LINKAGE OF FRUIT SHAPE AND COLOR GENES IN CAPSICUM

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Received July 9, 1958

In the course of some research on peppers, Capsicum annum (Smith and Heiser 1951), conducted at the Citrus Experiment Station, Riverside, California, several striking, heritable fruit characters were noted. Upon further analysis, a chromosome linkage was found to exist between two immature-fruit color genes and a gene determining pepper fruit shape. In addition the fruit shape difference between the two varieties tested was found to be due to a single gene difference.

MATERIALS AND METHODS

Parent 238 was obtained from Dr. P. G. Smith of the University of California at Davis. Parents 254 and 256 are Bureau of Plant Introduction accessions No. 203, 522 and 203, 524 respectively. The Floral Gem parent was obtained from Clarence Brown of San Juan Capistrano, California. Each line used in this study was uniform and this suggests a high degree of homozygosity.

The shape of ripe fruit was measured with a millimeter-ruled pair of calipers and recordings were made to the nearest millimeter. Length is measured as the linear distance from the ovary-style fusion to the ovary base (with the receptacle removed). This is called the polar diameter. The equatorial diameter is the maximum width of the ovary. The shape index is calculated by dividing the polar diameter by the equatorial diameter. For isodiametric or round fruit the shape index is one; for elongate fruit, it is more than one.

Measurements were made of ten pepper fruits from each plant, the shape index computed for each fruit, and a mean shape index obtained for each plant.

Description of parents, F₁, F₂, and backcross progeny

There are three different parents involved in the crosses that are analyzed in this report.

Parent 238: The foliage, stems, flowers and immature fruit of these plants are dark purple. This purple anthocyanin color in the fruit results from exposure to the sun, and unexposed areas such as the tissue beneath the receptacle at the basal end of the fruit are green: purple is epistatic to green in sun exposed areas. Mature fruit color is red. From the measurement of the fruit of two plants, fruit size was found to be uniform: the mean length was 1.21 ± .09 cm and width, 1.18 ± .34 cm. The fruit shape index is 1.06 ± .02 which is indicative of nearly
isodiametric fruit. Fruits of the 238 and Floral Gem parents, the \( F_1 \) and \( F_2 \) progeny, are shown in Figure 1.

*Parent 256* is similar to 238 in the purple coloration of foliage, stem, flower and fruit, but the tissue unexposed to the sun is yellow-green. Mature fruit color is

**Figure 1.**—Fruit of parents—Floral Gem and 238 (small purple). The \( F_1 \). On the bottom line, selfed progeny including parental and recombinant types—from left to right, purple round, purple long, nonpurple round, and nonpurple long.
red. Fruit size is uniform and measurement of the fruit of two plants gave an average length of 1.25 ± .11 cm and a width of 1.30 ± .23 cm. The shape index is .96 ± .02: this fruit is more oblate. Parent 254 is also purple and is similar to 256 except in fruit shape. The fruit of 254 is elongate. Purple fruit color in these purple families is associated with purple flower color (petals, style, filament and anthers). Some observed exceptions such as nonpurple style color could not be confirmed with F₁ tests.

The Floral Gem Parent has light green foliage and stems. The flowers have white petals, colorless filaments and styles and light blue anthers. The fruit is yellow when immature but turns red upon maturation. The fruit averaged 5.23 ± .51 cm in length and 2.44 ± .26 cm in width. Although fruit size was variable, the shape index was uniform, averaging 2.14 ± .08 which was twice that of either of the purple parents.

The F₁ generation: The F₁ plants from crosses of Floral Gem with parent 238 are lighter purple than parent 238 plants, but the F₁ fruit is a dark purple like the fruit of parent 238. Fruit size in the F₁ is intermediate between the two parents. (In this paper fruit size will not be evaluated.) The shape index of the F₁ fruit (from this Floral Gem × 238 cross) is uniform and averages 1.28 ± .22. The nonpurple immature fruit color is green.

The fruit of the F₁ from the Floral Gem × 256 cross is more spherical with the shape index averaging 1.22 ± .22. The nonpurple immature fruit color in plants resulting from this cross is yellow-green. The purple coloration of fruit and foliage is similar to that found in the F₁ plants of the 238 × Floral Gem cross except that the seedlings in this case are green.

The backcross and F₂ generations

Inheritance of purple and nonpurple fruit color: Ikeno (1913) observed many different shades of purple plant coloration in the F₂ of the cross—purple by non-purple. By combining all purples, he obtained a 3 purple:1 nonpurple F₂ ratio and postulated a monofactorial difference in purple color inheritance. Although Deshpande (1933) also observed a 3 purple:1 nonpurple F₂ ratio in a purple by nonpurple cross, he postulated the presence of a second locus to account for the various grades of purple.

A similarly wide range of purple coloration was noted in the foliage of the F₂ progeny of crosses of Floral Gem × 238 and 256. In fruit color classification, however, there is a clear and nonintergrading distinction between purple and nonpurple. In using only fruit color as an indicator of the purple gene, an F₂ ratio of 3 purple:1 nonpurple is obtained and a 1 purple:1 nonpurple ratio results from the testcross of the F₁ with Floral Gem (Table 1). (According to Deshpande, the purple gene is designated A. AA and Aa fruit are purple and aa, nonpurple).

Inheritance of green and yellow immature fruit color: Odland and Porter (1938) observed a 15 green (various shades):1 sulphur-white ratio in the F₂ of a cross between the varieties Ornamental (sulphur-white) and Oshkosh (cedar-green). They concluded that two pairs of alleles conditioned immature fruit color
TABLE 1

Segregating progeny from the cross AO/ao × ao/ao

<table>
<thead>
<tr>
<th>Origin of AO chromosome</th>
<th>AO</th>
<th>Ao</th>
<th>ao</th>
<th>Total</th>
<th>Percent recombination</th>
</tr>
</thead>
<tbody>
<tr>
<td>238</td>
<td>138</td>
<td>5</td>
<td>13</td>
<td>120</td>
<td>276</td>
</tr>
<tr>
<td>256</td>
<td>112</td>
<td>7</td>
<td>10</td>
<td>129</td>
<td>258</td>
</tr>
<tr>
<td>Total</td>
<td>250</td>
<td>12</td>
<td>23</td>
<td>249</td>
<td>534</td>
</tr>
</tbody>
</table>

Testcross segregation—\(A = 262, a = 273, O = 273, o = 264\).

Table 2

Segregating progeny from the cross AG\(_1\)/ag\(_1\) × ag\(_1\)/ag\(_1\)

<table>
<thead>
<tr>
<th>Origin of AG(_1) chromosome</th>
<th>AG(_1)</th>
<th>ag(_1)</th>
<th>aG(_1)</th>
<th>ag(_1)</th>
<th>Total</th>
<th>Percent recombination</th>
</tr>
</thead>
<tbody>
<tr>
<td>254</td>
<td>61</td>
<td>10</td>
<td>18</td>
<td>66</td>
<td>155</td>
<td>. . .</td>
</tr>
<tr>
<td>256</td>
<td>49</td>
<td>11</td>
<td>19</td>
<td>47</td>
<td>126</td>
<td>. . .</td>
</tr>
<tr>
<td>Total</td>
<td>110</td>
<td>21</td>
<td>37</td>
<td>113</td>
<td>281</td>
<td>20.64</td>
</tr>
</tbody>
</table>

Testcross segregation—\(A = 131, a = 150, G_1 = 147, g_1 = 134\).

in this cross: \(G_1G_2g_2g_2\) represents cedar-green, \(G_1G_2g_2g_2\) and \(g_1g_1G_2G_2\), lettuce-green, and \(g_1g_1g_1g_1\), sulphur-white.

In the backcross of the yellow-green \(F_1\) (256 × Floral Gem) by Floral Gem a 1 yellow-green:1 yellow ratio is obtained (Table 2). (In these crosses no distinction was made between yellow and sulphur-white: the yellow-green type is distinctive). Further backcrosses of yellow-green by yellow give a similar 1 yellow-green:1 yellow ratio.

The \(F_2\) fruit from the Floral Gem by 238 cross is green but in further test-crossing with Floral Gem, a yellow-green type was isolated. In testcrosses of this yellow-green fruit type by Floral Gem a 1 yellow-green:1 yellow ratio was obtained (Tables 2 and 3). The 1 yellow-green:1 yellow testcross ratio indicates that the yellow-green fruit are heterozygous for one of the \(G\) loci and can therefore be designated \(G_1g_1g_1g_1\). With reference to Odland and Porter's symbols for green and yellow fruit color inheritance, the 256 parent is \(G_1g_1g_2g_2\), parent 238 is \(G_1G_2G_2G_2\) and the Floral Gem parent is \(g_1g_1g_1g_1\). The yellow-green fruit color results from the segregation of \(G_1\) or \(G_2\) in the \(G_1G_2g_2g_2\) × \(g_1g_1g_1g_1\) testcrosses.

Round and elongate shape: In a cross between round (oblate) and elongate fruit type, Kaiser (1935) observed a monofactorial segregation for fruit shape in the \(F_2\). Khambananda also postulated a major gene for fruit shape based on trimodal logarithmic distributions. In these two cases incomplete dominance of
the oblate type results in a distinction between the oblate homozygote, OO, the heterozygote, Oo, and the elongate, oo.

In all the crosses between the purple and Floral Gem parents which this author has observed, there are two and only two shapes segregating (Figures 1 and 2). The round have a shape index of approximately 1 and the elongate, which are twice as long as wide, have a shape index of 2 (Figure 3). In the F_2 of the 238 × Floral Gem cross, a 3 round:1 elongate ratio is observed (Figure 3 D). In the backcross of the F_1 to the Floral Gem parent, a 1 round:1 elongate ratio results among the testcross progeny (Table 2). In both the F_2 and testcross progenies the two classes are distinct and nonoverlapping (Figure 3 E). In this case, therefore, a major gene, O (round), is completely dominant to its recessive allele, o (elongate). (The round fruit shape is designated OO or Oo and the elongate as oo).

The slight differences between the fruit shape indices of the purple parents, 238 and 256, are also evident among their testcross progeny. (Figures 3A and 3C versus Figure 3F).

From the above data it is therefore possible to represent the genotypes of the four parents under consideration as follows: 238—AAOG,G,G,G, 256—

<table>
<thead>
<tr>
<th>Origin of O chromosome</th>
<th>OG,</th>
<th>Og,</th>
<th>og,</th>
<th>Total</th>
<th>Percent recombination</th>
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<tbody>
<tr>
<td>256</td>
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<td>15</td>
<td>19</td>
<td>79</td>
<td>198</td>
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</table>

Testcross segregation—O = 100, o = 98, G = 104, g = 94.

<table>
<thead>
<tr>
<th>Origin of AOG chromosome</th>
<th>AOG,</th>
<th>AOG,</th>
<th>AOG,</th>
<th>AOG,</th>
<th>AOG,</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>238</td>
<td>85</td>
<td>10</td>
<td>1</td>
<td>3</td>
<td>10</td>
<td>24</td>
</tr>
<tr>
<td>256</td>
<td>34</td>
<td>7</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>Total</td>
<td>119</td>
<td>17</td>
<td>2</td>
<td>5</td>
<td>11</td>
<td>33</td>
</tr>
</tbody>
</table>

Recombination—A = 143, a = 153, G = 152, g = 144, G = 152, g = 131,

Testcross segregation—A = 143, a = 153, G = 152, g = 131.

<table>
<thead>
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<th>Percent</th>
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</table>

### TABLE 3

**Segregating progeny from the cross**

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<th>Linkage between O and G</th>
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<tr>
<td>Origin of O chromosome</td>
</tr>
<tr>
<td>------------------------</td>
</tr>
<tr>
<td>256</td>
</tr>
</tbody>
</table>

Testcross segregation—O = 100, o = 98, G = 104, g = 94.

### TABLE 4

**Segregating progeny from three point linkage test in cross**

<table>
<thead>
<tr>
<th>Origin of AOG chromosome</th>
<th>AOG,</th>
<th>AOG,</th>
<th>AOG,</th>
<th>AOG,</th>
<th>AOG,</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>238</td>
<td>85</td>
<td>10</td>
<td>1</td>
<td>3</td>
<td>10</td>
<td>24</td>
</tr>
<tr>
<td>256</td>
<td>34</td>
<td>7</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>Total</td>
<td>119</td>
<td>17</td>
<td>2</td>
<td>5</td>
<td>11</td>
<td>33</td>
</tr>
</tbody>
</table>

Recombination—A = 143, a = 153, G = 152, g = 131,

Testcross segregation—A = 143, a = 153, G = 152, g = 131.

| Percent | 19.25 |
FIGURE 2.—Testcross progeny of Floral Gem and 256. First and second row—parental types. Top row—purple round AO/ao; second row—nonpurple long ao/ao. Third row— the recombinants nonpurple round and purple long. In the second row three yellow-green and one yellow (on the right). Third row left to right, round, yellow and round, yellow-green.
Figure 3.—Frequency distribution of fruit shape indices of parents (A), F₁ (B), progeny of testcross Oo × oo (C), testcross progeny of a selected Oo (D) and a self of Oo (E) from the original cross of 238 × Floral Gem (FG). In (F), testcross progeny from 256 × Floral Gem. Each value represents the average shape index of ten fruits from a plant.

**Linkage of loci A, 0, and G₁**

A and 0: In the analysis of testcross progeny of the two different purple F₁'s (256 × Floral Gem and 238 × Floral Gem) by Floral Gem, it was observed that with some exception all the round fruit are purple and all the elongate fruit are nonpurple. Pooled data from numerous testcross progenies are presented in Table 1 (all crosses are in coupling). The two loci A and 0 are linked and 6.5 percent crossing over occurs between them. The segregation of purple vs. nonpurple and round vs. elongate is clearly monofactorial.

A and G₁: It was also observed that most of the nonpurple fruit are yellow and most of the purple fruit are yellow-green. Pooled data, including other purple parents that did not have the 0 gene, are presented in Table 2. A and G₁ are linked and 20.64 percent crossing over occurs between them.

0 and G₁: Using the round, nonpurple recombinant, OG₁/oG₁, obtained in the testcross progeny as well as A0G₁/a0G₁, it was found that the percent of recombination between 0 and G₁ is 18.8 percent (Table 3). These data indicate that A, 0, and G₁ are on the same chromosome and in this linear order.

Further verification of this linkage order was obtained from three point testcross data (Table 4). These tests clearly show the order of genes to be A·0·G₁, and the provisional map of this chromosome is as follows:

![](https://example.com/chromosome_map.png)

**DISCUSSION**

The most intensive analysis of genetic characters in Capsicum was made by Deshpande (1933). He postulated three instances of linkage all of which seem questionable. He calculated 44 percent crossing over between the A (purple immature fruit) and R (red mature fruit) genes. This result, however, was obtained from F₂ data and could easily represent the expected frequency based upon independent assortment. (In the author’s experiments to test A·0·G₁ linkage with other genes, the R gene appears to be independent.) In Deshpande's second case of linkage, also obtained from F₂ progeny, three percent crossing over was postulated between the genes for thick fruit base and calyx not enclosing the fruit base. It is more likely that these two characteristics are interdependent one upon the other. The third case involved the genes for fruit length and fruit position. Fruit length, however, did not segregate as a single gene. Moreover, it is possible that the longer fruit becomes pendent as a consequence of increased length while the
shorter fruit remains erect. DESHPANDE also indicated that shorter fruit are more often associated with purple color. He did not, however, give any linkage data on this nor did he consider shape. (This does agree, however, with the linkage reported here in that the longer fruit, those with a shape index of 2, are non-purple).

HOLMES (1934) found no linkage between the \( L \) gene (localized necrosis to tobacco mosaic virus) and six other genes including \( A \) (purple), \( R \) (red mature fruit), \( S \) (smooth stem), \( D \) (pointed apex), \( P \) (pendent fruit position), and \( M \) (pungent fruit). HAGIWARA and OOMURA (1947) observed 20 to 24 percent recombination between the genes for purple style and purple pistil and approximately 15 percent recombination between pendent peduncle and a gene for variegated leaf.

\[ \text{Control of fruit shape} \]

In this paper a major dominant gene that controls fruit shape in peppers is described. This evidence is derived from an analysis of \( F_2 \) and testcross progenies. In these progenies the fruit shape indices are distinct and nonoverlapping (Figure 3 C,D,E,F). In the testcross \((00 \times oo)\) progenies the heterozygotes are round with a shape index of approximately 1 and the homozygous recessives are elongate with a shape index of approximately 2. In the selfed progeny the homozygotes \((OO)\) and heterozygotes \((Oo)\) are round and their shape index is approximately 1 (Figure 3 E). This similarity between \(OO\) and \(Oo\) in the shape index analysis of \(F_2\) progenies indicates that the \(O\) allele is completely dominant.

Such a gene controlling fruit shape in peppers was hypothesized by KAISER (1935) and KHAMBONANDA (1950). In their studies, however, trimodal curves of \(F_2\) populations indicated only partial dominance of the oblate type. (It is not known whether the \(O\) gene of the crosses discussed in this paper is similar to the shape controlling gene described by KAISER and KHAMBONANDA).

Although a single gene that determines fruit shape is demonstrated in the crosses reported here, there appear to be other genes which also govern fruit shape. This is evident in studying backcross progeny of crosses of the 238 parent with longer fruited types (shape index = +4). These result in progeny of intermediate fruit shape and in addition the backcross progeny segregate less sharply. Similar results were obtained by DALE (1929). His data show a continuous distribution among the progeny of peppers with parents of very dissimilar fruit types, and he concluded therefore that fruit length inheritance is based on genes with proportionate effects. (In DALE's crosses, the extremes between the parents probably represent more than one gene difference).

The difference in shape index between the 238 and 256 parental types and the distribution of shape indices in their progeny (Figure 3 C, F) is due to segregating modifiers and not to a difference in the particular alleles of the original parents. This conclusion is based on a study of a derivative of the backcross progeny of the 238 allele. After two successive backcrosses, the segregation of round and elongate types is sharper and, as the curves (Figure 3 D) indicate, there is a definite shift to the left resulting in a curve similar to that derived from
the progeny of the 256 allele. This probably results from the segregation of modifiers that cause elongation of the fruit.

A number of cases have been reported of genes governing fruit shape in other plants. Sinnott (1927) found that two pairs of alleles differentiate the disk from the elongate fruit type in Cucurbita. In Lycopersicum, Lindstrom (1927) analyzed a major incompletely dominant gene controlling fruit shape. In Solanum melongena, Gotoh (1954) hypothesized that major genes control fruit shape.

The control of shape in terms of gene action was considered by Sinnott (1935) and Kaiser (1935) working with the squash and pepper, respectively. They concluded that shape differences result from differences in genes which control the relative rates of growth between the polar and equatorial dimensions. This conclusion was based on data which showed a sharper segregation of shape indices than of dimensional traits among F2 progeny. Although a clear bimodality was evident for length in both the squash and pepper, the segregation was not so sharp as for shape. A smooth curve was obtained for width. From this the authors concluded that there is a gene governing shape and that therefore there is no direct genic control upon individual dimensions (length and width). They further concluded that any apparent segregation for length was the indirect result of "interactions between genes controlling dimensional relationships". (Kaiser 1935).

In the studies reported here the lengths and widths of the two genotypes, Oo (round), and oo (elongate) from the cross Oo × oo, are plotted and analyzed separately. Using this type of analysis, there is observed a distinct though slightly overlapping segregation for the fruit lengths of the two fruit types (Figure 4). This difference between the mean lengths of the elongate and round fruit is highly significant—P = < .01 (Table 5). The widths of the elongate and round fruit overlap to a considerable extent. The difference between the means of the two fruit widths, however, is significant—P = < .05 (Table 6). There is evident also a negative correlation between length and width in the backcross progeny. This would be expected since the elongate fruit becomes narrower as it elongates while the width of the round fruit remains unaffected. (Sinnott 1935, found a similar negative correlation between length and width among the F2 progeny of

<table>
<thead>
<tr>
<th>TABLE 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean lengths and variances of round and elongate fruit from the cross Oo × oo</td>
</tr>
<tr>
<td>---------------------------------</td>
</tr>
<tr>
<td>n</td>
</tr>
<tr>
<td>Round Oo</td>
</tr>
<tr>
<td>Elongate oo</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>pooled variance</td>
</tr>
<tr>
<td>s (X₁ - X₂)</td>
</tr>
<tr>
<td>t</td>
</tr>
</tbody>
</table>

* Significantly different from 0 cm difference. P = < .01.
squashes.) Therefore a change in shape can be explained by postulating a change in length which causes a coincident change in width. Such is the case with a rubber band: if stretched, the width coincidentally narrows. Thus only a single action is necessary to cause such a difference in shape.

From these results—the clear segregation for fruit length and the negative
correlation between length and width—it is postulated that the factor controlling linear dimension is the major influence in governing shape. On this basis, the O gene controls shape by controlling length.

This is opposed to Sinnott’s and Kaiser’s views on shape control which are based upon the belief that shape is controlled by genes which coordinate many pathways of growth. Such a multifunctional role for genes is not consistent with present day views which hypothesize that genes control single steps and one action (Horowitz 1956; Horowitz and Fling 1956).

Sinnott (1931) also established that size of fruit is independent of shape. This is evident in the pepper crosses reported here. Although the size of the round fruit of the backcross progeny is nearly double the fruit size of parent 238 (Figure 1) the shape index of 1 is maintained in the presence of the O gene.

In all these cases (tomato, squash, eggplant and pepper) it is the dominant alleles that tend to flatten the fruit while elongate fruit develop in the presence of the recessive alleles.

**SUMMARY**

1. Linkage of three loci in peppers is here reported. These include the genes A (purple versus nonpurple immature fruit color), O (round versus elongate fruit shape) and G, (yellow-green versus yellow immature fruit color). The linear order and the map distances of the genes is as follows: A—6.5—O—18.8—G,

2. Among the progeny of selfed and testcrossed heterozygotes, Oo, the two fruit shapes—round and elongate—are distinct and nonintergrading.

3. The O gene governing fruit shape is completely dominant.

4. Although the O gene is completely dominant, other genetic modifiers also govern fruit shape.

5. The O gene controls shape independent of size.

6. Fruit shape is postulated to depend primarily on fruit length.

7. The role of genes in the control of shape is discussed.
LITERATURE CITED


