivar were inoculated with TEV in the same manner as previously described. Plants of each cultivar were rated for disease symptoms one week after inoculation and subsequently at weekly intervals for a period of 6 weeks. The classification for TEV resistance was based on several symptoms which were observed and described by others (21,30,47): (1) symptomless; (2) mild to severe mottle; (3) an upward curling of the leaves; and (4) wilting of the plants. After six weeks, plants of each variety which showed mild to severe mottle, wilt, or an upward curling of the leaves were classified as susceptible. Those having none of these symptoms were rated as resistant to TEV.

The progenies from 3 crosses (P.I.152225 X Tabasco), (LP-1 X Tabasco), and (Almeda X LP-1) were used in statistical analyses (41) to study the inheritance of TEV. The accession P.I.152225 was used as a parent because of reported resistance to TEV (21). LP-1 was selected because of apparent resistance to TEV, while Tabasco and Almeda were considered susceptible to the disease.

Some botanical characteristics of the parents LP-1 and Almeda are:
LP-1: Figure 1 shows an LP-1 plant in the field. The plant is erect, compact in form, with an average height of about 36.6 cm (in the field), and approximately 86.1 cm in width at the top. The leaves are entire, and dark green in color. Flowers have a white corolla, and the fruit are borne one, two and occasionally three at a node. The pods are erect, ranging from 1.2 to 1.5 cm in length, and 0.6 to 1.2 cm in diameter at the base. Color of the immature fruit is sulfur-yellow
to orange, becoming red with maturity.

**Almeda:** The Almeda plant is shown in Figure 2. It is small, compact in form, erect, with a cluster bearing habit. The fruit are erect, and greenish-yellow in the immature stage, turning red at maturity. Average length of the fruit is 4.1 cm, with a diameter of 1.1 cm at the base. Average height of the plant is about 65 to 75 cm.

**P.I.152225 X Tabasco**

This cross was made in the summer of 1967 in the greenhouse, using 1 plant of each parent. Flowers of plants were pollinated and subsequently tagged. Fruits were allowed to mature when seeds were collected from maternal parent P.I.152225.

The F₁ seeds were planted in sterilized soil in the greenhouse. Three F₁ plants were hand pollinated in order to insure selfing. F₂ seeds were subsequently obtained from these 3 F₁ plants.

In February of 1969, seed of each parent, F₁ and F₂ progenies, were grown in greenhouse benches. Fifty seedlings of each of the parents, 25 F₁ and 346 F₂ segregates were included in the experiment.

In March of 1969, the parents and progenies were inoculated with TEV, using the carborundum method previously described. Plants were evaluated for disease resistance one week after inoculation and at weekly intervals thereafter for a period of 6 weeks. Those which were wilted, or showed moderate to severe leaf mottle, were classified as susceptible. Plants showing no wilt symptoms, or having slight leaf mottle were rated as resistant to TEV, as reported by Greenleaf (23).
Figure 1. LP-1 pepper

Figure 2. Almeda pepper
**LP-1 X Tabasco**

The cross between these 2 cultivars was made in the summer of 1968 in the greenhouse, using 1 plant of each parent. Hybridization was accomplished by hand pollination as previously described.

Ten \( F_1 \) seeds were obtained from LP-1, the female parent. These seeds were planted in soil sterilized with methyl bromide. Nine seeds germinated, but only 1 \( F_1 \) plant survived. The other 8 seedlings were killed by damping off.

In the latter half of 1969, 15 plants of each parent, 6 \( F_1 \) plants and 140 \( F_2 \) plants were grown in the greenhouse. The 6 \( F_1 \) plants were obtained by vegetative cuttings of the same plant from which the \( F_2 \) seeds were obtained.

Six weeks after seed was planted, the seedlings were inoculated with TEV as previously described. Plants were classified for disease symptoms 1 week after inoculations and at weekly intervals thereafter for a period of 8 weeks. Plants which were wilted or showed mild to severe leaf mottle were classified as susceptible, while plants showing no wilt symptoms, or having slight mottle were considered resistant to TEV (20,21).

**Almeda X LP-1**

Almeda and LP-1 were cross-pollinated in the summer of 1968 in the greenhouse, with 1 plant of each parent being used.

\( F_1 \) seeds were obtained from the Almeda parent and planted in sterilized soil in the greenhouse. Two \( F_1 \) plants from this planting were placed under insect-proof screen cages in the greenhouse to
facilitate self-pollination. $F_2$ seeds were subsequently obtained from these plants.

In December of 1969, plants of parents, $F_1$ and $F_2$ progenies were grown in peat pots in the greenhouse. Seventeen plants of each parent, 18 $F_1$ and 225 $F_2$ seedlings were used in this experiment. In February of 1970, plants were inoculated with TEV using the carborundum method previously described. The plants were reinoculated with the virus in March of 1970.

The seedlings were classified for resistance to TEV 1 week after the March inoculation and at weekly intervals thereafter for a period of 8 weeks. This classification was based on the same criteria (20,21), used in the cross between LP-1 and Tabasco. At the end of 8 weeks the data were analyzed statistically (41).

**CUCUMBER MOSAIC VIRUS (CMV)**

Early in the summer of 1968 several hundred pepper cultivars were screened for CMV resistance in the greenhouse. These cultivars were of LP-1, Almeda, Tabasco and 420 P.I. Capsicum accessions, which included 341 $C. \textit{annuum}$ L., 43 $C. \textit{frutescens}$ L., and 36 $C. \textit{sinense}$. Approximately 50 seeds of each cultivar were sown about 1/4 inch apart in rows 2 inches apart in greenhouse benches, using one row for each cultivar.

Seedlings of the cultivars were inoculated with CMV from Cayenne pepper ($C. \textit{annuum}$ L.) obtained from T. P. Pirone, and L. L. Black, Department of Plant Pathology, Louisiana State University,
Baton Rouge, Louisiana. This inoculum was applied in the same manner as described for TEV in previous experiments.

Following inoculation with the virus, plants were examined for disease symptoms 1 week after inoculation and at weekly intervals thereafter for a period of 5 weeks. Rating of plants was according to several symptoms which were observed and described by others (65): (1) systemic infection; (2) systemic infection with local lesions on the leaves; (3) local lesions without systemic infection; (4) severe defoliation and stem browning; (5) an upward curling of the leaves; (6) mild to severe mottle; and (7) slight leaf mottle, never becoming severe. Five weeks after inoculation, seedlings of each cultivar having no symptoms, slight leaf mottle, or local lesions without any systemic infection were classified as resistant. Those having any of the other symptoms were classified as susceptible.

**Almeda X LP-1**

\[ F_2 \] seeds of the cross Almeda X LP-1 were obtained from two \[ F_1 \] plants, which were grown under insect-proof screen cages. In December of 1969, 20 seedlings of each parent, 18 \[ F_1 \] plants, and 89 \[ F_2 \] seedlings were grown in peat pots in the greenhouse.

On February 4, 1970, the plants were inoculated with CMV from an infected Cayenne pepper.

Following the inoculations, data on the plants were recorded weekly for a period of 4 weeks. At the end of 4 weeks the \[ F_2 \] plants showing any symptoms of CMV were discarded and the remaining plants were reinoculated. After an additional 4 weeks, each plant of this
group was tested separately in order to see whether the virus could be recovered from any of the plants. Two to three young leaves from each of the F2 plants were ground, using a separate mortar, and pestle for each sample and applied in similar manner as previously described. One seedling of each Tabasco pepper (C.frutescens L.) and Tobacco plants (Nicotaina tabacum) cv. Havana 425, was inoculated for each of the F2 plants. Two weeks later these test plants were evaluated for any sign of CMV or other viruses, and the F2 plants were classified for CMV resistance. Fifteen F2 plants did not show CMV symptoms when inoculum was transferred to Tobacco and Tabasco plants. Ten weeks after the first inoculation, the data were analyzed statistically.

POD CHARACTERS

A cross between the cultivars Almeda and LP-1 was obtained by hand pollination in the greenhouse during the summer of 1968. The two parents were distinguishable by a number of clear-cut characters, which made them ideal for genetic study.

Six F1 plants were grown late in the fall of 1968 in the greenhouse and allowed to set fruit without controlled pollination. Consequently, F2 seeds were obtained from these six plants. Data in Table 2 show the characters of each parent and the F1 hybrids which were studied.
Table 2. Parental and F<sub>1</sub> characteristics of the cross Almeda X LP-1.

<table>
<thead>
<tr>
<th>Characters</th>
<th>Parental Varieties</th>
<th>F&lt;sub&gt;1&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Almeda</td>
<td>LP-1</td>
</tr>
<tr>
<td>Fruiting habit</td>
<td>Cluster&lt;sup&gt;1/&lt;/sup&gt;</td>
<td>Non-cluster</td>
</tr>
<tr>
<td>Immature fruit</td>
<td>Greenish-yellow</td>
<td>Yellowish-green</td>
</tr>
<tr>
<td>color</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>1/</sup> Three or more pedicels per node

During the summer of 1968, 516 F<sub>2</sub> plants were grown at 3 locations as follows: (1) 160 in the greenhouse, (2) 80 on the Hill farm, and (3) 276 on the Ben Hur farm.

The F<sub>2</sub> populations at the last two locations were spaced about 18 inches apart in rows, approximately 4 feet apart while the plants in the greenhouse were grown in 8 inch clay pots.

The F<sub>2</sub> populations were classified in the field for cluster Vs. non-cluster, immature greenish-yellow fruit Vs. yellowish-green, and associations between these characters.

It was noted that a few of the F<sub>2</sub> progenies segregated for a Cayenne pod type. However, none of this fruit type was observed among the 1970 material. These plants were not included in the 1969 results.

Two of the F<sub>1</sub> plants were deflowered, defruited, and placed under insect-proof screen cages to insure selfing and to prevent any possible pollen contamination.
During the spring of 1970 another generation of F2 seeds was obtained from the two F1 plants which were placed under the cages. Two hundred F2 plants were established in the greenhouse in peat pots along with about 60 plants of each parent. Later in the spring of 1970 the F2, and the parents were grown in the field, (Ben Hur). The plants were spaced about 2 feet apart in three rows approximately 4 feet apart.

The 1970 population was also classified in the field for cluster Vs. non-cluster type; immature greenish-yellow Vs. sulfur-yellow fruits, and associations between these characters. The data from 1969 and 1970 were analyzed statistically.
RESULTS AND DISCUSSIONS

Several hundred P.I. *Capsicum* spp. accessions, and the pepper cultivars, LP-1, Tabasco and Almeda (all *C. frutescens* L.) were evaluated for resistance to TEV and CMV. The P.I. group included 341 *C. annuum* L., 43 *C. frutescens* L., and 36 *C. sinense*.

TOBACCO ETCH VIRUS (TEV)

The crosses P.I.152225 X Tabasco, LP-1 X Tabasco and Almeda X LP-1, were used to study the inheritance of resistance to TEV for several reasons. Greenleaf reported that P.I.152225 was resistant to TEV (20,21), and preliminary experiments indicated that LP-1 possessed TEV resistance, while the Almeda and Tabasco cultivars seemed susceptible.

At the end of the 6 weeks all plants of P.I.152225 were healthy and symptomless, while the entire population of Tabasco showed wilt symptoms, (20,21). Seedlings of LP-1 also remained healthy while those of the Almeda and all of the P.I. varieties (except P.I.152225) had leaf-mottling or curling symptoms of TEV.

The results of the experiments indicated that each of the three pepper cultivars, and accession P.I.152225, were homozygous in their reaction to the disease. LP-1, and P.I.152225, were homozygous for resistance, while Almeda and Tabasco were homozygous for susceptibility.
The P.I.152225 parent was resistant to TEV, as reported by Greenleaf (20), while the Tabasco cultivar was highly susceptible, which is in agreement with others (20, 21, 56, 66). The F₁ progeny was susceptible to TEV. Table 3 shows that the susceptibility to TEV in the F₂ population was dominant over resistance. The chi-square test for goodness of fit for a 3:1 ratio gave a probability value of .50-.30. These data show that the segregation was in satisfactory agreement with the expected single factor hypothesis.

Table 3. Segregation of F₂ progenies of the cross P.I.152225 x Tabasco following inoculation with TEV.

<table>
<thead>
<tr>
<th>Phenotype</th>
<th>Observed</th>
<th>Calculated</th>
<th>Ratio</th>
<th>$x^2$</th>
<th>P.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Susceptible</td>
<td>252</td>
<td>259.5</td>
<td>3</td>
<td>.2167</td>
<td>.30-.50</td>
</tr>
<tr>
<td>Resistant</td>
<td>94</td>
<td>86.5</td>
<td>1</td>
<td>.6502</td>
<td>.866</td>
</tr>
</tbody>
</table>

Greenleaf (20) also found that the F₁ plants were susceptible to TEV when P.I.152225 was crossed with Tabasco. He reported that recessive genes $et^f$ and $et^a$ control TEV resistance in peppers, and that the ratio in the F₂ generation was 3:1.
**LP-1 X Tabasco**

Figure 3 shows a photograph of plants of LP-1 ($P_1$), Tabasco ($P_2$) and the $F_2$ from the cross between these varieties. None of the plants of LP-1, on the left, showed wilt or other symptoms, while all those of Tabasco, on the right, were severely wilted, and eventually died. The $F_1$ of this cross was resistant to TEV, as evidenced by the non-wilted plants in Figure 4, and other plants of this generation not shown. The $F_2$ progeny segregated in a 3:1 ratio of resistant to susceptible plants (Table 4).

Table 4. Segregation of $F_2$ progenies of the cross LP-1 X Tabasco following inoculation with TEV.

<table>
<thead>
<tr>
<th>Phenotype</th>
<th>Observed</th>
<th>Calculated</th>
<th>Ratio</th>
<th>$X^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resistant</td>
<td>98</td>
<td>105</td>
<td>3</td>
<td>.466</td>
<td></td>
</tr>
<tr>
<td>Susceptible</td>
<td>42</td>
<td>35</td>
<td>1.4</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The data from the $F_2$ of this cross are presented in Table 4. Of the 140 plants in the $F_2$ generation, 98 were resistant, while 42 were susceptible to TEV. A chi-square analysis was calculated and a value of 1.86 was obtained for a 3:1 ratio, with one degree of freedom which had a ($p$) of .20-.10. This showed that the inheritance of resistance to TEV in the cross LP-1 X Tabasco appeared to fit a 3:1 ratio with resistance being dominant over susceptibility.
Figure 3. Parents, LP-1 (P₁) left, Tabasco (P₂) right, and F₂ center.

Figure 4. F₁ of LP-1 X Tabasco, inoculated with TEV.
Almeda X LP-1

Almeda (P₁), LP-1 (P₂), and the F₁ hybrids from the cross between these 2 parents are shown in Figure 5. The Almeda plants (P₁) exhibited severe leaf-mottle and distortions, while those of LP-1 (P₂) appeared symptomless. The F₁ plants in the center also seemed symptomless, similar to the resistant parent (P₂). It should also be noted that there was no difference between the inoculated and non-inoculated F₁ plants, indicating that the resistance to TEV was dominant. Two F₂ plants of the cross between Almeda X LP-1 are shown in Figure 6. Note that the plant on the left appeared healthy while the one on the right had mottled and distorted leaves. These two plants were picked from the same F₂ population which had been inoculated with TEV.

The data from the F₂ generation of the cross Almeda X LP-1 are shown in Table 5. The F₂ plants segregated into 2 classes in a ratio of 3 non-mottled leaf plants : 1 mottled and/or curled leaf. A chi-square analysis was calculated for a goodness of fit for a 3:1 ratio, and a chi-square value of 1.81 was obtained. The probability (p) value for the chi-square of 1.81 with one degree of freedom was .20-.10. Therefore, the data obtained fit a 3:1 ratio, indicating that the inheritance of TEV resistance was completely dominant over susceptibility to TEV.
Figure 5. Almeda ($P_1$), Left. Center; $F_1$ hybrid. Right; $LP^{-1}$.

Figure 6. $F_2$ plants inoculated with TEV. Left plant appears symptomless. Right plant showing leaf mottle.
Table 5. Segregation of $F_2$ progenies of the cross Almeda X LP-1 following inoculation with TEV.

<table>
<thead>
<tr>
<th>Phenotype</th>
<th>Observed</th>
<th>Calculated</th>
<th>Ratio</th>
<th>$\chi^2$</th>
<th>P.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-mottled leaf</td>
<td>160</td>
<td>168.75</td>
<td>3</td>
<td>.453</td>
<td></td>
</tr>
<tr>
<td>Mottled leaf</td>
<td>65</td>
<td>56.25</td>
<td>1</td>
<td>1.361</td>
<td></td>
</tr>
</tbody>
</table>

1.81 .20-.10

Similar results were obtained when the resistant parent, LP-1 was crossed with another susceptible variety (Tabasco) in previous experiments. The $F_1$ progeny of the cross was resistant to TEV, as evidenced by non-wilted plants following inoculation with TEV.

Cook (10) stated that resistance to TEV in pl1 and p34 (S.C.4625), (C. annuum L.) peppers was inherited as a single recessive gene, designated $et^a$ by Greenleaf, and believed responsible for the TEV reaction of the pl1, and p34 (S.C. 4625) peppers.

CUCUMBER MOSAIC VIRUS (CMV)

The cross Almeda X LP-1 was chosen to study the inheritance of resistance to CMV. Preliminary experiments indicated that plants of LP-1 had only very slight leaf mottle, while all of the P.I. group, Tabasco, and Almeda had severe CMV symptoms.
Therefore, LP-1 was considered as resistant to CMV, while the others were classified as susceptible. The results of these experiments also showed that each of the parents were homozygous in their response to CMV.

There were no visible symptoms on any of the LP-1 plants during the first 4 weeks following inoculation, while all Almeda plants showed necrotic lesions (about 2 mm in diameter), on the leaves (Figure 7). During the second week, systemic symptoms on Almeda appeared on the upper leaves with brown spots on the stem, and severe leaf mottle.

The F₁ plants exhibited severe leaf mottle. This suggested that the resistance to CMV was recessive. Seventy-four of the F₂ segregates showed mild to severe leaf-mottle, with stem browning, or leaf mottle without brown spots on the stem, while 15 of the F₂ plants appeared symptomless or with slight leaf mottling. This segregation appeared to fit 3:1 ratio. A chi-square analysis was calculated, and a value of 3.149 was obtained for a 3:1 ratio, and 1 degree of freedom. The probability value from the chi-square, Table 6, for goodness of fit was .10-.05.

These data show that resistance to CMV in this cross was inherited as a simple mendelian factor with resistance being recessive to dominant, since all the F₁ plants were susceptible.
Figure 7. Almeda plants showing local lesions and leaf mottle after inoculation with CMV.
Table 6. Segregation of F\textsubscript{2} progenies of the cross Almeda X LP-1 following inoculation with CMV

<table>
<thead>
<tr>
<th>Phenotype</th>
<th>Observed (O)</th>
<th>Calculated (O)</th>
<th>Ratio</th>
<th>(x^2)</th>
<th>P.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mottle leaf</td>
<td>74</td>
<td>66.75</td>
<td>3</td>
<td>.787</td>
<td></td>
</tr>
<tr>
<td>Non-mottle leaf</td>
<td>15</td>
<td>22.25</td>
<td>1</td>
<td>2.362</td>
<td></td>
</tr>
</tbody>
</table>

\(x^2 = 3.149, \text{P.} = 0.10-.05\)

NON-CLUSTER VS. CLUSTER BEARING HABIT

In 1969 genetic material, Almeda (cluster) X LP-1 (non-cluster) was classified for non-cluster vs. cluster type. Of the 516 F\textsubscript{2} segregates, 398 were of the non-cluster type.

There were 22 out of the 200 F\textsubscript{2} segregates, which were killed in the field by damping off in 1970. The remaining 178 F\textsubscript{2} plants were classified for non-cluster vs. cluster character. Of these 178 F\textsubscript{2} plants, 129 were of the non-cluster type. Table 7 shows the number of F\textsubscript{2} plants which segregated for the non-cluster and cluster character.

Data in Table 7 show that the non-cluster type (in the F\textsubscript{2} population), was dominant over cluster. The chi-square test for goodness of fit for a 3:1 ratio in the 1969 material gave a probability value of .30-.20. The 1970 F\textsubscript{2} gave a probability value of
Table 7. Segregation of F₂ progenies of the cross Almeda X LP-1 for non-cluster vs. cluster

<table>
<thead>
<tr>
<th>Year</th>
<th>Observed number</th>
<th>Calculated 3:1</th>
<th>X²</th>
<th>P.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Non-cluster</td>
<td>Cluster (1)</td>
<td>Non-Cluster</td>
<td>Cluster (1)</td>
</tr>
<tr>
<td>1969</td>
<td>398</td>
<td>118</td>
<td>387</td>
<td>129</td>
</tr>
<tr>
<td>1970</td>
<td>129</td>
<td>49</td>
<td>133.5</td>
<td>44.5</td>
</tr>
</tbody>
</table>

(1) Three or more pedicels per node.

.50-.30. These results show that the segregation was in agreement with the expected single factor dominance ratio, with all the F₁ plants being of the non-cluster type.

Murthy and Murthy (44), Angeli (3), and Deshpande (13), reported that the cluster habit was recessive to the non-cluster type, and that the non-cluster habit was controlled by a single dominant gene.

**IMMATURE FRUIT COLOR**

The Almeda parent has greenish-yellow immature-fruit, while that of LP-1 is sulfur-yellow in color. However, the color of the mature fruit produced by both parents is red. The F₁ hybrid had greenish-yellow immature fruit. The F₂ plants segregated into 2 immature-fruit-color classes; greenish-yellow, and sulfur-yellow. Of the 516 F₂ segregates, 386 F₂ plants had greenish-yellow pods.
Deshpande (13) and Webber (64) concluded from their results that the difference between green and yellow immature-fruit color in their material was conditioned by a single gene with green color being dominant. However, in later work, Jesivani et al. (33), reported that green color was conditioned by 2 genes. Odland (47) concluded that immature fruit color was found to be controlled by several "cumulative" factors, and the green color would result when two or more pairs of these factors are in the dominant condition. Halsted (22) found that the $F_1$ of a cross between a "pale green variety" and an "ordinary green variety" was "pale green". The results obtained from the cross Almeda X LP-1 in this experiment are presented in Table 8. The immature-fruit color of the $F_1$ was classified as greenish-yellow and appeared to be dominant over sulfur-yellow.

Table 8 also shows that in 1969 386 $F_2$ segregates had greenish-yellow immature-fruit color, and 130 had sulfur-yellow pods. In 1970 genetic material also segregated in 3:1 ratio, with 130 $F_2$ plants producing greenish-yellow colored pods and 48 segregates sulfur-yellow immature fruit. The calculated chi-square value of .0102 for the 1969 $F_2$ progenies fit a 3:1 ratio, with a probability value of .90. The 1970 $F_2$ population had a chi-square value of .366, and with one degree of freedom, had a probability of .70-.50. This indicated that the deviation of the observed value from the expected one was not significant, therefore, it suggests that the
genetic behavior of this character was conditioned by 1 pair of genes in this study.

Table 8. Segregation of the F\textsubscript{2} of the cross Almeda X LP-1 for immature fruit color.

<table>
<thead>
<tr>
<th>Year</th>
<th>Observed number</th>
<th>Calculated number</th>
<th>( x^2 )</th>
<th>P.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Greenish-yellow</td>
<td>Sulfur-yellow</td>
<td>Greenish-yellow</td>
<td>Sulfur-yellow</td>
</tr>
<tr>
<td>1969</td>
<td>386</td>
<td>130</td>
<td>387</td>
<td>129</td>
</tr>
<tr>
<td>1970</td>
<td>130</td>
<td>48</td>
<td>133.5</td>
<td>44.5</td>
</tr>
</tbody>
</table>

Associations Between Pedicels Per Node and Fruit Color

The Almeda variety has greenish-yellow colored immature fruit, which is borne in clusters (from 5-10 pedicels per node). LP-1 has sulfur-yellow immature fruit, borne 1, 2, and occasionally 3 per node (non-cluster).

The 1969 and 1970 progenies were classified for the following characters: non-cluster-greenish-yellow; non-cluster-sulfur-yellow; cluster-greenish-yellow and cluster-sulfur-yellow.

The F\textsubscript{1} plants in 1969 and 1970 had greenish-yellow colored fruit borne in non-cluster fashion. The 1969 F\textsubscript{2} progenies (Table 9) segregated in a ratio of a 9 non-cluster-greenish-yellow, 3 non-cluster-sulfur-yellow, 3 cluster-greenish-yellow, and 1 cluster type sulfur-yellow. The 1970 F\textsubscript{2} material was in agreement with that of 1969, as shown in Table 10. In 1970 the chi-square value was
3.372, as shown in Table 10, and gave a probability of .50-.30.

This indicated that there was no significant difference between the observed value and the theoretical in both chi-square tests. No apparent linkage existed between bearing habit and pod color.

Table 9. 1969 Segregation for fruiting habit and fruit color in F2 progeny of Almeda X LP-1.

<table>
<thead>
<tr>
<th>Non-cluster Vs. cluster and greenish-yellow V. sulfur-yellow</th>
<th>Observed (O)</th>
<th>Calculated (C) 9:3:3:1</th>
<th>O-C</th>
<th>((O-C)^2/c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-cluster greenish-yellow</td>
<td>302</td>
<td>290.25</td>
<td>11.75</td>
<td>.4756</td>
</tr>
<tr>
<td>Non-cluster sulfur-yellow</td>
<td>96</td>
<td>96.75</td>
<td>.75</td>
<td>.0058</td>
</tr>
<tr>
<td>Cluster-greenish-yellow</td>
<td>84</td>
<td>96.75</td>
<td>12.75</td>
<td>1.6802</td>
</tr>
<tr>
<td>Cluster-sulfur-yellow</td>
<td>34</td>
<td>32.25</td>
<td>1.75</td>
<td>.0949</td>
</tr>
</tbody>
</table>

\[X^2 = 2.246\]
\[P = .70-.50\]

Table 10. Segregation of fruiting habit and fruit color in F2 progeny of Almeda X LP-1.

<table>
<thead>
<tr>
<th>Non-cluster Vs. cluster and greenish-yellow</th>
<th>Observed (O)</th>
<th>Calculated (C) 9:3:3:1</th>
<th>O-C</th>
<th>((O-C)^2/c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-cluster greenish-yellow</td>
<td>98</td>
<td>100.125</td>
<td>2.125</td>
<td>.045</td>
</tr>
<tr>
<td>Non-cluster sulfur-yellow</td>
<td>31</td>
<td>33.375</td>
<td>2.375</td>
<td>.169</td>
</tr>
<tr>
<td>Cluster-greenish-yellow</td>
<td>32</td>
<td>33.375</td>
<td>1.375</td>
<td>.056</td>
</tr>
<tr>
<td>Cluster-sulfur-yellow</td>
<td>17</td>
<td>11.125</td>
<td>5.875</td>
<td>3.102</td>
</tr>
</tbody>
</table>

\[X^2 = 3.372\]
\[P = .50-.30\]
SUMMARY

Several hundred P.I. Capsicum spp. accessions, and the pepper cultivars, LP-1, Tabasco, and Almeda (all C. frutescens L.) were evaluated for resistance to TEV and CMV. The P.I. group included 341 C. annuum L., 43 C. frutescens L., and 36 C. sinense.

Seedlings of P.I. 152225 and LP-1 were resistant to TEV, while those of the other accessions, Tabasco and Almeda, showed leaf-mottling, curling, or wilting symptoms of TEV.

The mode of inheritance of TEV resistance was studied in the crosses P.I.152225 X Tabasco, LP-1 X Tabasco, and Almeda X LP-1. CMV resistance, pod color, and fruit bearing habit were studied in the cross Almeda X LP-1.

The F₁ population of the cross between P.I.152225 X Tabasco was susceptible to TEV and in the F₂ generation a 3:1 ratio of susceptibility to resistance was obtained. Resistance to TEV was controlled by a simple recessive gene. However, in the crosses LP-1 X Tabasco, and Almeda X LP-1, resistance to TEV was dominant over susceptibility, as the F₁ hybrids of both crosses were resistant to the virus. The segregating ratio in the F₂ generations suggested that the resistance to TEV was inherited as a simple Mendelian factor, with a 3:1 ratio.

In studying the mode of inheritance of CMV resistance, crosses were made between Almeda (CMV susceptible) and LP-1 (CMV resistant).
The F₁ progenies were highly susceptible to CMV, and complete dominance of susceptibility over resistance was suggested. The F₂ segregated in a 3:1 ratio. These data pointed out that resistance might be inherited on a monofactorial basis.

Inheritance of non-cluster vs. cluster bearing habit was studied in the cross Almeda (cluster) X LP-1 (non-cluster). The cluster bearing habit appeared to be controlled by a single recessive gene. The F₁ plants were of non-cluster habit, and segregated in the F₂ progeny in a 3:1 ratio of non-cluster to cluster bearing habit. This character seemed to be inherited as a simple Mendelian factor, with the non-cluster factor being dominant over cluster bearing habit.

The inheritance of immature fruit color was analyzed in the cross Almeda (greenish-yellow) X LP-1 (sulfur-yellow). The greenish-yellow color was dominant over sulfur-yellow. The F₂ progenies segregated in a 3:1 ratio. Therefore, it was postulated that this character was qualitative in nature, and that the sulfur-yellow color was conditioned by a simple recessive gene.

Inheritance of pod color and fruit bearing habit and associations between them was also investigated in the F₁ and F₂ generations of the cross Almeda (cluster, greenish-yellow) X LP-1 (non-cluster, sulfur-yellow). It was observed that there was no linkage between these two characters. The F₁ plants were all of the non-cluster, greenish-yellow type, while the F₂ progeny segregated in a 9:3:3:1
ratio. This confirmed that the cluster vs. non-cluster and greenish-yellow vs. sulfur-yellow pod types were simply inherited, and segregated independently in the $F_2$ generation.
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Major Field:  Horticulture

Title of Thesis:  The Inheritance of Resistance to Tobacco Etch and Cucumber Mosaic Viruses and Some Other Characters in Several Capsicum Species

Approved:

[Signatures]

Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

Date of Examination:

July 23, 1970