FIRST-CHROMOSOME GENES IN THE TOMATO¹

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INTRODUCTION

The linear order of the four known genes on the first chromosome of the tomato has never been critically established. The genes concerned are as follows: *Dd* (tall-dwarf growth habit), *Pp* (smooth-pubescent epidermis), *Oo* (oblate-ovate, major fruit shape) and *Ss* (simple-compound inflorescence).

Several years ago I succeeded in developing the quadruple recessive form essential for the requisite backcross. This was inbred for two generations and then crossed reciprocally with the quadruple dominant, in this case the commercial variety Marglobe. Reciprocal backcrosses of this F_1 to the quadruple recessive type were grown, and these furnish the major portion of data for this report. This backcross may be designated as follows:

$$F_1(ddp\textit{pooss} \times DDPP\textit{POSS}) \times ddp\textit{pooss}.$$

The dwarf, peach, ovate, compound-cluster parent was small-fruited while the Marglobe parent was large-fruited.

The determination of the fruit-shape genes, *Oo*, was obtained from measurements of the equatorial and blossom-stem end (polar) diameters of ten fruits from each plant, a shape index being calculated therefrom. This is necessary because these *Oo* genes are not the only oblate or ovate shape factors in the tomato. They are one of the major pairs however.

Fruit size as measured by fruit weight was also obtained from ten fruits per plant.

Complete data were secured from a greenhouse planting of 139 backcross plants, and this was repeated in a field planting of 150 plants.

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LINEAR ORDER OF FIRST-CHROMOSOME GENES

The combined results of the greenhouse and field plantings are arranged in table 1 so as to show the data from the reciprocal backcrosses separately.

TABLE 1

Backcross data involving four pairs of linked genes from the cross $F_1(DPOS \cdot dpos) \times ddppooss$ and reciprocal.

COMBINATIONS	F ₁ AS FEMALE	F ₁ AS MALE	TOTAL	PERCENT
<i>DPOS</i>	79	46	125	
<i>dpos</i>	52	33	85	72.7
<i>DPoS</i>	7	7	14	
<i>dPoS</i>	15	5	20	11.8
<i>DPOs</i>	13	3	16	
<i>dpoS</i>	5	8	13	10.0
<i>Dpos</i>	2	2	4	
<i>dPOS</i>	4	0	4	2.8
<i>DPoS</i>	4	2	6	
<i>dPoS</i>	0	0	0	2.1
<i>DpoS</i>	1	0	1	
<i>dPOs</i>	1	0	1	0.7
Total	183	106	289	100.1
Number of crossovers	52	27	..	..
Percent	28.4	25.5	..	..

Three sets of single and two of double crossovers were noted, but no triple crossing over occurred. The linear order of the genes proved to be *D-P-O-S*. In this experiment the relative map distances between the genes were as follows: *D* 3.5 *P* 13.9 *O* 12.8 *S*. Additional data to be recorded later will give better measures of linkage values. These, coupled with MACARTHUR'S (1928) data, afford verification of the linear order and relative map distances noted above.

Double crossing over in the adjoining *P-O-S* regions occurred 2.1 percent of the time where 1.8 percent would be expected with no interference. This gives a coincidence value of more than one, indicating no interference in these relatively long regions. The same general situation was found in respect to double crossing over in the more widely separated regions *D-P* and *O-S*.

The data in table 1 show that in this particular cross the total amount of crossing over in microsporogenesis was 25.5 percent and in megasporogenesis 28.4 percent. The difference of 2.9 percent is not significant in terms of its probable error. Approximately equal crossing over in the two sexes of the tomato has been reported earlier by MACARTHUR (1928) and LINDSTROM (1927).

TABLE 2

Additional linkage data on first-chromosome genes. F_2 generations.

PEDIGREE NUMBER-PARENTS	XY	$\bar{X}\bar{y}$	zY	zy	PERCENT CROSSING OVER	PUBLISHED* PERCENTS	BACKCROSS DATA FROM TABLE 1
684— $DP \times dp$	112	7	3	38			
619—($XY \times xy$)	89	1	0	28			
691—	132	2	7	38			
872—	141	1	4	46			
1087—	234	5	7	44			
Total	708	16	21	194	4.0	3.4	3.5
684— $DO \times do$	106	13	11	30			
872—	134	8	10	40			
Total	240	21	21	70	12.6	11.4 11.0	17.4
684— $PO \times po$	106	9	11	34			
872—	137	8	7	40			
Total	243	17	18	74	10.3	8.6 10.9	13.9
684— $Os \times os$	76	41	42	1	14.4	20.0	12.8
684— $Ds \times ds$	80	39	38	3			
691—	101	33	41	4			
Total	181	72	79	7	29.7	28.3	24.6
684— $Ps \times ps$	75	40	43	2			
691—	105	34	37	3			
Total	180	74	80	5	25.4	24.5	22.5

* Combined data from MACARTHUR (1928) and LINDSTROM (1925, 1926, 1927, 1928).

Additional linkage data involving the $D-P-O-S$ genes are available in table 2 where a comparison of the linkage values from several sources has

been arranged. While there are the inevitable variations in crossing-over percentages, the data on the whole are in good accord.

The combined data afford a more accurate estimate of the linkage intensities of these first-chromosome genes. It has not seemed advisable to average mathematically all the results since many of the earlier determinations were based on F_2 repulsion data which are often notoriously unreliable.

For practical, present-day purposes the map of the first chromosome may be given approximately as follows:

FRUIT-SIZE RELATIONS WITH THE FIRST-CHROMOSOME GENES

Earlier reports (LINDSTROM 1926, 1927, 1928) have predicated the existence of a major fruit-size gene on this first chromosome of the tomato. The backcrosses already referred to bear on this situation directly since the quadruple-recessive parent was small fruited and the quadruple-dominant P_1 (Marglobe) was large fruited. The backcross to the small-fruited type does not afford the most critical evidence on size inheritance because of the partial dominance of the smaller size. But since no large-fruited, ovate, dwarf, peach, compound-cluster types are in existence, the present arrangement is the only possible test.

In table 3 are given the frequency distributions of fruit size as measured by fruit weight in the greenhouse and field plantings of the backcross generations, involving the parental, single and double crossover combinations of the four linked genes.

A comparison of the fruit weights in the first two columns ($DPOS$ and $dpos$) shows a very evident association of the larger fruits with the dominant $DPOS$ genes as well as of the smaller fruits with the $dpos$ genes. The most critical evidence is afforded in the weight distributions of the single crossover $DPoS$ and $dPoS$ (third and fourth columns) combinations. Here it is plainly evident, in both plantings, that fruit size is associated with something in the $O-S$ end of the chromosome. The next two columns (five and six) which are differentiated on the Ss genes exhibit no marked differences in fruit weight. Accordingly fruit size (or weight) is apparently affected by something very near the Oo genes. That this something is a size gene cannot be proved by these data, although experiments already

reported (LINDSTROM 1928) and some not yet concluded indicate that such is actually the case.

TABLE 3

Distribution of fruit weights in relation to the four pairs of linked genes on the first chromosome.
P₁—small size ddppooss×large size DDPPOOSS.

WEIGHT IN GRAMS	DPOS	dpos	DPoS	dPOS	DPOs	dpoS	Dpos	dPOS	DPoS	DpoS	dPOs
GREENHOUSE PLANTING											
23	..	2	2	..	..	..	..	..	..	..	..
26	1	3	1	..	..	..	..	..	..	..	..
29	3	10	2	..	..	3	..	..	1	..	..
32	5	7	4	..	..	4	..	..	1	..	..
35	8	8	1	1	3	3	1	1	1	..	..
38	11	5	..	3	4	1	0	0	1	..	..
41	5	2	..	0	4	0	1	0	..	..	..
44	8	2	..	1	..	0	..	1	..	..	..
47	1	..	..	2	..	1	..	..	..	..	..
50	0	..	..	0	..	..	..	..	..	..	..
53	5	..	..	2	..	..	..	..	..	..	..
56	2	..	..	1	..	..	..	..	..	..	..
Total	49	39	10	10	11	12	2	2	4	..	..
FIELD PLANTING											
25	3	5	2	..	1	..	..	..	..	..	..
30	6	5	2	..	1	..	..	..	1	..	..
35	17	9	..	..	1	..	..	..	0	..	..
40	16	14	..	..	0	1	2	..	0	..	1
45	17	9	..	2	0	..	..	..	0	..	..
50	10	2	..	1	1	..	..	2	1	..	..
55	6	1	..	3	1	..	..	..	..	1	..
60	0	..	..	1	..	..	..	..	..	..	..
65	0	..	..	0	..	..	..	..	..	..	..
70	1	..	..	3	..	..	..	..	..	..	..
Total	76	45	4	10	5	1	2	2	2	1	1

MANIFOLD EFFECTS OF THE Ss GENES

The Ss genes have been named for their most obvious expression which is concerned with the inflorescence, simple or compound. The source of the recessive, compound-cluster s gene in the material reported above was the commercial variety Grape Cluster. It was observed that there were two other important effects of this gene. First, the number of flower clusters formed on the compound type was always less than is formed on the ordinary varieties of tomatoes. Whereas the usual number of nodes, or

number of leaves between the various flower clusters, on the main stem of the standard type is three, the number on compound-cluster types is usually four or five.

Second, the compound-cluster variety, Grape Cluster, carries noticeably beaked fruits. In some cases the blossom end of the fruit is sharply beaked, the beak extending as far as 4-5 millimeters beyond the normal end of the fruit.

It is of interest to determine whether or not these developments, thus associated with the *s* gene, are invariably correlated with this gene. Quantitative data for the number of nodes between flower clusters are available in the backcross generations of the greenhouse planting shown in table 4. Here the number of leaves between each of the first three flower clusters is averaged and arranged in relation to the linked *OoSs* genes.

TABLE 4

Relation of genes OoSs and the number of leaves between each of the first three flower clusters.

AVERAGE NUMBER OF LEAVES BETWEEN FRUIT CLUSTERS	<i>OS</i>	<i>Os</i>	<i>oS</i>	<i>os</i>	<i>S</i>	<i>s</i>	<i>O</i>	<i>o</i>
3	41	1	10	3	51	4	42	13
4	19	6	4	33	23	39	25	37
5	1	4	2	15	3	19	5	17
Total	61	11	16	51	77	62	72	67

Evidently the *Ss* genes are more closely correlated with the number of leaves than are the *Oo* genes. The average number of leaves between flower clusters is 3.4 for the *S* type and 4.2 for the *s* type, a significant difference. The data indicate a rather close relation between the *Ss* genes and number of nodes, although some variation exists. It must be recalled that all the simple-cluster individuals in this experiment were heterozygous *Ss*, and since the *S* gene does not show complete dominance, although it approaches it closely, there probably is some diluting effect on the other manifestations of this gene.

The degree of beaking in relation to these same *OoSs* genes is given in table 5.

Here again it is the *Ss* genes that show the closest association with the beaking of the fruit. Such evidence makes it clear that these genes have a very pronounced and deep-seated influence on both plant and fruit characters. That this influence traces to the single genes *Ss* and not to other genes linked with them is not proved by the foregoing data. Only general

experience with the compound-cluster gene in other crosses leads me to suggest the hypothesis of manifold effect.

TABLE 5
Relation of OoSs genes and beaking of fruits.

	<i>OS</i>	<i>O_s</i>	<i>oS</i>	<i>os</i>	<i>S</i>	<i>s</i>	<i>O</i>	<i>o</i>
Non-beaked	53	0	10	0	63	0	53	10
Slightly beaked	8	2	6	3	14	5	10	9
Medium beaked	0	5	0	32	0	37	5	32
Strongly beaked	0	4	0	16	0	20	4	16
Total	61	11	16	51	77	62	72	67

SUMMARY

The linear order of the four known genes on the first chromosome of the tomato was established by a four-point, backcross test as *D-P-O-S*.

Evidence is presented of the probable location of an important fruit-size gene on the first chromosome. This gene is located very near the *Oo* fruit-shape genes.

The manifold effects of the *Ss* inflorescence genes are described and measured. They influence not only the type of the flower clusters but also the number of clusters and the beaking of the fruit.

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