JOURNAL OF AGRICULTURAL RESEARCH

CONTENTS

Sesquidiploid F$_1$ Hybrids of Lycopersicon esculentum and L. Peruvianum (Key No. G-1393) ........................................ 33
G. W. BOHN

Seasonal Variations of Carotene and Other Nutritionally Important Constituents in the Two Pasture Grasses Dallis and Carpet (Key No. La.-7) ........................................ 55
J. R. KUPPERS, L. L. RUSOFF, and D. M. SEATH
Articles for publication in the Journal must bear the formal approval of the chief of the department bureau, or of the director of the experiment station from which the paper emanates. Each manuscript must be accompanied by a statement that it has been read and approved by one or more persons (named) familiar with the subject. The data as represented by tables, graphs, summaries, and conclusions must be approved from the statistical viewpoint by someone (named) competent to judge. All computations should be verified.

Station manuscripts and correspondence concerning them should be addressed to V. R. Gardner, Director, Michigan Agricultural Experiment Station, East Lansing, Mich., who is chairman of the Station subcommittee.

Published with the approval of the Director of the Budget. Issued on the 1st and 15th of each month. This volume will consist of 12 numbers and the contents and index.

Subscription price:
Entire Journal: Domestic, $2.25 a year (2 volumes)
Foreign, $3.00 a year (2 volumes)
Single numbers: Domestic, 10 cents
Foreign, 15 cents

Articles appearing in the Journal are printed separately and can be obtained by purchase at varying prices depending on their size. When purchased in quantity of 100 or more, a reduction of 25 percent in the cost will be made. If separates are desired in quantity, they should be ordered at the time the manuscript is sent to the printer. Address all correspondence regarding subscriptions and purchase of numbers and separates to the Superintendent of Documents, Government Printing Office, Washington 25, D. C.
SESQUIDIPLOID F₁ HYBRIDS OF LYCOPERSICON ESCULENTUM AND L. PERUVIANUM ¹

By G. W. Bohn ²

INTRODUCTION

Lycopersicon peruvianum (L.) Mill., a green-fruited wild tomato from South America, possesses several characters that would be valuable if they could be incorporated into tomato stocks possessing cultural size and quality. The determination of mosaic严密性 in a collection of L. peruvianum var. dentatum Dun. (L. chilense Dun.) and the successful hybridization of this collection with L. esculentum Mill. by Holmes (8, 9) ⁴ stimulated interest in this species as a potential source of desirable economic characters. Virgin (25), Blood (8), and others reported collections of L. peruvianum to be resistant to curly top, and Wright and Lincoln (28) and others found some collections to be resistant to defoliation diseases. Bailey (2) and others reported nematode resistance in this species. Alexander, Lincoln, and Wright ⁵ surveyed this and other species in the genus Lycopersicon for reactions to several tomato diseases. Smith (23) and others reported that some collections of L. peruvianum are resistant to spotted wilt. Reynard and Kanapaux (21) and Lincoln and others (12) stated that this species contains considerably more ascorbic acid than does L. esculentum. Yeager and Purinton (30) recently reported high ascorbic acid content in lines derived from a cross between L. esculentum and L. peruvianum.

Observations on natural infestations among mixed species plantings at Cheyenne, Wyo., indicated that, like the commercial tomato, Lycopersicon peruvianum is attacked by tomato psyllids (Paratrioza cockerelli (Sulc)) but, unlike the commercial tomato, it does not develop marked symptoms of psyllid yellows.

F₁ hybrids were obtained fairly readily from crosses of Lycopersicon esculentum with certain collections of L. peruvianum by Holmes (9),

¹ Received for publication October 7, 1947.
² Thanks are extended to Paul Hepler, formerly junior scientific aid, Division of Fruit and Vegetable Crops and Diseases, for able assistance with all phases of the experimental work in 1944 and 1945; to Paul Desjardins and Robert Hildreth, formerly junior scientific aids, who made the pollinations in 1946; and to Mary E. Riner, formerly scientific aid, who recorded the data in 1946.
³ The species name, unless stated otherwise, is used herein in its broad sense and includes the typical species and its varieties.
⁴ Italic numbers in parentheses refer to Literature Cited, p. 52.
Wright and Lincoln (28), Yeager and Hepler (29), Virgin (26), and Lesley and Lesley (11). Certain other collections of *L. peruvianum* did not respond to the usual techniques of hybridization. Cross-pollinations between *L. esculentum* and this type of *L. peruvianum* made by the writer at the University of Missouri, Columbia, Mo., in 1935 failed to produce seeded fruits, as did those of Lesley (10), MacArthur and Chiasson (15), and several other workers at various locations. Hybridization of *L. esculentum* with collections that do not cross readily is desired because such collections have factors for resistance that do not occur in those that do cross readily with *L. esculentum*.

V. R. Boswel suggested to the writer that hybrids between *Lycopersicon esculentum* and "difficult" collections of *L. peruvianum* might be obtained more readily at the Cheyenne Horticultural Field Station at Cheyenne, Wyo., than at other locations. The environmental conditions there are particularly favorable for fruit setting and seed production in the tomato (18). Since 1943, when these investigations were started, Smith (22) and McFarlane, Hartzler, and Frazier (16) have reported hybrids from crosses of "difficult" collections of *L. peruvianum* with *L. esculentum* by culturing young embryos from immature fruits on aseptic culture media. Porte and Walker (20) have obtained hybrids by using a small-fruited collection of *L. esculentum*, and Cooper and Brink (5) have obtained viable seeds from the cross tetraploid *L. pimpinellifolium* × diploid *L. peruvianum*. The results of the writer's experiments are reported herein.

**MATERIALS AND METHODS**

In preliminary experiments with diploids in 1943, two collections of *Lycopersicon peruvianum* (P. I. 126944 and P. I. 128645) that were known to cross with *L. esculentum* with difficulty or not at all were cross-pollinated reciprocally with several horticultural varieties of *L. esculentum* and with *L. pimpinellifolium* (Jusl.) Mill. P. I. 79532. Many fruits and a few abortive seeds, but no hybrid seedlings, were obtained. These data are not reported in detail. After the failure to obtain hybrids from cross-pollinations between diploid races, experiments were conducted with diploid and tetraploid races. The varieties Danmark (1) (early, determinate) and Waltham Forcing (5) (early, indeterminate) were used to represent *Lycopersicon esculentum* because they are prolific and early in pot cultures in the greenhouse at Cheyenne and would therefore yield more data per unit of space and per unit of time than other varieties. *L. peruvianum* P. I. 128645 was used in crosses with both of these horticultural varieties. Tetraploid seedlings of each of these three varieties were obtained from seeds soaked in colchicine solution as reported elsewhere (4).

---

6 Principal horticulturist, Division of Fruit and Vegetable Crops and Diseases.
7 P. I. is used herein to indicate plant introductions imported through the Division of Plant Exploration and Introduction or its precursors.
8 Received from H. L. Blood, formerly plant pathologist, Division of Fruit and Vegetable Crops and Diseases.
9 Bay State, Bonny Best, Bounty, Break o’Day, Danmark, Earliana, Globe, Oxheart, Ponderosa, and Waltham Forcing.
In 1943 and 1944 the plants were obtained directly from colchicine-treated or nontreated seeds. All plants from treated seeds that were used in the breeding work were identified as tetraploids by chromosome counts at meiosis in acetocarmine smears of pollen mother cells. Because the autotetraploids were readily identified by the gross morphological characters described by Winkler (27) and others, it was necessary to count the chromosomes only in plants actually used in the breeding work. Three plants of each variety from nontreated seeds were similarly identified as diploids. In 1943 only diploid races of *Lycopersicon esculentum* and diploid and tetraploid *L. peruvianum* were available. In the experiment conducted in the greenhouse during the winter of 1944, 30 tetraploid plants and 12 diploid plants of each variety of *L. esculentum* and of *L. peruvianum* were used.

For later experiments, conducted in the greenhouse in 1945 and 1946, seedlings from self-pollinated tetraploids and diploids of *Lycopersicon esculentum* and of *L. peruvianum* were used. Three or more plants of each line were verified as tetraploid or diploid by chromosome counts. In addition, a few plants of diploid and tetraploid *L. pimpinellifolium* P. I. 79532 and its diploid and amphidiploid (allotetraploid) \(^{11}\) hybrid with *L. esculentum* variety Marglobe were used in crosses with *L. peruvianum*. The tetraploids and amphidiploids were obtained from colchicine-treated seeds. These and the diploids were identified by chromosome counts. *L. pimpinellifolium* and its hybrid with *L. esculentum* were used to determine whether they might serve as bridges in the attempt to transfer chromosome material from *L. peruvianum* to *L. esculentum*.

A few plants were grown in the field, but most of them were grown in 2-gallon, glazed-stone jars or 7-inch clay pots of soil in the greenhouse. The plants cultured in the greenhouse were maintained in a vigorous condition by adding 100 ml. of a nutrient solution containing 200 p. p. m. of N and 100 p. p. m. each of P and K made from commercial ammonium sulfate, treble superphosphate, and potassium sulfate at approximately 10-day intervals.

In preliminary experiments in both the field and greenhouse pollinations were made on emasculated flowers (except those selfed) that were protected from contamination by foreign pollen with paper or cloth bags. In later experiments performed entirely in the greenhouse such contamination was controlled by other methods. The plants were sorted into groups according to use; the pistillate parents were separated from the staminate ones by space on the greenhouse bench. Some plants were used alternately as staminate and pistillate parents by transferring them from one group to the other. With a few exceptions (see p. 44) all flowers on the pistillate parents were emasculated on the day before normal anthesis. The success of this method of control was demonstrated by the very rare occurrence of contamination under conditions in which such contamination could be readily determined.

\(^{11}\) Although the tetraploid hybrid from *Lycopersicon esculentum* × *L. pimpinellifolium* produces progenies that segregate unit characters in ratios typical of autotetraploids, the present usage of species names is followed and the 48-chromosome hybrid is therefore considered to be an amphidiploid (allotetraploid) rather than a tetraploid (autotetraploid).
Figure 1.—Seed masses compressed in petri dishes to show the arbitrarily selected size classes of tomato ovules and seeds: A, Class 1, ovules barely or not at all enlarged; B, class 2, ovules slightly enlarged; C, class 3, ovules moderately enlarged; D, class 4, indicated by arrows, ovules much enlarged (poorly filled seeds); E and F, class 5, seeds large, plump. The larger seeds in D also belong to class 5. The actual crosses that were made to obtain the ovules and seeds shown were as follows: A, 2n L. esculentum ♀ × 4n L. esculentum ♂; B, 2n L. esculentum ♀ × 2n L. peruvianum ♂; C, 4n L. esculentum ♀ × 4n L. peruvianum ♂; D, 4n L. esculentum ♀ × 2n L. peruvianum ♂; E, 2n L. esculentum selfed; F, 4n L. esculentum selfed. × 5.4.
Pollen was collected on alcohol-cleaned, dry slides with the use of an electric vibrator and placed on the stigmas on the day anthesis would normally occur and again 2 days later. Some flowers were pollinated the day before and the day after anthesis. Usually two or three flowers but occasionally more were used on a single cluster; the unused flowers were removed before anthesis. Flowers on the staminate parents were self-pollinated at the time pollen was collected for the cross-pollinations.

To determine the relative sizes of ovules or seeds, the seed mass in each fruit was removed to the lid of a 90-mm. petri dish and the inverted dish was pressed against the seed mass to render the individual ovules or seeds readily visible. In most cases the ovules and seeds were grouped into the five arbitrary size classes shown in figure 1. The size classes shown were used for rating seed masses from fruits of diploid *Lycopersicon esculentum*. For rating seed masses from other pistillate parents, large seeds in fruits from self-pollinated flowers of the respective pistillate parents were considered to be size 5. The extra large, plump seeds from tetraploid *L. esculentum* selfed (fig. 1, F) were considered to be size class 5 for this pistillate parent.

**RESULTS**

Because similar results were obtained from all trials of any one type of cross-pollination that was repeated, the data from all experiments have been summarized (table 1) and are discussed together. The data in table 1 are grouped according to the chromosome complements of the plants crossed to agree with the sequence in the discussion. Although minor differences occurred, Danmark, Waltham Forcing, and other commercial varieties yielded similar results in all combinations; the data from them are therefore combined under *Lycopersicon esculentum*. This procedure necessitated the use of weighted averages for the fruit weights and average numbers of seeds in fruits. The weighted averages were obtained by using equal numbers of fruits of Danmark and Waltham Forcing as composite samples. Although size 5 seeds frequently produced larger percentages of seedlings than did size 4 seeds, the data on size 4 and size 5 seeds, including the average numbers in a fruit and the percentages that produced seedlings, were combined for brevity.

**SELF-POLLINATED DIPLOIDS**

Self-pollinated flowers of diploid races of *Lycopersicon esculentum*, *L. pimpinellifolium*, and their *F₁* hybrid set fruits with normal complements of well-developed seeds during both the summer and the winter (fig. 1, E, and table 1). The seed number in the hybrid was intermediate between the seed numbers in the parent species. Self-pollinated and naturally pollinated flowers of diploid *L. peruvianum* set fruits with normal complements of well-developed seeds during the summer, but they failed to set fruits or set fruits with few seeds during the winter (table 1). In addition to the results reported in table 1, 110 self-pollinated flowers on 6 plants produced 7 small, single-seeded fruits during the winter of 1943 and naturally pollinated flowers set no fruit. These results were obtained whether the flowers were pollinated first at anthesis or 1 or 2 days before anthesis.
<table>
<thead>
<tr>
<th>Type of cross and species of pistillate parent</th>
<th>Species of staminate parent</th>
<th>Season</th>
<th>Flowers pollinated</th>
<th>Flowers setting fruits</th>
<th>Average weight of fruits</th>
<th>Fruits with largest ovules or seeds as indicated</th>
<th>Average seeds per fruit, sizes 4 and 5</th>
<th>Seeds planted, sizes 4 and 5</th>
<th>Seeds producing seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Self-pollinated diploids:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>56</td>
<td>90</td>
<td>18.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>L. pinninellifolium</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>48</td>
<td>92</td>
<td>1.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>44</td>
</tr>
<tr>
<td>L. esculentum × L. pinninellifolium F&lt;sub&gt;1&lt;/sub&gt;</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>20</td>
<td>90</td>
<td>17.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>43</td>
<td>91</td>
<td>7.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>39</td>
</tr>
<tr>
<td>L. esculentum × L. pinninellifolium F&lt;sub&gt;1&lt;/sub&gt;</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>100</td>
<td>5</td>
<td>2.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>46</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>162</td>
<td>53</td>
<td>54.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>85</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>44</td>
<td>82</td>
<td>61.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>40</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>17</td>
<td>77</td>
<td>7.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>13</td>
</tr>
<tr>
<td>L. esculentum × L. pinninellifolium F&lt;sub&gt;1&lt;/sub&gt;</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>40</td>
<td>93</td>
<td>8.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>37</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>48</td>
<td>75</td>
<td>4.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>34</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>162</td>
<td>53</td>
<td>54.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>85</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>44</td>
<td>82</td>
<td>61.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>40</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>17</td>
<td>77</td>
<td>7.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>13</td>
</tr>
<tr>
<td>L. esculentum × L. pinninellifolium F&lt;sub&gt;1&lt;/sub&gt;</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>40</td>
<td>93</td>
<td>8.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>37</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. pinninellifolium</td>
<td>Winter</td>
<td>48</td>
<td>75</td>
<td>4.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>34</td>
</tr>
<tr>
<td>Diploids × diploids (interspecific):</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>20</td>
<td>100</td>
<td>55.1</td>
<td>1</td>
<td>10</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>66</td>
<td>92</td>
<td>61.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>48</td>
<td>92</td>
<td>61.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>48</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>35</td>
<td>91</td>
<td>4.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>35</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>14</td>
<td>91</td>
<td>4.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>33</td>
<td>91</td>
<td>4.8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>33</td>
</tr>
<tr>
<td>Tetraploids × tetraploids (interspecific):</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>127</td>
<td>80</td>
<td>48.1</td>
<td>0</td>
<td>18</td>
<td>81</td>
<td>1</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>9</td>
<td>90</td>
<td>61.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>12</td>
<td>92</td>
<td>61.3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>16</td>
<td>81</td>
<td>5.0</td>
<td>0</td>
<td>3</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>L. esculentum</td>
<td>Winter</td>
<td>88</td>
<td>3</td>
<td>1.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>88</td>
</tr>
</tbody>
</table>
### Diploids × Tetraploids (interspecific)

<table>
<thead>
<tr>
<th></th>
<th>L. peruvianum</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Winter</td>
<td>177</td>
<td>91</td>
<td>38.6</td>
<td>13</td>
<td>82</td>
<td>62</td>
<td>2</td>
<td>2</td>
<td>0.61</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>87</td>
<td>92</td>
<td>10</td>
<td>70</td>
<td>60</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.61</td>
<td>10</td>
</tr>
<tr>
<td>L. esculentum</td>
<td>do</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>19</td>
<td>76</td>
<td>5</td>
<td>10</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>29</td>
<td>97</td>
<td>0</td>
<td>27</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. esculentum × L. pimpinellifolium</td>
<td>do</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>8</td>
<td>100</td>
<td>5.0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>42</td>
<td>0</td>
<td>5</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. peruvianum</td>
<td>L. esculentum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>148</td>
<td>5</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Tetraploids × diploids (interspecific)

<table>
<thead>
<tr>
<th></th>
<th>L. peruvianum</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>L. esculentum</td>
<td>Winter</td>
<td>20</td>
<td>85</td>
<td>70.4</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>15</td>
<td>19</td>
<td>228</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>124</td>
<td>88</td>
<td>0</td>
<td>0</td>
<td>30</td>
<td>11</td>
<td>68</td>
<td>59</td>
<td>186</td>
<td>24</td>
</tr>
<tr>
<td>L. pimpinellifolium</td>
<td>do</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>19</td>
<td>84</td>
<td>1.8</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>15</td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>31</td>
<td>65</td>
<td>7.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>20</td>
<td>23</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. esculentum × L. pimpinellifolium</td>
<td>do</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>52</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>12</td>
<td>47</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>55</td>
<td>7</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>12</td>
<td>47</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The unfruitfulness of diploid *Lycopersicon peruvianum* during the winter apparently resulted from the effect of environmental factors on the young pistil or on the flower after pollination. Detrimental effects of high temperature comparable with those reported by Lesley and Lesley (11) would not seem to be the limiting factor in these experiments. The plants were vigorous and flowered profusely. The flowers appeared to be normal at anthesis and produced abundant pollen that functioned in crosses with *L. esculentum*. Furthermore, the day temperature in the greenhouse during the winter usually was kept within the range 75° to 85° F. and exceeded 90° for only brief periods on sporadic occasions. Day temperature in the greenhouse during the summer, when this species sets fruits, was usually somewhat higher and exceeded 90° frequently. No irregularities were observed in meiosis in the pollen mother cells of plants on which chromosome counts were made. The failure of diploids of this species to set fruits during the winter and their ability to set abundant seeded fruits in both the greenhouse and the field at Cheyenne during the summer suggest that light may be an important factor.

The percentages of seedlings produced by seeds of the diploid races planted in steamed soil served as checks for evaluating the percentages of seedlings produced by other seeds.

**SELF-POLLINATED TETRAPLOIDS**

Relatively fewer self-pollinated flowers of tetraploid *Lycopersicon esculentum* set fruits than did those of the diploid in the winter, but they set fruits as readily in the summer (table 1). The fruits of the self-pollinated tetraploids were smaller and contained fewer but larger seeds (fig. 1, F) than the fruits of the corresponding diploids. Relatively fewer of the seeds of the tetraploids planted in steamed soil produced seedlings than did those of the corresponding diploids. The tetraploid seedlings grew more slowly and were readily distinguished by their thicker stems and broader cotyledons.

These results are in agreement with those obtained from autotetraploids of other varieties of *Lycopersicon esculentum* by other investigators. Upcott (24) attributed the low fertility of autotetraploid *L. esculentum* to the formation of quadrivalents and numerical nondisjunction at meiosis. This was supported experimentally by Oka's (19) report that 8 percent of the seeds from self-pollinated tetraploids yielded heteroploid seedlings with 49 to 54 chromosomes. Lindstrom and Koos (14) attributed extreme sterility in a tetraploid derived from a haploid to complete homozygosity. It is of interest to note the relatively numerous seeds in fruits of tetraploid plants of the Danmark and Waltham Forcing varieties used in the present experiments. Danmark yielded an average of 41.3 seeds in size classes 4 and 5 in fruits from tetraploid plants derived from colchicine-treated seeds and an average of 30.0 seeds in fruits from plants derived from the *S*<sub>1</sub> (first selfed) generation. These tetraploids were obtained from several diploid plants in a line that had been inbred for 10 generations after it was received at the Cheyenne station. Tetraploid plants of Waltham Forcing were obtained from diploid plants in a line inbred for 2 generations after it was received. Fruits from these plants obtained from colchicine-treated seeds yielded an average of 44.5 seeds; those...
from the S1 generation yielded 42.7 seeds. Probably the degree of homozygosity in these inbred lines does not approach that in the tetraploid derived from the haploid.

The tetraploids of *Lycopersicon pimpinellifolium* yielded results similar to those obtained from *L. esculentum* except that the weight of the tetraploid fruits was as great as that of the diploid *L. pimpinellifolium* or greater (table 1). There were fewer seeds in a fruit, of course, than in a fruit of *L. esculentum*.

The amphidiploid hybrid between *Lycopersicon esculentum* and *L. pimpinellifolium* yielded results similar to those obtained from the parent species except that its fruit weight was definitely greater than that of the diploid hybrid (table 1). Although the proportion of self-pollinated flowers that set fruits was as high in the amphidiploid as in the diploid, the average number of seeds in a fruit was considerably lower. High fertility of the amphidiploid from this species cross has been reported by Lindstrom and Humphrey (13).

In contrast with flowers of diploid *Lycopersicon peruvianum*, the self-pollinated and naturally pollinated flowers of tetraploid *L. peruvianum* set seeded fruits readily in the greenhouse during the winter. Individual plants in 7-inch clay pots produced as many as 100 fruits. The tetraploids also set fruits in the field and greenhouse during the summer. The fruits were approximately twice as heavy as seedy fruits of the diploid. These results contrast with those obtained on fruit size in diploid and tetraploid *L. esculentum* and *L. pimpinellifolium* in these and other investigations.

The seeds were fewer and larger in fruits of tetraploid *Lycopersicon peruvianum* than in fruits of the diploid. As in the diploid, the number of seeds varied in different plants. Some of the tetraploids in the S1 generation had only 1 or 2 seeds in a fruit. These may have been similar to the unfruitful autotetraploids of *L. esculentum* reported by Lindstrom and Humphrey (13); or they may have been heteroploids similar to those obtained by Oka (19). Chromosome counts were not made on the S1 plants with exceptionally few seeds. Observations on meiosis in 3 of their more fertile sibs and in 30 tetraploids derived directly from colchicine-treated seeds showed that 1 pair of chromosomes frequently fails to synapse (fig. 2) or lags on the spindle at anaphases I and II in pollen mother cells. Seedling emergence of the self-pollinated tetraploids was less and somewhat slower than that of the self-pollinated diploids. However, the tetraploid seedlings were larger than the diploid ones and had thicker stems and broader cotyledons. The growth rate of tetraploid *L. peruvianum* seedlings approached that of its diploid, and its initial size advantage was maintained during early growth.

The results from the self-pollinations serve as a basis for evaluating those from the cross-pollinations.

**DIPLOIDS X TETRAPLOIDS (INTRASPECIFIC)**

A few intraspecific cross-pollinations were made between diploid and tetraploid races for comparison with the interspecific crosses. Five fruits set by 6 flowers of diploid *Lycopersicon esculentum* pollinated with pollen from its tetraploid contained only abortive ovules.
in size classes 1, 2, or 3 (fig. 1, A, B, and C). Twelve fruits set by 14 flowers of tetraploid *L. esculentum* treated with pollen from its diploid contained abortive ovules and 6 seeds. The seeds were similar in appearance to those obtained from self-pollinated tetraploid *L. esculentum*. They produced triploid seedlings. These results are in agreement with those reported by Cooper and Brink (5).

Although self-pollinated flowers of diploid *Lycopersicon peruvianum* usually failed to set fruits during the winter, 1 single-seeded fruit was obtained from 10 flowers of this race treated with pollen from tetraploid *L. peruvianum*. This seed produced a triploid plant that was intermediate between the diploid and tetraploid plants in appearance.

![Figure 2](image_url)

**Figure 2.**—Early anaphase I in microsporocytes of tetraploid *Lycopersicon peruvianum* showing unpaired chromosomes that failed to reach the plate area and were left in the cytoplasm. × 696.

**DIPLOIDS X DIPLOIDS (INTERSPECIFIC)**

As in earlier experiments, emasculated flowers of diploid plants of all of the varieties of *Lycopersicon esculentum* set fruits readily if pollinated with pollen from diploid *L. peruvianum* (table 1). Similar results were obtained if pollen from diploid *L. peruvianum* was applied to emasculated flowers of diploid *L. pimpinellifolium* or of its F₁ hybrid with *L. esculentum*. Most of the fruits contained ovules that were slightly or moderately enlarged (fig. 1, B and C). These failed to yield viable seedlings in steamed soil in the greenhouse. Selected size 3 ovules removed from ripe fruits and from young fruits 20 days after pollination and planted under aseptic conditions on nutrient-salt-dextrose agar also failed to show any indications of growth. The histological studies of Cooper and Brink (5) indicated that such ovules do contain small embryos. Furthermore, Smith (23) secured hybrid
seedlings from excised embryos that were removed from young fruits and cultured aseptically, and McFarlane, Hartzler, and Frazier (16) obtained seedlings from similar ovules cleaned of ovarian residue but left intact. Possibly growth of the embryos was inhibited by the surrounding ovarian tissue in the studies reported herein, although an effort was made to remove fruit residue from the ovules by rubbing them on a sterile wood surface.

Four seeds classified in size classes 4 and 5 were obtained from 81 fruits from cross-pollinations between diploid *Lycopersicon esculentum* and diploid *L. peruvianum* (table 1). One of these seeds was similar in appearance to those from the self-pollinated diploid *L. esculentum*. As it yielded a seedling like the pistillate parent, it may have resulted from chance contamination by a single pollen grain of *L. esculentum* or from development of an unfertilized diploid megagamete. The other 3 seeds were extra large, green, and apparently immature. Two seeds of this type also occurred in single-seeded fruits from the cross between the diploid *L. esculentum* × *L. pimpinellifolium* F₁ hybrid and diploid *L. peruvianum*. The similarity of these seeds to those from the successful crosses between tetraploid *L. esculentum* and diploid *L. peruvianum* (p. 45) suggests that they may have resulted from fertilization of diploid megagametes. Like the latter, these seeds contained well-developed endosperms and small but differentiated embryos. The embryos were too weak to break through the seed coats of the intact seeds on moist blotters in a seed germinator. They enlarged after they were dissected from the seed coats and placed on clean blotters, but they failed to produce mature plants.

As in earlier experiments, flowers of diploid *Lycopersicon peruvianum* emasculated and treated with pollen from diploid *L. esculentum* failed to set fruits (table 1). The failure to obtain fruits from this cross during the winter probably is not significant because self-pollinated flowers of diploid *L. peruvianum* rarely set fruits during this season. However, flowers cross-pollinated during the summer, when self-pollinations were successful, dropped a few days after anthesis, as did emasculated, nonpollinated control flowers. During the winter of 1943 emasculated flowers of diploid *L. peruvianum* were pollinated with pollen from diploid *L. esculentum* and induced to set by applying to the pedicels 0.1-percent indolebutyric acid in lanolin emulsion. In 33 fruits (not included in table 1) obtained by this technique most of the ovules had enlarged very little or not at all. Two plump seeds produced in these fruits yielded seedlings identical with the pistillate parent. These results indicate that cross-fertilization did not occur. Whether this resulted from failure of the haploid pollen tubes of *L. esculentum* to grow normally in the diploid pistils of *L. peruvianum* was not determined.

**TETRAPLOIDS X TETRAPLOIDS (INTERSPECIFIC)**

Tetraploid *Lycopersicon esculentum*, tetraploid *L. pimpinellifolium*, and their amphidiploid hybrid pollinated with pollen from tetraploid *L. peruvianum* yielded results similar to those obtained from the same type of pollination with diploids (table 1 and fig. 1, B and C). Most of the fruits contained size 3 ovules. Six shriveled seeds in size class 4 obtained from 121 fruits from these crosses failed to yield
viable seedlings. They were not green like the seeds from the cross between diploids, but they were not dissected for comparison of internal tissues. Possibly the amphidiploid (allotetraploid) hybrid between \textit{L. esculentum} and \textit{L. peruvianum} could be obtained from this type of cross by Smith's (23) embryo-culture technique.

Emasculated flowers of tetraploid \textit{Lycopersicon peruvianum} pollinated with pollen from tetraploid \textit{L. esculentum} usually failed to set fruits (table 1). The few fruits that did set were much smaller than control fruits from self-pollinated flowers and contained nonenlarged ovules. Twelve fruits were set by 22 emasculated, cross-pollinated flowers late in the pollinating period when lower clusters of nonemasculated flowers on the same plants were cross-pollinated. These flowers and fruits were not included in table 1 because it seems likely that small amounts of pollen from the nonemasculated flowers reached the stigmas of some or all of them. Of the 12 fruits, 5 contained size 2 and size 3 ovules and 7 contained small numbers of plump seeds. Only tetraploid \textit{L. peruvianum} seedlings were obtained from these plump seeds, indicating that some or all of the 12 fruits were set as the result of chance self-pollination. Although some of the fruits were seedless, it is not certain that they were set as the result of the application of pollen from tetraploid \textit{L. esculentum}; they may have resulted from stimulation by pollen tubes from pollen of tetraploid \textit{L. peruvianum} that reached the stigmas too late to permit fertilization and seed development to occur.

Numerous technical difficulties were encountered in the manipulation of both diploid and tetraploid \textit{Lycopersicon peruvianum} as pistillate parents in crosses. The styles on these plants were long, slender, and curved, and the anthers were not easily separated from the abundant hairs on the bases of the styles. During emasculation the styles frequently broke off at the point of attachment to the ovary. After apparently successful emasculation of flowers the day before anthesis would occur, the long slender styles frequently dried out before the petals reflexed; these were not pollinated. A small proportion of the cross-pollinated flowers of tetraploid \textit{L. peruvianum} recorded in table 1 may have dropped as a result of the drying of the styles after pollination, but most of them retained healthy styles for several days. There was little indication that stimulation followed applications of pollen from tetraploid \textit{L. esculentum}. The flowers usually dropped 3 to 7 days after anthesis. Three very small fruits with nonenlarged ovules were obtained.

Because of the difficulties mentioned, pollen from tetraploid \textit{Lycopersicon esculentum} was used on nonemasculated flowers of tetraploid \textit{L. peruvianum}. The flowers were pollinated as soon as the styles extruded from the staminal cone, and pollinations were repeated daily until anthesis. An effort was made not to disturb flowers that had begun to shed pollen. It was considered possible that ovary stimulation and self-fertilization in a few ovules after self-pollination with a few pollen grains might permit fertilization in some ovules by microgametes from the applied \textit{L. esculentum} pollen and the development of these ovules containing hybrid embryos. Flowers so treated usually dropped a few days after anthesis or remained attached to the plants without ovary enlargement. A few produced fruits containing various
numbers of plump seeds and ovules of different sizes. The latter contained complements of ovules and seeds similar to those in fruits from naturally pollinated flowers. Seeds from fruits that contained 17 (half the number obtained in fruits from self-pollinated flowers) seeds or fewer were planted in steamed soil in the greenhouse. None of the resulting seedlings was a hybrid; all were fertile *L. peruvianum* tetraploids comparable with those obtained after self-pollination.

The results from emasculated and nonemasculated flowers indicated that tetraploid *Lycopersicon esculentum* was impotent as a fruit-setting agent on tetraploid *L. peruvianum*. Whether this resulted from failure of fertilization to occur, from failure of the diploid pollen tubes of *L. esculentum* to grow in the tetraploid styles of *L. peruvianum*, or from some other cause was not determined. This type of cross-pollination showed little promise as a means of obtaining species hybrids.

**DIPLOIDS X TETRAPLOIDS (INTERSPECIFIC)**

Emasculated flowers of diploid *Lycopersicon esculentum*, diploid *L. pimpinellifolium*, and their diploid F₁ hybrid treated with pollen from tetraploid *L. peruvianum* set fruits readily. Most of the fruits contained ovules that were slightly to moderately enlarged (table 1 and fig. 1, B and C); the ovules were similar in appearance to those in fruits from cross-pollinations between lines with equal chromosome numbers. Four fruits from the *L. esculentum* parent contained three seeds in size class 4 and seven seeds in size class 5. These were similar in appearance to seeds in these size classes from self-pollinated *L. esculentum*, but they failed to produce seedlings in steamed soil.

Most of the flowers of diploid *Lycopersicon peruvianum* pollinated with pollen from tetraploid *L. esculentum* failed to set fruits. The results obtained during the winter probably are not significant, because self-pollinated flowers of diploid *L. peruvianum* rarely set fruits during this season. However, similar results were obtained during the summer when self-pollinated flowers set readily. Eight small fruits from this cross-pollination contained nonenlarged ovules (table 1). This cross-pollination showed little promise as a means of obtaining hybrids.

**TETRAPLOIDS X DIPLOIDS (INTERSPECIFIC)**

Flowers of tetraploid *Lycopersicon esculentum* pollinated by diploid *L. peruvianum* set fruits as readily as self-pollinated flowers (table 1). The average weight of these fruits was greater than that of fruits set on either diploid or tetraploid *L. esculentum* from applications of pollen from any other source (table 1). Tetraploid *L. pimpinellifolium* if used as the pistillate parent yielded similar results. A lower percentage of the flowers of the amphidiploid hybrid *L. esculentum* × *L. pimpinellifolium* F₁ set fruits, but the weight data were similar.

In contrast with fruits from other cross-pollinations, the fruits from these crosses contained some large, plump seeds (table 1 and fig. 1, D). These seeds differed in shape from those following self-pollinations (compare fig. 1, D and F). They had a distinctive green color that contrasted sharply with the light brown of seeds from self-pollinated diploid and tetraploid *Lycopersicon esculentum* and *L. pimpinellifolium* and with the reddish brown of seeds from self-pollinated
diploid and tetraploid *L. peruvianum*. With a few exceptions previously noted (p. 43), the enlarged ovules or seeds in fruits from other cross-pollinations did not possess this green color.

The large, green seeds from these successful crosses appeared to be immature. It was noted that the period from anthesis to fruit and seed maturity was considerably longer in diploid and tetraploid *Lycopersicon peruvianum* (70 to 80 days) than in diploid and tetraploid *L. esculentum* (50 to 60 days) under the conditions of these experiments. Fruits from cross-pollinated flowers picked ripe and stored in brown paper bags in the laboratory at 65° to 70° F. for 30 days yielded brown seeds that were apparently more nearly mature.

Comparatively few seeds classified as sizes 4 and 5 from the successful cross tetraploid *Lycopersicon esculentum* × diploid *L. peruvianum* produced seedlings (table 1). Higher percentages of seedlings were produced from seeds left in the fruits for 90 days after pollination than from those removed as soon as the fruits were ripe. On dissection, seeds that failed to germinate were found to have well-developed endosperms and comparatively small embryos. These embryos were apparently slow in initiating growth and too weak to break the seed coats.

The hybrid plants from this successful cross were vigorous and had morphological characters intermediate between those of the parents (fig. 3). In appearance they were very similar to those described by Porte and Walker (20). Counts of chromosomes at meiosis in 8 plants showed that these hybrids had 36 chromosomes. These counts and those of chromosomes in the parents (48 chromosomes in tetraploid *Lycopersicon esculentum* and 24 chromosomes in diploid *L. peruvianum*) showed that the hybrids were sesquidiploids (7, p. 275) (allotriploids) that contained 2 sets of chromosomes (24) from *L. esculentum* and 1 set of chromosomes (12) from *L. peruvianum*.

Vigorous hybrids were obtained also from the cross amphidiploid *Lycopersicon esculentum* × *L. pimpinellifolium* F₁ × diploid *L. peruvianum*. These plants could not be distinguished readily from plants from the cross tetraploid *L. esculentum* × diploid *L. peruvianum*. Although these plants might be expected to vary in appearance because of variations in the relative numbers of *L. esculentum* and *L. pimpinellifolium* chromosomes they contained, such variation was not observed among 10 plants grown in pots in the greenhouse.

No seeds from the cross tetraploid *Lycopersicon pimpinellifolium* × diploid *L. peruvianum* were planted.

Most of the flowers of tetraploid *Lycopersicon peruvianum* pollinated by diploid *L. esculentum* dropped a few days after pollination (table 1). Apparently, diploid *L. esculentum* functions poorly as a fruit-setting agent on tetraploid *L. peruvianum*. One fruit from this cross contained 47 size 4 seeds. These seeds failed to produce seedlings from plantings made in steamed soil. Similar results had been obtained in earlier experiments. These results suggest that this cross may yield hybrids from repeated trials or by the use of other parental varieties or techniques. However, seeds from fruits set by nonemasculated, cross-pollinated flowers produced only tetraploid *L. peruvianum* seedlings.
Figure 3.—Tomato plants grown in the greenhouse, Cheyenne, Wyo., summer, 1945: A, Tetraploid *Lycopersicon esculentum*; B, sesquidiploid; C, diploid *L. peruvianum*.
VARIATION IN LINES OF DIPLOID Lycopersicon peruvianum P. I. 128645

Differences were obtained in the average number of seeds in fruits from crosses between tetraploid Lycopersicon esculentum and diploid L. peruvianum P. I. 128645 in the winter and in the summer (table 1). In the summer similar differences occurred in crosses involving different inbred lines from the same introduction of L. peruvianum. These data are presented in greater detail in table 2. The 12 S1 plants of diploid L. peruvianum used during the winter and the 9 S2 plants used during the summer all had their origin in a single plant of L. peruvianum P. I. 128645 self-pollinated in the greenhouse in 1943. The 9 S2 plants used in the summer consisted of 3-plant progenies from 3 field-grown sibs of the 12 S1 plants used in the earlier experiment. Considerable variation occurred in stem, leaf, fruit, and seed characters in the S1 generation grown in the field.

Tetraploids of Lycopersicon esculentum varieties Danmark and Waltham Forcing produced relatively few seeds in fruits from flowers treated with pollen from lines 5 and 7 of diploid L. peruvianum P. I. 128645. Larger numbers of seeds were produced in fruits of these varieties, especially Waltham Forcing, from flowers pollinated with pollen from line 6. Similar results were obtained if pollen from these lines was used on flowers of tetraploid L. pimpinellifolium. Pollen from all three lines produced relatively large numbers of seeds in fruits set on the amphidiploid species hybrid.

There was little indication that these differences were caused by differences in meiotic instability in the different lines comparable with that reported by Lesley and Lesley (11). Although meiosis was not studied extensively in this material, chromosome counts demonstrated that all nine plants used here were normal diploids and no irregularities in meiosis were observed. Chromosome distribution at anaphases I and II was normal. Differences in average number of seeds in fruits...
set by self-pollinated flowers did occur, but all nine plants produced abundant viable seeds.

The variation in efficiency of pollen in crosses with tetraploid *Lycopersicon esculentum* and *L. pimpinellifolium* among plants of diploid *L. peruvianum* P. I. 128645 and the variation in morphological characters in a field-grown progeny from a single plant both indicate considerable genetic diversity in this plant introduction. This is in agreement with the polymorphic nature of this species of *Lycopersicon* as described by Muller (17).

**TETRAPLOID Lycopersicon esculentum × DIFFERENT COLLECTIONS OF DIPLOID L. PERUVIANUM**

Taxonomic studies, plant-breeding experiments, and disease-reaction studies all indicate the diverse genetic nature of different collections of *Lycopersicon peruvianum*. It was therefore considered desirable to determine how different collections of it would respond in crosses with tetraploid *L. esculentum*. In the summer of 1946, three collections received as typical *L. peruvianum* P. I. 126926, P. I. 126944, and P. I. 128656 and two collections received as *L. peruvianum* var. *dentatum* P. I. 128645 and P. I. 128654 were used as pollen parents in crosses with tetraploid *L. esculentum* varieties Danmark and Waltham Forcing.\(^{12}\)

There were considerable differences in the distribution of fruits among classes based on the size of the largest seed contained in each fruit (table 3). Many of the fruits set from flowers pollinated by

**Table 3.—Results from pollinations of tetraploid Lycopersicon esculentum by different collections of diploid L. peruvianum in the greenhouse at Cheyenne, Wyo., 1946**

<table>
<thead>
<tr>
<th>Staminate parent</th>
<th>Flowers pollinated</th>
<th>Flow-</th>
<th>Flow-</th>
<th>Fruits with largest ovules or seeds in size class indicated</th>
<th>Total seeds</th>
<th>Average seeds per fruit, sizes 4 and 5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>Percent</td>
<td>Number</td>
<td>Number</td>
<td>Number</td>
<td>Number</td>
</tr>
<tr>
<td>P. I. 126926</td>
<td>37</td>
<td>86</td>
<td>1</td>
<td>7</td>
<td>15</td>
<td>7</td>
</tr>
<tr>
<td>P. I. 126944</td>
<td>39</td>
<td>72</td>
<td>2</td>
<td>5</td>
<td>15</td>
<td>7</td>
</tr>
<tr>
<td>P. I. 128645</td>
<td>23</td>
<td>70</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>P. I. 128654</td>
<td>55</td>
<td>91</td>
<td>2</td>
<td>14</td>
<td>30</td>
<td>3</td>
</tr>
<tr>
<td>P. I. 128656</td>
<td>25</td>
<td>76</td>
<td>1</td>
<td>8</td>
<td>8</td>
<td>1</td>
</tr>
</tbody>
</table>

*Lycopersicon peruvianum* P. I. 126944 and P. I. 128645 contained seeds in size classes 4 and 5. Seeds were less numerous in fruits from the former cross. Relatively fewer of the fruits set from flowers pollinated by P. I. 126926 contained seeds and most of these were placed in size class 4. Fruits set from flowers pollinated by P. I. 128656 and P. I. 128654 rarely contained seeds in size classes 4 and 5. Some

\(^{12}\) P. I. 126434 and P. I. 126949, received as *Lycopersicon glandulosum*, were also used. The plants from both seed samples produced red fruits and were morphologically identical with *L. pimpinellifolium*. They reacted like diploid *L. pimpinellifolium* in crosses with diploid and tetraploid *L. esculentum* as reported by Cooper and Brink (5); that is, they were cross-fertile with diploid *L. esculentum* and nearly cross-sterile with its tetraploid.
extra large, plump seeds with the characteristic appearance of seeds containing sesquidiploid embryos were obtained from each cross. These results indicate that sesquidiploid hybrids can be obtained from crosses between tetraploid *Lycopersicon esculentum* and various collections of diploid *L. peruvianum* and its varieties. However, the differences obtained from crosses involving different collections suggest that the degree of interfertility of a particular collection in such crosses cannot be predicted from present knowledge of this group.

**DISCUSSION**

Many workers have attempted to cross diploid *Lycopersicon esculentum* with diploid *L. peruvianum* and its varieties with varying degrees of success (p. 33). All collections of the 2 species that have been reported, including those reported herein, that have been studied cytologically have been found to have 12 pairs of chromosomes. The F₁ hybrids would therefore be expected to have 24 chromosomes (the diploid number). Lesley and Lesley (11) obtained diploid hybrids from crosses between diploid *L. esculentum* and Holmes' collection of *L. peruvianum* but obtained both triploid and amphidiploid plants in progenies derived from them. Dermen ¹³ found one of Porte and Walker's hybrids to be triploid.

The experiments reported herein demonstrate that sesquidiploid F₁ hybrids with 2 chromosome sets (24) from *Lycopersicon esculentum* and 1 chromosome set (12) from *L. peruvianum* can be obtained with relative ease. These results are in accord with those obtained by Cooper and Brink (5) from crosses between *L. pimpinellifolium* and *L. peruvianum* P. I. 128646 and P. I. 128649.

In practical breeding work it seems likely that the diploid and the sesquidiploid hybrids offer two modes of attack on the problem of incorporating into economically valuable tomatoes genetically controlled ability either to produce high ascorbic acid concentration or to exhibit disease resistance. The diploid hybrid may offer the possibility of exchange of chromosomes or parts of chromosomes between *Lycopersicon peruvianum* and *L. esculentum*. This is suggested by the cytological studies of Lesley and Lesley (11), who found apparently normal pairing at diakinesis and first metaphase in the diploid hybrids of *L. esculentum × L. peruvianum* and quadrivalent associations in amphidiploids. If pairing in the diploid hybrid is comparable with that observed in the parents, it should be possible to obtain new diploid forms from backcrosses to *L. esculentum* by using methods suggested by Smith (23).

The sesquidiploid offers the possibility of obtaining an entirely different type of tomato. Whether the 36 chromosomes form 12 trivalents, 12 bivalents and 12 univalents, or combinations between these extremes, most of the spores would have about 18 chromosomes with greater and smaller numbers occurring at lower frequencies. Lagging univalents would result in higher proportions of spores with the lower numbers of chromosomes. Occasional spores with 12 *Lycopersicon esculentum* chromosomes and 1 or 2 *L. peruvianum*

¹³ Haig Dermen, associate cytologist, Division of Fruit and Vegetable Crops and Diseases, in personal discussion in 1943.
chromosomes should occur. From self-polhnations or from cross-
pollinations with diploid *L. esculentum* these should yield aneuploids 
with 25 or 26 chromosomes (\(2n + 1\) and \(2n + 2\)). The aneuploids 
in turn should yield on selfing 26-chromosome plants with 13 pairs 
of chromosomes. Although aneuploids could occur in progenies 
from diploid \(F_1\) hybrids, they might be expected to occur more 
frequently in progenies from sesquidiploids. Of 12 possible aneuploid 
lines of this type some should be fertile and have potential value as 
cultigens with disease resistance or high vitamin content. If the 
aneuploids should prove to be sterile, they would still have value in 
determining the genetic factors involved in disease resistance: Such 
knowledge would be invaluable in the attack on the problem of utilizing 
disease resistance from this species in practical breeding programs.

A breeding program with the objective of obtaining aneuploid 
tomato lines has certain advantages and certain limitations that do 
not apply to a breeding program with the objective of obtaining diploid 
lines. With the latter objective it is possible that progress will be 
limited by sterility and testing difficulties in segregating populations. 
On the other hand, the possible number of new combinations may 
approach infinity. Regardless of how many offspring are obtained, 
tested, and found wanting in some essential character, there is always 
the possibility that a new individual with a new genotype will combine 
the desired potentialities.

With aneuploid lines as the objective, the breeding and testing 
programs may be simplified. Once obtained, a 26-chromosome (13-
pair) aneuploid line should breed true, except for possible difficulties 
caused by the formation of trivalents or tetravalents and irregular 
chromosome distribution at meiosis. The aneuploid lines would 
permit the use of line tests rather than individual plant tests for fer-
tility, disease resistance, high vitamin content, and other characters. 
When these characteristics have been determined for any one aneu-
ploid line, the potential value of that line is thereby established. The 
potential number of 26-chromosome lines is, of course, limited.

Although natural aneuploid species or varieties are not known in the 
genus *Lycopersicon*, natural aneuploid series are known in other 
species or genera in many plant families including the Solanaceae. 
Gerstel (6) produced potentially valuable aneuploid lines in *Nicotiana*. 
The assumption that aneuploid tomato varieties can be produced from 
species hybrids is therefore supported by evidence from other genera.

**SUMMARY**

Interspecific cross-polhnations were made between diploid and 
tetraploid races of *Lycopersicon esculentum* and *L. peruvianum* 
P. I. 128645. Similar crosses were made by using *L. pimpinellifolium* 
or its \(F_1\) hybrid with *L. esculentum* in place of *L. esculentum*. Tetraploid 
*L. esculentum* was also pollinated by diploid *L. peruvianum* P. I. 
128654, P. I. 126926, P. I. 126944, and P. I. 128656. Each collection 
and tetraploid race was also self-polhninated.

Viable sesquidiploid seedlings were obtained from the cross tetra-
ploid *Lycopersicon esculentum* pollinated by diploid *L. peruvianum* P. I. 
128645. Similar results were obtained from tetraploid *L. pimpinelli-
ofolium* and its amphidiploid hybrid with *L. esculentum* pollinated by
the same collection of *L. peruvianum*. Seeds similar to those obtained from these crosses were obtained from tetraploid *L. esculentum* pollinated by *L. peruvianum* P. I. 126926, P. I. 126944, P. I. 128654, and P. I. 128656.

Other cross-pollinations produced no fruits or produced fruits with aborted ovules that failed to germinate from plantings of entire ovules or seeds in steamed soil or on an agar culture medium under aseptic conditions.

Marked seasonal variation in fruit-setting ability was found in diploid *Lycopersicon peruvianum* P. I. 128645, but not in its auto-tetraploid derivative or in diploid or tetraploid races of *L. esculentum* or *L. pimpinellifolium*. Variations were found also in morphological characters including number of seeds per fruit in inbred diploid lines of *L. peruvianum* P. I. 128645. These inbred lines also varied in seed-producing efficiency in crosses with tetraploid *L. esculentum*. Similar, but greater, differences in seed-producing efficiency in such crosses were found among different collections of *L. peruvianum*.

Fruit size of tetraploid *Lycopersicon peruvianum* exceeded that of the diploid. Fruit size of tetraploid *L. esculentum* exceeded that of the diploid only in fruits set by flowers pollinated by diploid *L. peruvianum*.

**LITERATURE CITED**

(1) BABB, M. F., and KRAUS, J. E. 1939. RESULTS OF TOMATO VARIETY TESTS IN THE GREAT PLAINS REGION. U. S. Dept. Agr. Cir. 533, 12 pp., illus.


(9) 1943. A TENDENCY TO ESCAPE TOBACCO-MOSAIC DISEASE IN DERIVATIVES FROM A HYBRID TOMATO. Phytopathology 33: 691–697, illus.


(12) LINCOLN, R. E., Zscheile, F. P., Porter, J. W., and others.  
1943. provitamin a and vitamin c in the genus lycopersicon. Bot. 
(13) LINDSTROM, E. W., and HUMPHREY, L. M.  
1933. comparative cyto-genetic studies of tetraploid tomatoes 
(14) ——— and Kooos, K.  
1931. cyto-genetic investigations of a haploid tomato and its 
410, illus.
(15) MACARTHUR, J. W., and CHIASSON, L. P.  
1947. cytogenetic notes on tomato species and hybrids. Genetics 
32: 165–177, illus.
(16) MCFARLANE, J. S., HARTZLER, E., and FRAZIER, W. A.  
1946. breeding tomatoes for nematode resistance and for high 
vitamin c content in hawaii. Amer. Soc. Hort. Sci. Proc. 47: 
262–270, illus.
(17) MULLER, C. H.  
Pub. 382, 29 pp., illus.
(18) OBA, G. I., RINER, M. E., and SCOTT, D. H.  
1945. experimental production of hybrid tomato seed. Amer. Soc. 
(19) OKA, T. H.  
89–92, illus. [In Chinese. English summary, pp. 91–92.]
(20) PORTE, W. S., and WALKER, H. B.  
1945. a cross between lycopersicon esculentum and disease-re-
sistant l. peruvianum. (Phytopath. note) Phytopathology 35: 
931–933, illus.
(21) REYNARD, G. B., and KANAPAUX, M. S.  
1942. ascorbic acid (vitamin c) content of some tomato varieties 
(22) SMITH, P. G.  
1944. embryo culture of a tomato species hybrid. Amer. Soc. Hort. 
(23) ———  
1944. reaction of lycopersicon spp. to spotted wilt. (Phytopath. 
note) Phytopathology 34: 504–505.
(24) UPCOTT, M.  
1935. the cytology of triploid and tetraploid lycopersicum escu-
(25) VIRGIN, W. J.  
1940. the chilean tomato, lycopersicon chilense, found resistant 
to curly top. (Phytopath. note) Phytopathology 30: 280.
(26) ———  
Rpt. (1941) 49 (Bul. 244): 41.
(27) WINKLER, H.  
1916. über die experimentelle erzeugung von pflanzen mit ab-
weichenden chromosomenzahlen. Ztschr. f. Bot. 8: 417–544, 
illus.
(28) WRIGHT, V., and LINCOLN, R. E.  
1940. resistance to defoliation diseases in tomato. Ind. Agr. Expt. 
(29) YEAGER, A. F., and HEPLER, J. R.  
(30) ——— and PURINTON, H. J.  
1946. lycopersicon peruvianum as a parent in the development of 