INHERITANCE STUDIES OF CERTAIN FRUIT AND PLANT
CHARACTERS IN CAPSICUM FRUTESCENS

DISSERTATION

Presented in Partial Fulfillment of the Requirements
for the Degree Doctor of Philosophy in the
Graduate School of the Ohio State University

By
ALVIN HUGH DEMPSEY, B.S.A., M.S.A.
The Ohio State University
1953

Approved by:

[Signature]
ACKNOWLEDGEMENTS

The author wishes to express his appreciation to Dr. F. S. Howlett for his criticism of the original problem outline and encouragement throughout the progress of this study.

He also wishes to thank Dr. E. K. Alban and Dr. E. F. Laddock for serving on his special committee, and for their willingness to provide help and advice in the early stages of the problem. The writer is indebted to Dr. Walter N. Brown for his time and aid in correcting the original draft of the manuscript.

To his wife, Sue, the writer wishes to express his sincere appreciation for the typing of the thesis and her constant encouragement throughout his graduate study and execution of the problem.

Acknowledgement is made to Mr. B. B. Brantley for his assistance in the preparation of the photographs and criticism of the manuscript.

Thanks are due Dr. F. F. Cowart, Director of the Georgia Experiment Station, and Dr. E. F. Savage for their help in obtaining a leave of absence to do graduate study at the Ohio State University.
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>REVIEW OF LITERATURE</td>
<td>4</td>
</tr>
<tr>
<td>Plant Habit</td>
<td>4</td>
</tr>
<tr>
<td>Fruit Characters</td>
<td>4</td>
</tr>
<tr>
<td>Other Characters</td>
<td>7</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>10</td>
</tr>
<tr>
<td>EXPERIMENTAL RESULTS</td>
<td>21</td>
</tr>
<tr>
<td>PLANT HABIT</td>
<td>21</td>
</tr>
<tr>
<td>Inheritance of Plant Height</td>
<td>21</td>
</tr>
<tr>
<td>Inheritance of Stem Diameter</td>
<td>24</td>
</tr>
<tr>
<td>FRUIT CHARCTERS</td>
<td>27</td>
</tr>
<tr>
<td>Segregation for Fruit Length and Width</td>
<td>28</td>
</tr>
<tr>
<td>Inheritance of Fruit Shape</td>
<td>31</td>
</tr>
<tr>
<td>Inheritance of Fruit Wall Thickness</td>
<td>36</td>
</tr>
<tr>
<td>OTHER CHARACTERS</td>
<td>42</td>
</tr>
<tr>
<td>Inheritance of Pungency</td>
<td>42</td>
</tr>
<tr>
<td>Inheritance of Fruit Position</td>
<td>44</td>
</tr>
<tr>
<td>Association of Pungency and Fruit Position</td>
<td>45</td>
</tr>
<tr>
<td>Linkage from F2 Data</td>
<td>48</td>
</tr>
<tr>
<td>Resistance to Bacterial Spot</td>
<td>50</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>52</td>
</tr>
<tr>
<td>SUMMARY</td>
<td>58</td>
</tr>
<tr>
<td>LITERATURE CITED</td>
<td>61</td>
</tr>
<tr>
<td>BIBLIOGRAPHY</td>
<td>65</td>
</tr>
</tbody>
</table>
LIST OF ILLUSTRATIONS

FIGURE 1. (Photograph) A-1 and B-1, the parents used in this study .................................................. 12
C-1, methods for controlled pollinations. ............................................. 16

FIGURE 2. (Graph) Frequency distribution for plant height of F2 generation of Santanka X Truhart .............................................................. 22

FIGURE 3. (Graph) Frequency distribution for stem diameter of F2 generation ........................................ 26

FIGURE 4. (Photograph) Fruits of parental lines and fruits from F2 generation ............................................. 30

FIGURE 5. (Graph) Fruit length in mm. .......................... 33

FIGURE 6. (Graph) Fruit width in mm. .......................... 33

FIGURE 7. (Graph) The distribution of fruit shape indices for F2 generation of Santanka X Truhart ......................... 35

FIGURE 8. (Photograph) Fruit positions and cross sections of fruits of Santanka (P1), Truhart Perfection (P2) and F1 of Santanka X Truhart .................................................. 38

FIGURE 9. (Graph) Fruit wall thickness in mm. ........... 41

FIGURE 10. (Graph) Fruit wall thickness in mm. Logarithmic Progression ............................ 41

FIGURE 11. (Photograph) F1 plants of Santanka X Truhart and F3 segregate ... 47
INHERITANCE STUDIES OF CERTAIN FRUIT AND PLANT CHARACTERS IN CAPSICUM FRUTESCENS

INTRODUCTION

For more than twenty-five years the pimiento has been one of the most important vegetable crops for canning in Georgia. The farmers of Georgia grow approximately 75 percent of the pimientos produced in the United States (7). The State average yield of pimientos in Georgia for 1926 was three tons per acre (37) but the average annual per acre yield of pimientos for Georgia during the last decade has been less than one ton (7). Diseases are chiefly responsible for the low yields of this crop (15) and the need for a disease resistant, improved pimiento variety is apparent.

The objectives of this investigation were to determine the segregation and inheritance of plant height, stem diameter; fruit length, width, shape, and fruit wall thickness; pungency, fruit position, and resistance to bacterial spot, Xanthomonas vesicatoria (Doidge) Dows. Data for this genetic study were obtained by crossing the commercial pimiento variety with a disease resistant pepper introduced from Japan. Information obtained from the present study should aid in planning a systematic breeding program for the development of a desirable pimiento variety with resistance to bacterial spot, one of the most serious diseases.
The pimiento belongs to the Solanaceae or nightshade family and the genus \textit{Capsicum}. The genus comprises a wide range of forms, particularly as to the shape and pungency of the fruit. Bailey (1) places all the cultivated peppers under \textit{Capsicum frutescens} L. Huskins and La-Cour (17) studied a dozen varieties among three subspecies and found only normal figures of twelve chromosomes in the haploid and twenty-four in the diploid condition. Dixit's (9) results agree with these and aceto-carmine smears of pollen mother cells of the parents used in this study gave the haploid number of twelve.

Although much work has been done on the inheritance of some characters in the genus \textit{Capsicum}, it seems desirable to study the transmissibility of plant and fruit characters using inbred lines. Greenleaf (12) has suggested line breeding as a method of improving the pimiento but he did not report the use of inbred lines for hybridization. Previous workers have used many types of peppers in their genetic studies and there is disagreement on inheritance of some characters such as pungency, fruit position, and the ability to hybridize Tabasco with cultivated varieties. It appears that controlled inbreeding might aid in obtaining more uniform results.

There are many wild types of \textit{Capsicum} whose varied potentialities must be tested. By means of laborious controlled self- and cross-pollinations and selection in
segregating generations - diverse types may be combined and recombined with wider limits. A thorough knowledge of the mode or pattern of inheritance of the characters contributing to yield, desirable horticultural fruit and plant characteristics, and resistance to diseases is essential for the intelligent planning and successful completion of a breeding program for the improvement of the pimiento. This information on inheritance furnishes a basis for transferring gene complexes from one type to another. Occasionally transgressive segregation occurs for quantitative characters and the recombination of genetic factors leads to the production of new and desirable individuals unlike either parent.
REVIEW OF LITERATURE

Plant Habit

In his study of hybrid vigor of eggplant, Kakizaki (21) determined stem diameters and heights of thirty intervarietal crosses. The F_1 plants showed a mean stem diameter and height increase of six percent over the mean of the parents. Dale (4) found in his work with peppers that the tall plant habit was dominant to the dwarf. Segregation in the F_2 was three tall to one dwarf.

The branching habit of pepper was shown by Webber (40) and others to be controlled by several factors as evidenced by the intermediate character of the F_1 and the occurrence of all gradations of habit in the F_2.

Fruit Characters

Halsted (13 & 14), in his summary of experiments with peppers, reported the results of his study involving twenty different crosses of pepper. He stated, "In the study of fruit measurements it is highly proper to confine one's study to a single cross at a time, as the total brings together greatly different sets of combinations." The average "breadths" (widths) of fruits for the F_1 and F_2 generations of most crosses in his study were closer to the average widths of the smaller parents. In his cross of Golden Queen (57.1 mm.) X Red Cluster (6.2 mm.), the F_1 had an average width of 17.9 mm. Halsted did not suggest a mode of inheritance for fruit width, length and shape.
Khambanonda (22), in his report on inheritance of fruit size in red pepper, found the mean of the F₁ generation for fruit length larger than either parent. The F₂, F₃ and F₄ distributions were positively skewed and transgressive far beyond the parental and F₁ values. In his cross of Red Chili X Sunnybrook, the fruit width of the F₁ was intermediate between the parents. Fruits, the same width as the fruits of the small parent, were recovered in the selfed generations; whereas, none as wide as the other parent was recovered.

Dale (5), reporting fruit-length studies in Capsicum, obtained skewed curves when he plotted distributions of pod length for the F₂ generation against intervals of equal arithmetical magnitude, but normal curves when plotted on a logarithmic basis. He concluded that several undetermined factors for pod length exerted proportionate rather than additive effects, and there was no disturbing influence of dominance.

Sinnott (31) and Sinnott and Durham (32) offered a theory that factors controlling shape exist.

Cochran (3) used shape index for the classification and identification of varieties of Capsicum.

Webber (40) in his report on pepper hybrids found fruit size to be controlled by several factors. As a result of his study of heredity correlation of size and color characters in tomatoes, Lindstrom (25) made the following
comments, "In this connection it may be noted that size characters in tomato are somewhat peculiar in their $F_1$ behavior. Whereas the $F_1$ tomato plant ordinarily shows the marked vegetative vigor of heterosis, the $F_1$ fruits themselves are characteristically smaller than the parental average, thus exhibiting no heterosis. This has been attributed to the influence of the dominance of the factors for small size, a fact which is verified to some extent in the $F_2$ generation which shows some skewness, the mode being nearer the smaller end of the distribution."

Trimodal logarithmic distributions of segregating generations for fruit shape in pepper were reported by Khambanonda (22) to fit a one-gene hypothesis. He found the oblate fruit partially dominant to the elongated. Kaiser (20) demonstrated the effects of genes determining fruit shape in pepper.

In his section under the study of the wall of pepper fruits, Halsted (13) stated,"there is some correlation between the size of the fruit and the thickness of the wall." Other workers report that the distributions of fruit size (weight) of $F_2$, $F_3$, and $F_4$ generations are positively skewed but become normalized by logarithmic transformations. The effects of genes and environment on fruit weight were found to be multiplicative; the same gene produced a greater effect in some genotypes than in others.
Other Characters

Capsaicin, a volatile alkaloid that is soluble in alcohol, is the chemical that causes peppers to be pungent (10). The percentage of capsaicin varies greatly and Micko (27) found that some peppers had twenty times as much capsaicin as others. Erwin (10) states, "Generally speaking the percentage of capsaicin or pungency is inversely proportional to the size of the fruit."

Webber (40) reported pungent dominant to non-pungent and he obtained three pungent to one mild in the F2. Miller and Fineman (28) found pungent to be dominant in the F1 but recessive in the F2. They made the F2 classification under cool fall conditions and suggest that under such conditions pungency fails to develop in the heterozygous types.

Ting (36) found by use of a chemical test for the determination of the degree of pungency in peppers that considerable variation exists in capsaicin content among varieties ordinarily classified as hot. Marked variations also occur within some varieties. With his test he classified Argentine Wonder (very hot), Red Chili (hot), Long Red Cayenne (slightly hot), Sweet Roumanian (sweet), and Oakview Wonder (sweet).

Odland (29) compared an F2 culture consisting of 15 plants of the cross Sunnybrook variety with Cayenne variety for pungency. Five plants were recorded as pungent, seven
as medium pungent, and three as non-pungent. He stated, "the ratio suggests monohybrid segregation."

From his study of the fruit position of peppers, Odland (29) drew the following conclusions: First, that a single-factor P differentiates positive and negative geotropic response. Second, that fruit position, while dependent primarily upon factor P, may be influenced by other factors, namely; length of peduncle, size of fruit, and general "supporting strength" of the plant as influenced by environment.

It has been proved experimentally by Inkeno (18) and Kaiser (20) with the use of a clinostat and by inversion of potted plants that gravity does influence the position of the pepper fruits.

Walker (39) describes the organism *Xanthomonas vesicatoria* (Doidge) Dows. and its life cycle as follows: "The bacterium has a single polar flagellum. Capsules are formed. On nutrient agar, colonies are circular with entire edges, wet-shining yellow. Some strains hydrolyze starch; others do not. The organism is carried as a contaminant on the surface of tomato and pepper seeds. It was shown by Diachun and Valleau (8) to be a soil invader which may live over winter in association with wheat roots. The optimum temperature for growth of the organism on agar is 27° C. Moist weather and spattering rain are favorable
for the dissemination and penetration. The pathogen enters cotyledon, leaf, and stem through stomata and progresses intercellularly. The fact that the organism may subsist as a saprophyte on plant refuse other than tomato may explain some spasmodic occurrences of the disease in spite of rotation and seed treatment."

Higgins (15) and Weber (41) have reported that the disease is also destructive in Georgia and Florida, respectively. Horsfall and McDonnell (16) observed that there were wide differences in relative susceptibility to bacterial spot disease which appeared in epiphytotic form in a large varietal and strain collection of sweet peppers at the University of Connecticut and that resistance is probably inherited as a dominant factor.

Stuckey (34) reported, that inoculations of F₁ hybrid pepper plants with a suspension of Xanthomonas vesicatoria, indicated that resistance to the organism was a recessive character.

Martin (26) rated six varieties of pepper highly resistant to moderately resistant to bacterial spot in his test of eleven varieties. All of the resistant lines were classified either hot or very hot.
MATERIALS AND METHODS

Two varieties of red pepper (*Capsicum frutescens* L.) were used for this investigation. Santanka (*P1*) originated from a Japanese introduction received from the Division of Plant Exploration and Introduction of the United States Department of Agriculture. Truhart Perfection (*P2*) is a commercial pimiento variety released by the Georgia Experiment Station in 1943 (2). It is in reality an inbred selection from the original Perfection variety (38).

Santanka (*P1*) has small, erect, elongated fruits which are pungent. The fruits are compressed at the base and appear above the foliage. The plants are compact and medium in size. This selection belongs in the tabasco group according to Erwin's (10) system of classification. See figure B-1. Santanka was found to be resistant to bacterial spot, *Xanthomonas vesicatoria* (Doidge) Dows., in a disease nursery. Its resistance is of the type in which the host reacts by hypertrophy and hyperplasia of the mesocarp cells beneath the lesion. A layer of cells with suberized walls is formed directly beneath the necrotic tissue, and delimits the enlargement of the lesion.

Truhart Perfection (*P2*) has conical or heart-shaped, pendent fruits which are non-pungent. The plant is medium to large and the branches are semi-erect to erect. Truhart Perfection is susceptible to the bacterial spot organism.
Figure A-1. Truhart Perfection (P₂) showing pendent fruits with erect plant habit.

Figure B-1. Santanka (P₁) showing erect fruits and medium height plant.
This variety belongs in the perfection group based on Erwin's key to cultivated groups of Capsicum. See figure A-1.

Both parental lines were selfed three times ($S_3$) before cross pollinations were attempted. They were uniform for phenotypic characteristics. Crosses were then made between the two varieties with Santanka as the female parent. The $F_2$ seeds were obtained by selfing the $F_1$ plants. Some $F_2$ plants were selfed in order to obtain the seeds for the $F_3$ families to be studied. Several methods were attempted to prevent the contamination of the controlled self-and cross-pollinations by foreign pollen. Caging of individual plants and the use of a special cone were found to be the most satisfactory procedures. The frames of the cages were made of one inch by two inch wood strips. They were twenty inches square and three feet in height. Two sides of the cages were closed with cellulose acetate treated cord (a type of glass substitute) to allow an abundance of sunlight to reach the plants. The other two sides and top were covered with unbleached sheeting which permitted the free movement of air. In spite of these precautions, the percentage of successful pollinations was small when cages were used. The cones were of the type used by Frank Van Haltern of the Georgia Experiment Station in
controlled pollination with cantaloupes. See figure C-1 for details of the cones.

**Plant Habit**

The seeds of the $P_1$, $P_2$, $F_1$ and $F_2$ were planted in the greenhouse and transplanted to the field for the plant and fruit studies. A site for the experimental planting was selected which would eliminate environmental variation as much as possible. Rows were three and one-half feet apart and the plants were spaced thirty inches apart in the row. The $F_3$ families used for the pungency and fruit position study were grown in the field during the summer of 1953.

Plant height was measured to the nearest centimeter from soil level to the highest terminal bud. Stem diameter was measured at the soil level to the nearest millimeter.

**Fruit Characters**

The first five mature fruits from each plant were harvested for the fruit length, width and shape studies. Length was measured from the calyx edge to the distal end of individual fruits and width was determined at the midpoint of the length to the nearest millimeter.

A cross section was made at the midpoint of the fruit and the fruit wall thickness measured to the nearest tenth millimeter with a vernier caliper.
Figure C-1. Bagged and tagged pepper blossom; using a special cone to prevent contamination.

Figure D-1. Completed cone and the materials needed for its construction.
The five measurements were averaged for each individual plant. The shape index of the fruit was obtained by dividing length by width.

**Fungency**

Plant breeders and seed growers who work with hot peppers have often encountered difficulty in determining the pungency of lines and individual plant selections by organoleptic methods. Direct tasting of the fruit has proved unsatisfactory because the taste is quickly "destroyed", and the non-pungent fruits cannot then be identified.

Ting (36) made certain simplifications in the procedure of Fodor (11) and Tice (35) which would permit rapid application of a chemical test for the degree of pungency in peppers. The test is as follows:

1. A level ½ teaspoonful of the ground fruit is placed in a small bottle to which is added 10 milliliters of diethyl ether.

2. The bottle is stoppered and allowed to stand for five minutes.

3. About five milliliters of the extract is decanted into a dry test tube and the indicator added until no further color change takes place.

The ether extracts the pungent principle, capsaicin. The indicator consists of a one percent solution of vanadium oxytrichloride in carbon tetrachloride. Sweet pepper
extracts show no green color reaction while those of hot peppers vary from a greenish yellow to a dark green as the content of capsaicin increases. Because of the instability of the green color, a series of color standards are prepared from malachite green and napthal yellow. The color standard series runs from a number 1 yellow (sweet) through number 10 green (hot).

Ting (36) suggested that each dried sample be ground separately in a mortar for extraction. In the work reported herein an intermediate model Wiley Mill, a modification of the Wiley Mill that is especially suitable for the preparation of small samples of desiccated plant tissue, was used for grinding the samples. A delivery tube with a 40 mesh sieve top was used in the milling of the dried fruits. In order to compare the two methods of preparing the plant material, samples from the same fruit were ground by the mortar and the Wiley Mill and then extracted with ether. The vanadium indicator was added to the extracted samples and no difference in the color reaction was observed. This indicated the milling had not affected the color reaction.

Upon completion of the measurements for fruit length and width, fruit samples from individual plants were dried in an oven at 135° F. in preparation for the chemical pungency test. The seeds were removed from the
dried fruits and the pericarp, placenta and interlocular septae were ground for ether extraction. Erwin (10) states, "The capsaicin was found most abundant in the enlarged sub-epidermal cells, but was also abundant in nearly all the cells of the ovary wall, which are especially well supplied with chromatophores."

**Resistance to Bacterial Spot**

The seedlings for the study of resistance to *Xanthomonas vesicatoria* were grown in flats in the greenhouse during the fall and winter of 1952, under environmental conditions optimum for the development and spread of the organism. This disease affects both the leaves and fruits but the greatest damage occurs on the leaves. The lesions on the leaves are at first raised and wart-like but after a few days the tissues usually dry and collapse, leaving a small dark-brown spot. Infected leaves of the susceptible varieties turn yellow and drop. Inoculations were attempted on the young seedlings before the true leaves developed, but the usual symptoms of the disease did not develop on the cotyledons sufficiently to allow definite classification of the plants for susceptibility to *Xanthomonas vesicatoria*.

The inoculation method used was a modification of that used by Knight and Clouston (23 & 24) and Weindling (42) for testing resistance of cotton seedlings to
Xanthomonas malvacearum (E.F. Sm) Doneson.

The plants were inoculated with a water suspension of the bacterium when they were approximately ten centimeters in height. After inoculation the flats were placed inside a chamber made of two layers of tobacco cloth and kept moist by frequent sprays with water. The suspension of the organism was prepared from 7 day old Petri dish cultures of the bacterium.

Observations were made ten days after inoculation. Plants were classified as resistant if there were no infection or only occasional delimited lesions on the youngest leaves. If leaves developed numerous lesions usually followed by defoliation, the plants were recorded as susceptible.
EXPERIMENTAL RESULTS

The results are presented in three parts: (1) Plant Habit - inheritance of plant height and stem diameter; (2) Fruit Characters - segregation for fruit length and width, inheritance of fruit shape, and inheritance of fruit wall thickness; (3) Other Characters - inheritance of pungency, inheritance of fruit position, association of pungency and fruit position, linkage from F$_2$ data, and resistance to bacterial spot.

PLANT HABIT

For the study of plant height and stem diameter, fifty plants of the P$_1$, P$_2$ and F$_1$ and a sample of 504 plants of the segregating F$_2$ generation were available. The records for the plant habit studies were obtained at the same time of the harvest of the fruits for the fruit measurements. The study of plant height and stem diameter was undertaken to arrive at some indication of plant vigor as a distinguishing characteristic.

Inheritance of Plant Height

The frequency distribution for plant height of the F$_2$ generation for the cross of Santanka (P$_1$) X Truhart (P$_2$) is given in figure 2.
Figure 2 – Frequency distribution for plant height of $F_2$ generation of Santanka X Truhart
Table 1. - Plant Height of Parents and Hybrid Generations.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number of plants</th>
<th>Mean (cm.)</th>
<th>Standard deviation (cm.)</th>
<th>Coefficient of variability (cm.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P₁(Santanka)</td>
<td>50</td>
<td>35.1 ± .43</td>
<td>3.01 ± .30</td>
<td>8.57 ± .71</td>
</tr>
<tr>
<td>P₂(Truhart)</td>
<td>50</td>
<td>85.8 ± .92</td>
<td>6.48 ± .65</td>
<td>7.55 ± .77</td>
</tr>
<tr>
<td>F₁ (S x T)</td>
<td>50</td>
<td>58.2 ± .84</td>
<td>5.93 ± .59</td>
<td>10.18 ± .98</td>
</tr>
<tr>
<td>F₂</td>
<td>504</td>
<td>59.7 ± .44</td>
<td>9.80 ± .31</td>
<td>16.42 ± .53</td>
</tr>
</tbody>
</table>

From Table 1 the average of P₁ ± P₂ means is 60.45 centimeters. Therefore, the F₁ mean (58.2 cm.) closely approaches the average of the parents, while the F₂ mean (59.7 cm.) more nearly approaches it. There is no significant difference in the F₁ and F₂ means and they are intermediate between those of the parental lines. The intermediate nature of the F₁ and F₂ means for plant height suggests the presence of duplicate, cumulative, non-dominant genes which are sometimes referred to as polymeric genes (30). The F₂ was more variable than the F₁ which was expected with an intermediate F₁.

Assuming three pairs of duplicate, cumulative, non-dominant genes to be interacting for plant height, the F₂ sample was compared with (a / b)² in Table 2.
Table 2. - Comparison of observed F₂ sample for plant height with \((a \neq b)^{60} N = 504\).

<table>
<thead>
<tr>
<th>Class center (cm.)</th>
<th>Class range (cm.)</th>
<th>Relative frequencies</th>
<th>Number calculated</th>
<th>Actual number</th>
<th>(X^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>30</td>
<td>25-34</td>
<td>0.0156</td>
<td>8</td>
<td>10</td>
<td>0.50</td>
</tr>
<tr>
<td>40</td>
<td>35-44</td>
<td>0.0938</td>
<td>47</td>
<td>52</td>
<td>0.53</td>
</tr>
<tr>
<td>50</td>
<td>45-54</td>
<td>0.2343</td>
<td>118</td>
<td>126</td>
<td>0.54</td>
</tr>
<tr>
<td>60</td>
<td>55-64</td>
<td>0.3125</td>
<td>158</td>
<td>161</td>
<td>0.06</td>
</tr>
<tr>
<td>70</td>
<td>65-74</td>
<td>0.2343</td>
<td>118</td>
<td>107</td>
<td>2.45</td>
</tr>
<tr>
<td>80</td>
<td>75-84</td>
<td>0.0938</td>
<td>47</td>
<td>43</td>
<td>0.30</td>
</tr>
<tr>
<td>90</td>
<td>85-94</td>
<td>0.0156</td>
<td>8</td>
<td>5</td>
<td>1.12</td>
</tr>
</tbody>
</table>

\(X^2, df = 6, P = 0.50-0.30\) 5.50

Results of comparing the \(F₂\) generation with \((a \neq b)^{60}\) support the assumption of polymeric genes. In Table 2, it may be noted that for plant height, the observed frequencies agree with the calculated frequencies of \((a \neq b)^{60}\) assuming interaction of duplicate, cumulative, non-dominant genes, and these data favor the hypothesis that three pairs of polymeric genes were involved in the inheritance of plant height for this cross.

Inheritance of Stem Diameter

Plants with a stem diameter large enough to provide sufficient supporting strength to the plants and fruits can survive mechanical hazards best.
Below are given the results of the measurements for stem diameter made at the soil level of the plants.

Table 3. - Plant stem diameter of Parental lines and Hybrid generations.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number plants</th>
<th>Mean mm.</th>
<th>Standard deviation mm.</th>
<th>Coefficient variability mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>P₁ (Santanka)</td>
<td>50</td>
<td>17.3 ± .41</td>
<td>2.90 ± .29</td>
<td>16.76 ± 1.70</td>
</tr>
<tr>
<td>P₂ (Truhart)</td>
<td>50</td>
<td>26.7 ± .45</td>
<td>3.19 ± .32</td>
<td>11.94 ± 1.20</td>
</tr>
<tr>
<td>F₁ (S X T)</td>
<td>50</td>
<td>17.8 ± .48</td>
<td>3.40 ± .34</td>
<td>19.10 ± 1.96</td>
</tr>
<tr>
<td>F₂</td>
<td>504</td>
<td>19.2 ± .23</td>
<td>5.11 ± .16</td>
<td>26.66 ± 0.92</td>
</tr>
</tbody>
</table>

The F₁ mean for stem diameter of 17.8 millimeters is very near the P₁ mean of 17.3 millimeters showing dominance of the P₁ parent. The F₂ mean of 19.2 millimeters is larger than the F₁ mean which is expected with dominance of the P₁ parent. Figure 3 gives the frequency distribution of the F₂ generation for stem diameter. Referring to the graph for stem diameter, two definite modes may be observed; one at 18 mm. (P₁ = 17.3 mm.) and 26 mm. (P₂ = 26.7 mm.). The F₂ sample is divided into two classes as suggested by these two modes, assuming dominance of P₁ and 3:1 ratio in F₂. The results of a further breakdown of the segregating F₂ generation are presented in Table 4.
Figure 3.—Frequency distribution for stem diameter of $F_2$ generation.
Table 4. - Frequencies of stem diameter in F₂ generation of cross Santanka X Truhart.

<table>
<thead>
<tr>
<th>Class number (mm)</th>
<th>Observed classes</th>
<th>Modal classes</th>
<th>Observed number</th>
<th>Calculated 3:1*</th>
<th>( \chi^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>10-11</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12-13</td>
<td>51</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14-15</td>
<td>66</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16-17</td>
<td>89</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18-19</td>
<td>95</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20-21</td>
<td>76</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22-23</td>
<td>18</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24-25</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>26-27</td>
<td>31</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>28-29</td>
<td>27</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30-31</td>
<td>14</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>32-33</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>34-39</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\[ \chi^2 = 0.68, \text{ df } = 1, P = .50-.30 \]

*Assuming dominance of \( P_1 \) and modal classes from Figure 3.

The test for goodness of fit with a 3:1 ratio in Table 4 gave a chi-square value of 0.68 with a probability of .50-.30 and it may be concluded that the segregation of the F₂ generation for stem diameter fits a monogenic hypothesis.

**FRUIT CHARACTERS**

The fruits on the same pepper plant are fairly uniform in shape and general appearance but the size and weight exhibit a rather wide range of variation. Location on the plant and the lack of sufficient fecundation affect the size of the fruits as well as other environmental factors.
An average of five fruit observations was considered as being representative of the individual plants and the average of these five fruits per plant is presented in the results.

**Segregation for Fruit Length and Width**

Table 5.- Fruit length and width for Parental lines and Hybrid generations.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number plants</th>
<th>Mean length</th>
<th>Range length</th>
<th>Mean width</th>
<th>Range width</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>mm.</td>
<td>mm.</td>
<td>mm.</td>
<td>mm.</td>
</tr>
<tr>
<td>P₁(Santanka)</td>
<td>50</td>
<td>46.3</td>
<td>42.8-49.7</td>
<td>8.1</td>
<td>7.2-9.7</td>
</tr>
<tr>
<td>P₂(Truhart)</td>
<td>50</td>
<td>72.5</td>
<td>67.8-78.2</td>
<td>57.9</td>
<td>51.3-64.0</td>
</tr>
<tr>
<td>F₁ (S X T)</td>
<td>50</td>
<td>74.7</td>
<td>65.3-78.9</td>
<td>16.7</td>
<td>15.2-17.8</td>
</tr>
<tr>
<td>F₂</td>
<td>504</td>
<td>44.3</td>
<td>17.2-92.3</td>
<td>14.8</td>
<td>7.5-35.4</td>
</tr>
</tbody>
</table>

The F₁ mean (74.7 mm.) for fruit length is slightly larger than that of either parent. Transgressive segregation is found in the F₂ sample that contains individuals which are smaller than the small parent (P₁) and individuals larger than the large parent (P₂).

For fruit width the F₁ mean is smaller than 33.0 mm. - the average for the (P₁ × P₂). In the F₂ sample, individuals were recovered as small as the small parent (P₁) but none was recovered as large as the P₂. The largest individual in the F₂ sample was 35.4 mm. in width.
Upper row, left three fruits - Fruits of Truhart Perfection ($P_2$).

Upper row, right eight fruits - Fruits of Santanka ($P_1$).

Second, third and fourth rows from top - Fruits from thirty-seven individual $F_2$ plants.
Figure 4. Fruits of parental lines and fruits from $F_2$ generation.
The $F_2$ frequency distributions for fruit length and width are given in Figures 5 and 6. It should be noted that the ranges of the $F_1$ and $P_2$ for fruit length do not fall within the limits of the most frequent classes of the $F_2$ distribution. For fruit width the ranges of the $P_1$ and $F_1$ are found within the limits of the classes which have a greater number of individuals.

**Inheritance of Fruit Shape**

The possession of a specific form, both of the body as a whole and of its component parts, is one of the most distinctive features of organisms. The single gene difference between spherical and disk fruits in squash; between spherical and pear-shaped fruits in tomato; between lobed and entire leaves in Japanese morning glory; between single rose and pea combs in poultry; and between the many wing forms in Drosophila may be cited.

In recent work with pepper a positive correlation between length and width of fruit has been reported (22). This correlation suggests that shape is inherited as an unit factor.

The shape indices for the $P_1$, $P_2$, $F_1$ and $F_2$ generations were obtained by dividing the length by the width. The results are presented in Table 6.
Figure 5.- Frequency distribution for fruit length of F2 generation for cross of Santanka X Truhart.

Figure 6.- Frequency distribution for fruit width of F2 generation for cross of Santanka X Truhart. The range (51.3-64.0 mm.) for F2 is not within the limits of the scale on this figure.
Table 6.- Fruit Shape Indices for Cross of Santanka X Truhart.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number plants</th>
<th>Mean index</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1 (Santanka)</td>
<td>50</td>
<td>5.71</td>
<td>5.12-5.78</td>
</tr>
<tr>
<td>P2 (Truhart)</td>
<td>50</td>
<td>1.25</td>
<td>1.10-1.65</td>
</tr>
<tr>
<td>F1 (S X T)</td>
<td>50</td>
<td>4.43</td>
<td>4.21-4.80</td>
</tr>
<tr>
<td>F2</td>
<td>504</td>
<td>2.99</td>
<td>1.23-5.72</td>
</tr>
</tbody>
</table>

Figure 7 gives the frequency distributions of the fruit shape indices of the F₂ generation plotted on a logarithmic scale. It may be observed that there are three modes at shape indices 1.79, 2.88, and 4.01. Since these modes, when plotted on a logarithmic scale, suggest the action of one gene pair with incomplete dominance, separation of the F₂ sample was made using the class interval suggested by the modes. The goodness of fit of these classes are compared with the 1:2:1 ratio in Table 7.

Table 7.- Fruit Shape Indices of F₂ generation compared with 1:2:1 ratio.

<table>
<thead>
<tr>
<th>Modal class</th>
<th>Class interval</th>
<th>Observed</th>
<th>Calculated</th>
<th>X²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.79</td>
<td>1.21-2.14</td>
<td>128</td>
<td>126</td>
<td>0.03</td>
</tr>
<tr>
<td>2.88</td>
<td>2.15-3.57</td>
<td>236</td>
<td>252</td>
<td>2.03</td>
</tr>
<tr>
<td>4.01</td>
<td>3.58-5.71</td>
<td>140</td>
<td>126</td>
<td>1.55</td>
</tr>
</tbody>
</table>

\[ X^2 = 3.61, \text{df} = 2, \ P = .20-.10 \]
Figure 7.—The distribution of fruit shape indices for $F_2$ generation of Santonka X Truhart.
The observed frequencies for fruit shape indices in the $F_2$ generation agree with the calculated frequencies, assuming one gene pair, incomplete dominance, and class intervals suggested by the modes on a logarithmic progression. It should be noted that the $F_2$ data were plotted with classes equal logarithmically, which assumes multiplicative gene action.

**Inheritance of Fruit Wall Thickness**

Thickness of fruit wall is a character which was given attention in this program of work because fruits with thick walls are highly desired by both growers and processors of pimiento. Heavy, thick walled fruits can be processed with a minimum of labor and a minimum of loss due to trimming. Halsted (13) found a correlation between thickness of fruit wall and weight, and for the present study a measure of the fruit wall was used as an indication of this important horticultural characteristic.

Means and ranges for fruit wall thickness are given in Table 3. The frequency distribution of fruit wall thickness for the $F_2$ generation is presented in Figure 9.
Upper left - Santanka \((P_1)\) fruits erect and in clusters.

Upper right - Truhart Perfection \((P_2)\) fruits pendent with large peduncle.

Lower left - Fruits of \(P_1\) and \(P_2\).

Lower right - Fruits of \(F_1\) (Santanka \(\times\) Truhart).
Figure 8. Parental lines and F1 generation.
Table 8.- Fruit wall thickness of Parental lines and Hybrid generations.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number plants</th>
<th>Mean thickness mm.</th>
<th>Standard deviation mm.</th>
<th>Range mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>P₁ (Santanka)</td>
<td>50</td>
<td>0.90 ± .0072</td>
<td>.16 ± .0051</td>
<td>0.5-1.4</td>
</tr>
<tr>
<td>P₂ (Truhart)</td>
<td>50</td>
<td>5.30 ± .0076</td>
<td>.17 ± .0054</td>
<td>4.7-5.9</td>
</tr>
<tr>
<td>F₁ (S X T)</td>
<td>50</td>
<td>1.85 ± .0245</td>
<td>.55 ± .0173</td>
<td>1.5-2.1</td>
</tr>
<tr>
<td>F₂</td>
<td>504</td>
<td>1.80 ± .0169</td>
<td>.38 ± .0119</td>
<td>0.5-5.2</td>
</tr>
</tbody>
</table>

The F₁ mean of 1.85 mm. is closer to the P₁, the smaller parent, than to the P₂ and it is much smaller than the average of the two parents (3.0 mm.). The smaller parent (P₁) is recovered in the segregating F₂ sample, but the P₂ is not. Referring to Figure 9, it may be observed that the F₂ distribution does not follow an arithmetic scale when plotted against the expansion of the binomial with \((a/b)^N\) and assuming equal, cumulative non-dominant genes.

The data for fruit wall thickness were rearranged on a scale which grouped fruit wall thickness into classes determined by a logarithmic progression. Figure 10 gives the results. The observed frequencies are in fair agreement with the expected. Table 9 gives a comparison of the observed frequencies with the theoretical frequencies resulting from the expansion of \((a/b)^N\) which assumes eight pairs of genes and geometric progression which indicates the gene effects are multiplicative. The value
Figure 9. - Frequency distribution of F2 generation for fruit wall thickness of Santanka X Truhart.

Figure 10. - The distribution of fruit wall thickness in F2 generation of Santanka X Truhart arranged on logarithmic progression.
Figure 9 — Fruit wall thickness in MM

N = 504

F₂ Mean = 1.80 ± 0.0169

Frequency

Figure 10 — Fruit wall thickness in MM — Logarithmic Progression

Fruit wall thickness
Logarithmic scale

Theoretical curve (a + b)^6

Chi square = 14.33

P value lies between .10 and .05
of chi-square was found to be 14.33 with a probability of .10-.05. It is apparent that the inheritance of fruit wall thickness in this cross is following a geometric progression, and at least eight pairs of genes are involved.

Table 9.- Comparison of observed F2 with expansion of \((a / b)^{16}\) using logarithmic progression.

<table>
<thead>
<tr>
<th>Class center</th>
<th>Observed frequency</th>
<th>Calculated (a / b)^{16} frequency</th>
<th>(0-C)</th>
<th>((o-C)^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>.50</td>
<td>0</td>
<td>.0077</td>
<td></td>
<td></td>
</tr>
<tr>
<td>.60</td>
<td>2</td>
<td>.1230</td>
<td></td>
<td></td>
</tr>
<tr>
<td>.70</td>
<td>2</td>
<td>30</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td>.80</td>
<td>8</td>
<td>4.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>.95</td>
<td>18</td>
<td>14.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.10</td>
<td>43</td>
<td>34.00</td>
<td>49</td>
<td>2.38</td>
</tr>
<tr>
<td>1.30</td>
<td>67</td>
<td>62.00</td>
<td>45</td>
<td>.40</td>
</tr>
<tr>
<td>1.50</td>
<td>86</td>
<td>88.00</td>
<td>-2</td>
<td>.05</td>
</tr>
<tr>
<td>1.70</td>
<td>104</td>
<td>99.00</td>
<td>45</td>
<td>.25</td>
</tr>
<tr>
<td>2.00</td>
<td>84</td>
<td>88.00</td>
<td>-4</td>
<td>.18</td>
</tr>
<tr>
<td>2.30</td>
<td>48</td>
<td>62.00</td>
<td>-14</td>
<td>3.16</td>
</tr>
<tr>
<td>2.60</td>
<td>25</td>
<td>34.00</td>
<td>-9</td>
<td>2.38</td>
</tr>
<tr>
<td>3.00</td>
<td>8</td>
<td>14.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.50</td>
<td>5</td>
<td>4.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.00</td>
<td>2</td>
<td>17</td>
<td>20</td>
<td>-3</td>
</tr>
<tr>
<td>4.60</td>
<td>1</td>
<td>.1230</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5.30</td>
<td>1</td>
<td>.0077</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\[X^2 = 14.33, \ df = 8, P = .10-.05\] 14.33

OTHER CHARACTERS

Inheritance of Pungency

The cross of Santanka (pungent) X Truhart (non-pungent) was available for the study of the inheritance of pungency. An F2 sample consisting of 504 individuals of Santanka X Truhart was examined in 1952 to determine the segregation of this character. Nine F3 families were
classified in 1953 as to their pungency. Each F₃ family consisted of approximately 50 individuals from nine F₂ plants that had been selfed in 1952.

The milled samples of desiccated fruit tissue from the P₁, P₂, and F₁, F₂, F₃ generations were subjected to the chemical test for determination of pungency. Fresh fruits were harvested from all plants showing non-pungent reaction by the chemical test and they were checked for pungency by an organoleptic test. On tasting, no pungency could be detected in the samples used for the organoleptic recheck. The results of the chemical test are given in Table 10.

Table 10.- Fruit pungency of parental lines and hybrid generations.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number plants</th>
<th>Pungent</th>
<th>non-pungent</th>
<th>Ratio</th>
<th>P from X²</th>
</tr>
</thead>
<tbody>
<tr>
<td>P₁ (Santanka)</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P₂ (Truhart)</td>
<td>50</td>
<td>0</td>
<td>50</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P₁ (S X T)</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>504</td>
<td>370</td>
<td>134</td>
<td>3:1</td>
<td>.50-.30</td>
</tr>
<tr>
<td>F₃ (53.1)**</td>
<td>48</td>
<td>48</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.2)</td>
<td>45</td>
<td>45</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.3)</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.4)</td>
<td>46</td>
<td>34</td>
<td>12</td>
<td>3:1</td>
<td>.50-.30</td>
</tr>
<tr>
<td>F₃ (53.5)</td>
<td>47</td>
<td>47</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.6)</td>
<td>47</td>
<td>35</td>
<td>12</td>
<td>3:1</td>
<td>.90-.95</td>
</tr>
<tr>
<td>F₃ (53.7)</td>
<td>46</td>
<td>46</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.8)***</td>
<td>40</td>
<td>0</td>
<td>40</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.9)</td>
<td>38</td>
<td>0</td>
<td>38</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*X² = 3.841, df = 1, P = .05.

**F₃(53.1) through F₃(53.7) the F₂ plants were pungent.

***F₃(53.8) and F₃(53.9) the F₂ plants were non-pungent.
Referring to Table 10, it may be observed that pungent is dominant to non-pungent, F₁ all pungent, and the F₂ sample and two F₃ samples that were segregating for pungency fit a 3:1 monohybrid ratio.

**Inheritance of Fruit Position**

In the cross used in this study of Santanka (erect) x Truhart (pendent), the F₁ was pendent. An F₂ sample of 504 individuals was classified for fruit position. Nine F₃ families were studied for this character.

The results are presented in Table 11. It may be observed that the F₁ was pendent and the F₂ sample and the three segregating F₃ families fit a three pendent to one erect ratio which is typical of monogenic inheritance.

**Table 11. - Fruit position for parental lines and hybrid generations.**

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number of plants</th>
<th>Number of pendent</th>
<th>Number of erect</th>
<th>Calculated ratio</th>
<th>F from X²</th>
</tr>
</thead>
<tbody>
<tr>
<td>F₁ (Santanka)</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td>3:1</td>
<td>.30-.20</td>
</tr>
<tr>
<td>F₂ (Truhart)</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₁ (S × T)</td>
<td>50</td>
<td>50</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₂</td>
<td>504</td>
<td>366</td>
<td>138</td>
<td>3:1</td>
<td></td>
</tr>
<tr>
<td>F₃ (53.1)**</td>
<td>48</td>
<td>48</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.2)</td>
<td>45</td>
<td>45</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.3)</td>
<td>50</td>
<td>40</td>
<td>10</td>
<td>3:1</td>
<td>.50-.30</td>
</tr>
<tr>
<td>F₃ (53.4)</td>
<td>46</td>
<td>33</td>
<td>13</td>
<td>3:1</td>
<td>.70-.50</td>
</tr>
<tr>
<td>F₃ (53.5)</td>
<td>47</td>
<td>47</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.6)</td>
<td>48</td>
<td>34</td>
<td>14</td>
<td>3:1</td>
<td>.10-.05</td>
</tr>
<tr>
<td>F₃ (53.7)</td>
<td>46</td>
<td>46</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.8)***</td>
<td>40</td>
<td>0</td>
<td>40</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₃ (53.9)</td>
<td>38</td>
<td>0</td>
<td>38</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Χ² = 3.841, df = 1, P = .05
**F₃(53.1) through F₃(53.7) the F₂ plants were pendent.
***F₃(53.8) and F₃(53.9) the F₂ plants were erect.
Association of Pungency and Fruit Position

The fruits of the $P_1$ (Santanka) are erect and pungent, while the fruits of the $P_2$ (Truhart) are pendent and non-pungent. The fruits of the $F_1$ from the cross of Santanka $\times$ Truhart are all pendent and pungent which indicates that the pendent position and pungency are both dominant. However, there appeared to be an excess of plants producing fruits that were erect and pungent as well as an excess of plants producing fruits that were pendent and non-pungent in the $F_2$ generation. The excesses of the parental types indicate a possible linkage between position and pungency. An analysis of the data was made to determine if such a relationship existed.

Table 12 gives the results of a chi-square test for independence of the two factors, fruit position and pungency. The value of chi-square was found to be 22.77 with a probability of less than one percent in the test. The observed frequencies do not agree with the calculated frequencies of $9:3:3:1$ for independence of the two factors, therefore, a test for linkage was indicated.
Upper - $F_1$ plant with pendent fruits.

Lower - $F_3$ segregate with erect fruits.
Figure 11. F₁ plants of Santanka × Truhart and F₃ segregate.
Table 12.- Chi-square test for independence of two factors fruit position and pungency.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Frequencies observed</th>
<th>Frequencies calculated*</th>
<th>X²**</th>
</tr>
</thead>
<tbody>
<tr>
<td>P₁ (Santanka) Erect-pungent</td>
<td>50</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>P₂ (Truhart) Pendent-nonpungent</td>
<td>50</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>F₁ (S X T) Pendent-pungent</td>
<td>50</td>
<td>50</td>
<td></td>
</tr>
<tr>
<td>F₂ Pendent-pungent</td>
<td>250</td>
<td>283.5</td>
<td>3.95</td>
</tr>
<tr>
<td>Pendent-nonpungent</td>
<td>116</td>
<td>94.5</td>
<td>4.86</td>
</tr>
<tr>
<td>Erect-pungent</td>
<td>120</td>
<td>94.5</td>
<td>3.85</td>
</tr>
<tr>
<td>Erect-nonpungent</td>
<td>18</td>
<td>31.5</td>
<td>10.11</td>
</tr>
</tbody>
</table>

df = 3, X² = 22.77

*Χ² Calculated 9:3:3:1 ratio, pendent-pungent, pendent-nonpungent, erect-pungent, and erect-nonpungent.

**Χ² 11.34, df = 3, P = .01.

Linkage from F₂ Data

Using Immer's (19) method the crossover values were determined from the F₂ data. The genotypes of the parents may be represented as follows: Santanka, erect pungent ppHH; Truhart, pendent non-pungent PPhh; F₁ pendent pungent PhHh. This is a repulsion cross; the pH came from Santanka and the Ph from Truhart.

Let a, b, c, and d represent the numbers of individuals classified in the phenotypic classes, PH (pendent-pungent), Ph( pendent-nonpungent), pH (erect-pungent) and ph (erect-nonpungent), respectively. The value of p (crossover value)
is determined from the equation using the observed data from Table 12.

\[
p = \frac{\sqrt{-(bc - ad) \div \sqrt{(bc - ad)^2 \div ad (bc - ad)}}}{(bc - ad)} = \frac{\sqrt{-(116 \times 120 - 250 \times 18)}}{\sqrt{(116 \times 120 - 250 \times 18)^2 \div 250 \times 16}} / (116 \times 120 - 250 \times 18)
\]

\[
p = 0.3443
\]

The standard error of \( p \), when \( n \) is the total number of individuals, is then

\[
\sigma p = \sqrt{\frac{(1-p^2) (2 - p^2)}{2n (2 - 2p^2)}}
\]

\[
\sigma p = \sqrt{\frac{(1 - 0.3443 \times 0.3443) (2 - 0.3443 \times 0.3443)}{2 \times 504 (2 - 2)(0.3443 \times 0.3443)}}
\]

\[
\sigma p = 0.0387
\]

The crossover value of 0.3443 \( \neq \) 0.0387 for this material as measured from the \( F_2 \) data is high, indicating rather loose linkage.

This linkage resulted in the combinations of traits which occurred in the parents appearing much more frequently than they should have, while the new combinations or recombinations of characters different from those introduced by the parents appeared less frequently than expected.
Random assortment did not occur in the formation of gametes that functioned in producing the $F_2$ offspring and the genes for pungency and erect fruit position had a tendency to stay together in this cross.

**Resistance to Bacterial Spot**

Two flats each of $P_1$ (Santanka), $P_2$ (Truhart) and $F_1$ ($S \times T$) were planted for the studies of bacterial spot, *Xanthomonas vesicatoria* (Doidge) Dows. resistance. Eight flats were sown with $F_2$ seeds. Three resistant $F_2$ plants and five $F_2$ plants susceptible to the organism were selfed. Two flats each were planted of the eight $F_3$ families for the disease study.

The plants were inoculated with a water suspension of the bacterium as described earlier in this presentation under materials and methods. Most of the susceptible $P_2$ (Truhart) plants were completely defoliated but new foliage developed. The resistant plants developed some lesions but they appeared dry and the necrotic tissue would fall from the infected spots leaving a "shot hole" appearance. The resistant $F_2$ and $F_3$ plants were as resistant to the organism as the $P_1$, Santanka.

The parental lines and their hybrid progenies were classified for resistance or susceptibility to bacterial spot and the results are presented in Table 13.
Table 13.- Resistance to *Xanthomonas vesicatoria* of parental lines and hybrid generations.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Number plants</th>
<th>Number resistant</th>
<th>Number susceptible</th>
<th>Calculated ratio</th>
<th>P from $X^2*$ lies between</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_1$ (Santanka)</td>
<td>75</td>
<td>75</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_2$ (Truhart)</td>
<td>62</td>
<td>0</td>
<td>62</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_1 (S \times T)$</td>
<td>70</td>
<td>0</td>
<td>70</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_2$</td>
<td>330</td>
<td>78</td>
<td>252</td>
<td>3:1</td>
<td>.70-.50</td>
</tr>
<tr>
<td>$F_3 (G52.1)**</td>
<td>80</td>
<td>80</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_3 (G52.2)$</td>
<td>65</td>
<td>18</td>
<td>47</td>
<td>3:1</td>
<td>.70-.50</td>
</tr>
<tr>
<td>$F_3 (G52.3)$</td>
<td>78</td>
<td>78</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_3 (G52.4)$</td>
<td>64</td>
<td>64</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_3 (G52.5)$</td>
<td>82</td>
<td>22</td>
<td>60</td>
<td>3:1</td>
<td>.70-.50</td>
</tr>
<tr>
<td>$F_3 (G52.6)$</td>
<td>75</td>
<td>17</td>
<td>58</td>
<td>3:1</td>
<td>.80-.70</td>
</tr>
<tr>
<td>$F_3 (G52.7)**</td>
<td>77</td>
<td>0</td>
<td>77</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$F_3 (G52.8)$</td>
<td>63</td>
<td>0</td>
<td>63</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*$X^2 = 3.841, df = 1, P = .05.$

**$F_3 (G52.1)$, $F_3 (G52.3)$, and $F_3 (G52.4)$ were resistant in the $F_2$ generation.**

***$F_3 (G52.2)$, $F_3 (G52.5)$, $F_3 (G52.6)$, $F_3 (G52.7)$ and $F_3 (G52.8)$ were susceptible in $F_2$ generation.**

The segregating $F_2$ sample of 330 individuals when classified was found to fit a ratio of three-fourths susceptible and one-fourth resistant. A study of various $F_3$ families from this cross offers interesting support for an explanation of the inheritance of resistance. The three $F_3$ families that were segregating fit a three susceptible to one resistant ratio. It is apparent from these data that resistance was inherited as a monogenic, recessive character. It may be observed in Table 13 that three $F_3$ families were homozygous resistant. These $F_3$ families were progenies from three $F_2$ plants that were phenotypically resistant.
DISCUSSION

An experiment was outlined with two varieties of pepper which involved controlled self- and cross-pollinations so that reliable data could be collected for classification and interpretation. Data concerning the phenomena under investigation were obtained by observing the segregation of certain characters under controlled conditions. Attention was given to a single character at a time and not to the plant as a whole in collecting the data.

Tentative assumptions or hypotheses were framed to account for the observed segregation of certain characters investigated. In some instances, the observed data were found to fit a specific gene model as monogenic inheritance. The ratios produced in the segregating populations were not exactly those expected for a specific gene model and the chi-square test was applied to determine if the observed sample in reality fits the assumed model.

The intermediate nature of the means in F₁ and F₂ generations for the quantitative character, plant height, indicated that the expression of this character was the result of polymeric genes. Three pairs of polymeric genes (duplicate, cumulative, non-dominant) were assumed and the results of comparing the F₂ generation with (a ≠ b)⁶ support this assumption. Other similar cases of inherit-
ance have been explained by assuming the presence of polymeric genes, such as in DeHaan's (6) report that plant height in peas is determined by three pairs of genes.

Pungency, small stem diameter, pendent fruit habit, and susceptibility to *Xanthomonas vesicatoria* (Doidge) Dows. were all demonstrated to be segregating with a ratio of three to one in this material. A chi-square test for goodness of fit was applied to data for these characters and it was concluded that they were inherited as monogenic, dominant characters.

A chemical test for classifying segregating pepper generations for pungency was found to be superior to the organoleptic method. A search of the literature did not reveal to the writer any other report of a segregating generation of pepper being classified for pungency by a chemical test. The intermediate Wiley Mill was found to expedite the preparing of the samples of plant tissue for extraction. Twenty samples could be prepared in one hour with the mill, whereas only ten samples could be ground by the mortar in one hour.

Other workers reported it was rather difficult to classify some plants for fruit position, because certain plants with large fruits apparently produced fruits in a semi-erect position. In order to overcome this difficulty, observations were made at first grand fruit set and again when fruits were harvested.
Individuals appeared that exceeded both parental lines for fruit length, therefore, types as long as the commercial variety can be recovered in the hybrid generations.

In the F₂ generation no plants produced fruits as wide as Truhart Perfection, the large parent.

Loose linkage between pungency and erect fruit position was established from F₂ data. The high crossover value indicated that the genes controlling pungency and erect fruit position were located on the same chromosome but were not close together on the chromosome. A knowledge of linkage between specific characters in pepper will aid in the mapping of the genes on the chromosomes.

Using Snedecor's (33) approach the data of the segregating F₂ generation for fruit shape and fruit wall thickness were plotted on semi-logarithmic or ratio paper and the distributions were found to follow the exponential growth process. With this type distribution the effects of the genes for fruit shape and fruit wall thickness are multiplicative and the same gene may not have the same effect in every individual. This may be caused either by the effect of a gene being smaller, the greater the number acting in the same direction or by the effect being larger, the greater the number acting in the same direction.
The chi-square test of significance, in the case of the fruit shape indices, should not be too strongly emphasized. The deviations from the expected ratios depend much upon the partitioning of numbers in classes, which are not too well defined in Figure 7.

Differences have been reported in the relative susceptibility of varieties and strains of pepper to bacterial spot, but no systematic approach has been attempted to determine the actual mode of inheritance. None of the workers reporting the differences in susceptibility have attempted to classify segregating populations and to determine inheritance of resistance by crosses of a resistant with a susceptible variety.

Two $F_3$ families were homozygous for bacterial spot resistance. By hybridizing a resistant variety with a susceptible one, a homozygous resistant individual was obtained in the segregating population. Inoculation of seedlings in the greenhouse gives the plant breeder an opportunity to select resistant plants from large segregating populations. The selected individuals could then be transplanted to the field for further selection of desirable horticultural plant and fruit characters. There would be no necessity, when using this procedure, for growing large populations in the field for disease selection.
The recovery of plants with desirable plant and fruit characters in the segregating generations was found to be much more difficult than obtaining disease resistant individuals. The backcross method of breeding appears to be the best system to use for transferring bacterial spot resistance to Truhart Perfection, the commercial variety. There are two systems that might be followed; namely, (1) Repeated consecutive backcrossing, then self and select in advance generations for plants with disease resistance and other desirable characters. (2) Select resistant plants in the F_2 generation by inoculation of seedlings in the greenhouse and backcross to Truhart. Continue selfing alternate generations and backcrossing to Truhart Perfection.

Selfing of alternate generations would probably require more generations for developing an improved disease resistant type, but fewer controlled backcrosses would be needed; because only homozygous resistant hybrids would be backcrossed to Truhart Perfection.

Information from this study should give the practical plant breeder a knowledge of what he can expect when two types of peppers with different plant and fruit characters are hybridized. A systematic program can be developed for combining in a single variety the desirable characters of
two or more lines, species, or varieties. This work is considered to be of an interim nature and more will be learned about the genetics of pepper as other cases of linkage are established and the modes of inheritance of specific characters are determined. In the future, the genetics of *Capsicum frutescens* L. might be as well understood as the genetics of corn or Drosophila.
SUMMARY

Two varieties of red pepper (*Capsicum frutescens* L.) were used as parents for this study. The parental lines were self-fertilized three times before controlled crosses were made. Observations were made on the first, second and third filial generations. Photographic evidence is presented to show segregation of several characters investigated.

1. For the quantitative character, plant height, the $F_1$ and $F_2$ means were intermediate between the two parents. Results of comparing the $F_2$ generation with expansion of the binomial $(a/b)^6$ favor the hypothesis that three pairs of polymeric genes were involved in the inheritance of plant height for this cross.

2. In the study of stem diameter, the $P_1$ (17.3 mm.) was dominant to $P_2$ (26.7 mm.). It was concluded that the segregation of this character fits a monogenic hypothesis.

3. Segregation for fruit length and width was given. Transgressive segregation was reported for fruit length with some individuals that were smaller and some larger than either parent. For width, the small parent ($P_1$) was recovered but the larger ($P_2$) was not recovered in the $F_2$ generation. The trimodal nature of the curve for the distribution of the $F_2$ generation for fruit shape indices, when plotted logarithmically, revealed that shape was controlled by one gene pair with incomplete dominance.
4. It is obvious from Figure 9 that the segregating second filial generation for fruit wall thickness did not follow an arithmetic scale, but when plotted in classes which were logarithmically equal and assuming eight pairs of genes, a more nearly symmetrical curve resulted. These data revealed that eight pairs of genes with multiplicative, cumulative effects were operating to determine fruit wall thickness in this material.

5. A chemical test was used to classify population samples of the parental lines, the first, second, and third filial generations for pungency. The results of this investigation concurred with the hypothesis that pungency is inherited as a monogenic, dominant character.

6. The erect fruit habit was recessive to pendent fruit position. Linkage was established from F$_2$ data between the two characters, pungency and fruit position. Loose linkage was indicated by the high crossover value of 0.3443 ± 0.0387.

7. Sample populations of the parents, the F$_1$, F$_2$, and F$_3$ generations were observed for resistance to *Xanthomonas vesicatoria* (Doidge) Dows, with artificial inoculation under controlled conditions in the greenhouse. Resistance was demonstrated to be recessive and segregation in the F$_2$ was three susceptible to one resistant.
Homozygous resistant lines were recovered in the third filial generation from plants that were phenotypically resistant in the second filial generation. It is of interest from a plant breeding viewpoint to know that types resistant to bacterial spot organism were readily developed from crosses between susceptible and resistant peppers.

8. In general, it may be stated that the inheritance of the vegetative characteristics, plant height and stem diameter, was less complex than the inheritance of fruit length, width, shape, and fruit wall thickness where the development of a reproductive organ is involved.
LITERATURE CITED


BIBLIOGRAPHY


(7) ________. An Improved Method of Estimating the Number of Genetic Factors Concerned in cases of Blending Inheritance. Science 54., (1921), p. 223.


(44) _Polygenic Inheritance and Natural Selection_. Biol. Rev. 18 (1943), pp. 32-64.


AUTOBIOGRAPHY

I, Alvin Hugh Dempsey, was born in Butts County, Georgia, February 17, 1920. I received my secondary school education in the public schools of Butts County, Georgia. My undergraduate training was obtained at the University of Georgia, Athens, Georgia, from which I received the degree Bachelor of Science in Agriculture in 1942. My education and training were interrupted during World War II. From January 1943 to April 1946, I served as an officer in the Mechanized Calvary of the United States Army. Overseas duty was spent in the European Theater Operation. In 1946, I returned to the University of Georgia from which I received the degree Master of Science in Agriculture in 1947. While at that institution, I served as a graduate assistant for two years. During 1946-47 I acted in the capacity of assistant to Dr. Julian H. Miller. In January 1948 I received the appointment of Assistant Horticulturist at the Georgia Experiment Station. I was promoted to Associate Horticulturist in July 1949 and held this position until December 1949, at which time I was given a leave of absence to do graduate work in the Department of Horticulture at The Ohio State University. After completion of the course work, I returned to the Georgia Experiment Station and resumed my duties in the Horticulture Department while completing the requirements for the degree Doctor of Philosophy.