THE RELATION BETWEEN GENES AFFECTING SIZE AND COLOR IN CERTAIN SPECIES OF NICOTIANA¹

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INTRODUCTION

HEREDITARY factors which govern size are of interest in genetic theory because they usually exhibit a complex type of inheritance. They are of economic importance since such problems as yield of grains, weight of livestock, and size of fruits are involved. Unfortunately, many contributing causes make size characters more difficult to analyze than qualitative characters like color. For example:

1. Size is often affected by environment.
2. Separation into discontinuous classes is usually not obtained.
3. Many size genes appear to lack dominance.
4. Little, if anything, is known about the interaction of these genes.
5. There are probably a large number of genes affecting the size of most organs and organisms.
6. The various genes concerned all affect the same characteristic, although they may act differently during development.
7. It is necessary to select a measurement of size in order to obtain data. This selected standard may not reveal the true genetic situation. The treatment of the data is also important.

In spite of these difficulties, some significant contributions have been made to our knowledge of the inheritance of quantitative characters. From 1909, when NILSSON-EHLE and EAST independently promulgated the multiple factor hypothesis, until about 1923, the analysis of size inheritance was carried out almost entirely by a purely statistical treatment of data. The most valuable additions to our knowledge of quantitative inheritance, from the economic as well as from the theoretical point of view, were concerned with the development of the conception of multiple cumulative factors governing size.

There was no advance in thought or experimental technique in published work on size inheritance until investigations on linkages with qualitative characters began. SAX (1923), the first one to set up an experiment to test genetic associations between color factors and size, found that in a segregating F_2 population, beans having a pigment factor, P , were heavier

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on the average than the white segregants. Carrying out this same type of analysis, linkages between qualitative and quantitative characters were reported in tomatoes (LINDSTROM 1926), maize (LINDSTROM 1931), peas (RASMUSSEN 1927), barley (WEXELSON 1933, 1934), *Drosophila* (WARREN 1924), and mice (GREEN 1931, 1933).

All researches on multiple quantitative factors have shown them to be cumulative in effect. As to the question of how these gene-values accumulate, little is known. Two possible means have been suggested: (1) they are simply additive, though not necessarily by uninvolved arithmetical increments, each gene contributing an individual unchanging amount; and (2) they interact so that the contribution of each gene is dependent on the number and nature of the other size genes present. The results of WEXELSON (1933) support the former interpretation, and those of RICHEY and SPRAGUE (1931) indicate that at least some of the factors have an additive effect.

On the other hand, RASMUSSEN (1933) has formulated an interaction hypothesis, based largely on the experience of Svalöf plant geneticists, in which he assumes that "the effect of each factor on the genotype is dependent on all the other factors present, the visible effect of a certain factor being smaller the greater the number of factors acting in the same direction." He reported (1935) confirmation of this hypothesis from the interaction of factors for internode length and flowering time in peas.

It seems quite probable that some factors have an additive effect and that others interact.

TREATMENT AND GENERAL STATISTICS

Formulation of a size index

Nicotiana Langsdorffii, which was used as one of the original parents in these studies has a much smaller corolla than that of *N. Sanderae* (Sutton's Scarlet), the other parent species. Two measurements, designated as tube length and length of the maximum lobe, as shown in figure 1, were made on each corolla. EAST (1913; 1916a, b) has shown that tube length is a valuable measurement for size studies in *Nicotiana* since it is practically unaffected by external conditions; and, most certainly, a single significant measure is preferable to any index. However, the differences dealt with in linkages between genes affecting corolla size and color were often so small that it was thought advisable to combine lobe length and tube length into an index in order to formulate a more inclusive picture of the size differences involved. The coefficient of correlation between lobe length and tube length, as calculated from F_2 data, is $+0.58 \pm 0.03$. Since the tube is much longer than the lobe, it is probably best to obtain the geometric mean between the two in order to arrive at an index of size.

Another problem in the treatment of quantitative data is the determination of a scale by which to compare the values obtained. The following considerations led to the conclusion that a logarithmic scale was preferable to an arithmetic one.

1. The frequency distribution of tube length measurements in *N. Langsdorffii*, plotted in millimeters, shows a steep, narrow curve not at all comparable to that of the larger parent, *N. Sanderae* (figure 2). Since both

FIGURE 1. Two measurements of corolla size used in these experiments.

parents have been inbred for a number of generations they should be of comparable homozygosity and form approximately the same curve of variability. Comparison of the frequency distributions of the two species on a logarithmic scale, base 10, makes them approximately equally variable (figure 3). *N. Sanderae* still has a somewhat greater variability, which is probably a true picture of the genetic situation due to the presence of self-sterility factors in this species.

2. Growth involves essentially a multiplication of living substance. On the logarithmic scale, equal divisions on the graph signify equal amounts of multiplication; while, on the contrary, on the arithmetic scale they in-

indicate equal additions. Size is the "end product" of growth. Therefore, the treatment of size data on a logarithmic scale gives a more representative picture of the biological phenomenon concerned.

Two considerations in formulating a suitable size index of the corolla

FIGURE 2. Frequency histograms of measurements in millimeters of corolla tube length in *N. Langsdorffii*, *N. Sanderæ*, the *F₁*, and the *F₂* generation.

have been discussed, namely: (1) combining the two measurements, tube length and length of the maximum lobe, in a geometric mean; and (2) a logarithmic treatment of this mean. The size index, therefore, is $\log \text{tube length} + \log \text{maximum lobe length} / 2$; or, more conveniently, $1000 \times (\log \text{tube length} + \log \text{maximum lobe length})$. The division by 2 is eliminated because the paramount interest in these experiments is in comparative

rather than actual values. The product is multiplied by 1000 to do away with an unnecessary use of decimals. Size will be expressed in units of this index.

General statistics

A comparison of standard deviations (table 1) shows that *N. Sanderae* is more variable than *Langsdorffii*, and the F_1 is intermediate. The increase

FIGURE 3. Frequency histograms of corolla size index, $1000 \times (\log. \text{tube length} + \log. \text{maximum lobe length})$, in *N. Langsdorffii*, *N. Sanderae*, the F_1 , and the F_2 generation.

in variability of the F_2 over the F_1 is demonstrated by the standard deviations and frequency histograms (figure 3). The significant difference between the two F_2 's, 334 and 344, is not explained at present. A third F_2 , 354, grown more recently, had a mean of 768 ± 8 ; and the standard deviation was 156 ± 6 . This mean is still larger than that of 344, but it is interesting to note that it is almost exactly halfway between the means of *Langsdorffii*

and *Sanderae*. Perhaps the shifting F_2 means are caused by a nearer approach to homozygosity in the parents used.

In table 1 are listed, in addition, the means and standard deviations of four F_3 's, four F_4 's, and reciprocal backcrosses of the F_1 to the original parents. The reciprocal backcrosses to *Langsdorffii* are equal in magnitude and intermediate in size and variability between the F_1 and *Langsdorffii*. The reciprocal backcrosses to *N. Sanderae* are also approximately equal in magnitude and are intermediate in size and in variability between the F_1 and Sutton's Scarlet.

TABLE 1
Statistical constants of the size index in the parent species and in hybrid generations.

FAMILY NUMBER	PARENTAGE	n	DESIGNATION	MEAN	S.D.
341	33043-24 selfed	47	<i>N. Sanderae</i>	1292 ± 5	48 ± 3
330642, 3327, 342		62	<i>N. Langsdorffii</i>	37 ± 3	32 ± 2
33046, 3327, 3401		78	F_1 (<i>L.</i> × <i>S.</i>)	742 ± 4	46 ± 3
334	33046-19 selfed	139	F_2 (<i>L.</i> × <i>S.</i>)	568 ± 7	125 ± 5
344	3401-3 & 5	238	F_2 (<i>L.</i> × <i>S.</i>)	729 ± 6	136 ± 4
346	3401-3 × 33043-24	24	F_1 × <i>Sanderae</i>	1045 ± 14	99 ± 10
347	33043-24 × 3401-3	91	<i>Sanderae</i> × F_1	1085 ± 5	72 ± 4
336	33046-19 × 330642-1	159	F_1 × <i>Langs.</i>	317 ± 5	90 ± 3
335	330642-1 × 33046-19	120	<i>Langs.</i> × F_1	312 ± 7	107 ± 5
3402	334-3 selfed	28	F_3 (528)	489 ± 10	78 ± 7
34018	334-24 selfed	28	F_3 (401)	448 ± 6	44 ± 4
3425	334-7 selfed	60	F_3 (671)	547 ± 6	63 ± 4
3426	334-100 selfed	52	F_3 (701)	699 ± 9	101 ± 7
348	3402-3 selfed	26	F_4 (548)	408 ± 5	39 ± 4
349	3402-11 selfed	31	F_4 (431)	384 ± 6	52 ± 4
3411	3402-28 selfed	104	F_4 (660)	578 ± 4	53 ± 2
3412	34018-18 selfed	95	F_4 (413)	337 ± 5	72 ± 4

Individual plants from various points on the F_2 frequency curve gave F_3 populations differing markedly in their means and variability. No F_3 family was as variable as the F_2 . With one exception, all F_4 populations were less variable than the F_3 populations from which they came. With a single exception, the means of the F_2 , F_3 , and F_4 families were lower than the means of the F_1 , F_2 , and F_3 families from which they were derived, irrespective of whether the parent plant was below or above the mean of its family. The size of the F_2 and F_3 parent plants is listed in table 1 in parentheses after the designation of the F_3 and F_4 families to which they gave rise.

LINKAGE BETWEEN QUALITATIVE AND QUANTITATIVE CHARACTERS

Association between color and size in the F_2 and first backcross generations

Since the color genes contributed by each parent are known (SMITH 1937), the average size of flowers with a certain gene from the larger parent

may be calculated and compared with the average size of those having the corresponding allele (or alleles) from the smaller parent. The difference between the two averages is considered to represent the contribution to size of the quantitative factors which are linked with each color gene. The results of such a series of calculations in two F_2 families, 334 and 344, are listed in table 2. The most outstanding result is that every color gene from the larger parent is associated with larger-sized corollas. Most of the differences are statistically significant. In those cases which are questionable, the consistency of the results in this and in other groups of populations leaves no room for doubt that they are biologically significant.

TABLE 2
Summary of linkages between color characters and corolla size in the F_2 generation.

COLOR FACTORS	FAMILY 334			FAMILY 344		
	MEAN	DIFFERENCE	n=139 DIFF./PE	MEAN	DIFFERENCE	n=238 DIFF./PE
<i>pp</i>	484			667		
<i>P</i>	595	+111	7.9	744	+77	3.9
<i>very light</i>	515			620		
<i>light</i>	537	+22	1.2	695	+75	4.4
<i>intense</i>	634	+97	5.7	764	+69	6.6
<i>very intense</i>	676	+42	2.1	834	+70	5.3
<i>rr</i>	568			749		
<i>R</i>	667	+99	5.2	762	+13	0.9
<i>e1e1e2e2</i>	556			703		
<i>E1, E2, E1E2</i>	616	+60	3.5	748	+45	2.1
<i>G</i>	544			714		
<i>gg</i>	627	+83	5.9	835	+121	8.6
<i>B1B2</i>	559			699		
<i>white</i>	640	+81	4.8	796	+97	8.8

The average effect for each group of genes in the two F_2 's has been calculated (without weighting for differences in number) and listed in the first column in table 4. Each value obtained is an approximation of the size contribution of the chromosome in which that particular gene is located. Since the data can not be refined at present to make allowances for crossing over, the figures probably underestimate each chromosomal contribution. For means of comparison, if each one of the nine chromosomes added equally to the difference in size between the two original parents, their contribution would be 140 size units apiece. All the calculated values are less than this. There is no indication from these results nor from those in subsequent generations that any gene or group of genes has an outstanding large effect on size. A number of genes with comparatively minor effects probably are concerned.

Some of the genes for small size are associated with dominant color characters, so that smallness cannot be attributed to an accumulation of recessive genes other than those which visibly influence only size.

Within the group having green plastid color (*G*), the various degrees of greenness, namely green, yellow and cream, were found to be associated with size differences. Similarly, within the group which have blue pollen color (*B₁B₂*), the various degrees of blueness also were found to be associated with size differences.

Backcrosses of the *F₁* to *N. Langsdorffii* were useful only for an analysis of the size effect in *pp* versus *Pp* individuals. These results are listed below:

Family	<i>n</i>	<i>pp</i>	<i>Pp</i>	Difference	Diff./P.E.
335	120	280	338	+58	4.1
336	159	294	334	+40	3.4
345	31	312	384	+72	3.1

Families 335 and 336 are directly comparable with the *F₂* family 334. The difference in size between the means of *pp* and *Pp* is roughly half that of the difference between *pp* and (*PP*+*Pp*).

The backcrosses of the *F₁* to *N. Sanderae* could be used only for an analysis of pollen-color genes and size. The results were as follows:

Family	<i>n</i>	<i>B₁B₁B₂b₂</i>	White	Difference	Diff./P.E.
338	74	909	963	+54	6.0
346	23	1001	1045	+44	0.5

Family 338 is derived from the same *F₁* plant as *F₂*, 334. The effect of *B₁B₂* in the heterozygous condition is less than when either one or both pairs are homozygous, as in the *F₂*. Family 346 compared with 344 gave similar results. There appears to be good evidence that the size genes associated with *P* and with pollen color have less effect in the heterozygous than in the homozygous condition.

The reciprocal backcrosses of the *F₁* to *N. Sanderae* offer material for detecting size differences associated with the sterility alleles. Under the discussion of pollen color (SMITH 1937), genetic evidence was presented which demonstrated that the male gametes with the *Sf* allele from *Langsdorffii* were eliminated in the cross *Sanderae*×*F₁*. If genes for small size are linked with *Sf*, the population resulting from the cross *F₁*×*Sanderae* should be smaller than the reciprocal cross. Compare the means of family 346 and 347 in table 1. The difference between the two is 40 ± 14.9 . This result is in the predicted direction, but can not be considered statistically significant. The numbers are small, especially in 346. The reciprocal backcrosses 337 (*Sanderae*×*F₁*) and 338 (*F₁*×*Sanderae*) were not listed in the table because they were not derived from identically the same plants. 337 (33043-24×33046-9) has a mean of 1090 ± 6 . The mean of 338 (33046-19×33043-19) is 952 ± 5 , which obviously is a significant difference. It

was concluded that size genes are linked with the self-sterility locus. This result was predictable, since pollen color was found to be associated with size differences, and a gene for blue pollen is located in the same chromosome as the *s* alleles.

Association of color and size in subsequent generations

One of the most successful methods for consistently testing pronounced linkages between color and size, was to cross with *Sanderae* various small segregants with many recessives. The resulting F_1 's were selfed and crossed back to the small parent. Segregating populations from these types of crosses were obtained including four families from self-pollinations, namely: 3503, 3504, 3509, and 35011; and three families from backcrosses, namely:

TABLE 3

Association between color and size in families obtained from crossing various small segregants with Sanderae, then selfing the F_1 or backcrossing it to the small segregant.

FAMILY NUMBER	DIFFERENCE BETWEEN MEAN SIZES OF SEGREGATING COLOR ALLELES				
	<i>P-p</i>	<i>R-r</i>	<i>E-e</i>	<i>g-G</i>	<i>white-B1B2</i>
3503	+61 ± 28	+113 ± 36	+121 ± 28		+239 ± 19
3504	+15 ± 17	+20 ± 20			+64 ± 17
3509		+53 ± 13			
35010				+70 ± 42	
35011	+3 ± 25	+138 ± 26	+93 ± 32		+141 ± 26
35012	+48 ± 17	+38 ± 39	+102 ± 26		
35013			+85 ± 19		
Average	31.8	72.4	100.3	70.0	144.3

35010, 35012, and 35013. The average flower size associated with color genes in 35011 is illustrated in plate 1. A summary of the data on all these families is shown in table 3. The size genes associated with intensity of anthocyanin color are omitted in the table and will not be discussed further because of the difficulty in classifying and analyzing intensity. Nevertheless, the association was usually quite pronounced; for example, in family 35021 which is four generations removed from the original parents, the average size of *intense* (*I1I1i2i2*) segregants was 490 ± 7 , while that of *very intense* (*I1I1I2i2*) segregants was 512 ± 15 .

The average value for each color gene in the families in table 3 is listed in the third column of figures in table 4. These values are of interest because they should give a better estimate than F_2 data of the size contributed by genes close to each color gene. The increased size value over that in the F_2 of three of the genes, namely *R*, *b1b2*, and *E1E2* was unexpected. More data are needed before a satisfactory explanation can be offered.

PLATE I

Family 35011: segregation of color and size. Each flower illustrated is representative of a color class and is as near as possible to the mean size of that group. Means are expressed in size index units, 1000 (log tube length+log lobe length), below the representative flower for each color class. About $\frac{1}{2}$ natural size.

TABLE 4

*Average size values associated with color genes in different types of populations.
Size is expressed as the difference between two means.*

COLOR GENES	F ₂ <i>Langs. × Sand.</i>	F ₃ <i>Langs. × Sand.</i>	F ₁ (SEG. × Sand.) × SELF AND SEG.
<i>P</i>	+94.0	-3.0	+31.8
<i>R</i>	+56.0	+57.0	+72.4
<i>E₁E₂</i>	+52.5	+46.5	+100.3
<i>g</i>	+102.0	+86.0	+70.0
<i>b₁b₂</i>	+89.0	+71.3	+144.3

Linkages between color and size genes in some F₃ families are tabulated as averages in table 4. In each case, with the exception of size associated with the *R* factor, there is a marked numerical decrease from the F₂ values. This is to be expected if crossing over takes place; and is, therefore, a strong point favoring the interpretation that we are dealing here with separate genes affecting size rather than the manifold effect of genes which influence

TABLE 5

Five cumulative series made from F₂ data showing increased size with each single addition of a color character from the large parent.

FACTORIAL SERIES	FAMILY 334			FAMILY 344		
	n	MEAN	DIFF.	n	MEAN	DIFF.
1.						
<i>pGB₁B₂</i>	18	466		9	556	
<i>PGB₁B₁</i>	57	556	+90	91	694	+138
<i>PgB₁B₂</i>	21	651	+95	18	775	+81
<i>Pg white</i>	10	687	+36	15	900	+125
2.						
<i>rGB₁B₂</i>	12	484		20	693	
<i>rG white</i>	3	615	+131	15	776	+83
<i>RG white</i>	12	640	+25	40	791	+15
<i>Rg white</i>	7	696	+56	12	881	+90
3.						
<i>eGB₁B₂</i>	26	525		14	660	
<i>EGB₁B₂</i>	30	585	+60	77	701	+41
<i>EG white</i>	12	566	-19	62	776	+75
<i>Eg white</i>	9	667	+101	16	874	+98
4.						
<i>reG</i>	6	462		2	690	
<i>rEG</i>	8	555	+93	38	727	+37
<i>REG</i>	31	631	+76	100	750	+23
<i>REg</i>	15	689	+58	23	845	+95
5.						
<i>reB₁B₂</i>	8	483		2	690	
<i>rEB₁B₂</i>	11	579	+96	19	708	+18
<i>rE white</i>	4	613	+34	20	790	+82
<i>RE white</i>	16	661	+49	50	816	+26

both color and size. Another point supporting this argument is that in every segregating population it is possible to find some plants with large corollas but many qualitative characters from the small parent, and others with small corollas and many color factors from the larger parent. It is often not possible to determine which genes are associated with the larger size until the averages are calculated. In other words, crossovers are frequent.

TABLE 6

Increase in size by adding single genes or groups of genes in an accumulating series.

FAMILY 3503				FAMILY 3504			
COLOR FACTORS	n	MEAN	DIFF.	COLOR FACTORS	n	MEAN	DIFF.
<i>PrB₁B₂</i>	1	723		<i>PrB₁B₂</i>	4	933	
<i>PRB₁B₂</i>	6	919	+196	<i>Pr White</i>	5	983	+50
<i>PR White</i>	10	1045	+126	<i>PR White</i>	12	1012	+29
<i>pB₁B₂</i>	2	926		<i>pB₁B₂</i>	5	970	
<i>p white</i>	3	980	+54	<i>PB₁B₂</i>	10	935	-35
<i>P white</i>	13	1017	+37	<i>P white</i>	17	1015	+80
<i>Pri₂B₁B₂</i>	1	723		<i>Pri₂B₁B₂</i>	2	909	
<i>PRi₂B₁B₂</i>	2	880	+157	<i>PRi₂B₁B₂</i>	4	945	+34
<i>PRi₂ white</i>	4	1043	+163	<i>PRi₂B₁B₂</i>	3	910	-35
<i>PRI₂ white</i>	6	1046	+3	<i>PRI₂ white</i>	10	1049	+139

FAMILY 35011				FAMILY 35012			
COLOR FACTORS	n	MEAN	DIFF.	COLOR FACTORS	n	MEAN	DIFF.
<i>pB₁B₂</i>	10	698		<i>Pre</i>	4	455	
<i>PB₁B₂</i>	30	720	+22	<i>PrE</i>	2	515	+60
<i>P white</i>	3	842	+122	<i>PRE</i>	7	530	+15
<i>PreB₁B₂</i>	1	645		<i>eir₂</i>	4	394	
<i>PREB₁B₂</i>	7	716	+71	<i>e all other in-</i>			
<i>PREB₁B₂</i>	12	783	+67	<i>tensities</i>	4	455	+61
<i>PRE white</i>	3	842	+59	<i>E all other in-</i>			
				<i>tensities</i>	9	527	+72

Cumulative effect of size genes

So far we have seen that every color gene considered in these experiments is associated with size differences. If a series were made up in which each successive member contains one more qualitative gene from the larger parent, then the average size should increase with each additional group as the series progresses if the genes are cumulative. Five representative series were constructed from the F₂ data of families 334 and 344. They are arranged in table 5.

The results show definitely that each addition of a color gene and its associated size gene or group of genes from the larger parent causes an increase in corolla size. The genes are cumulative in effect.

Similar series were also constructed from the data on families 3503, 3504, 35011, and 35012 (table 6). These results, with two exceptions, were all in the expected direction. The classes are regrettably small in number.

INTERACTION OF SIZE GENES

The next step, after demonstrating that size genes are cumulative in effect, is to investigate the problem of the manner in which their values accumulate. The approximately symmetrical nature of the F_2 frequency distribution curve, after the simple and logical transformation $x^1 = \log x$, indicated that the variability is due to a *large* number of *independent, additive* factors with effects of *comparable magnitude*.

The following additional considerations support the conclusion that a large number of genes affect corolla size. (1) Neither of the two extremes of the F_2 distribution reached the parental classes. (2) The F_2 curve is not definitely bi- or multimodal. (3) By using the formula for estimating the number of size genes it was found that *not less* than twelve were involved. (4) Each color gene was associated with comparatively small size effects. There was no indication that genes with major effects on corolla size were operating. (5) Furthermore, if there were a few genes with effects comparable to all the others put together (or greater), there is likely to be marked negative skewness in the F_2 population.

The size genes are independent because they have been found to be linked with independent color genes. The results in table 2 indicate that they are probably of comparable magnitude.

If genes interact so that the visible effect of each gene is smaller the greater the number of genes acting in the same direction (RASMUSSEN 1933), then the F_2 distribution curve will be negatively skewed. In other words, after an appropriate scale has been chosen (in this experiment a logarithmic one) any departure from a normal curve in the direction of negative skewness may indicate interactions of the type described above. From the symmetrical nature of the F_2 curve, we are led to conclude that, in a general way, there is no indication that the genes interact. They appear to be additive in the sense that they add independent geometric (logarithmic) increments of size. The situation might be still more complex; for example, interactions of the RASMUSSEN type might occur but not be detectable on the scale used here because some size genes contributed increments exceeding regular geometric values.

If each size gene or group of genes which is associated with a certain color gene is entirely unaffected by the size genes associated with another color gene, then the difference in size between R and r , for example, should be the same in the P as in the p universe. Any significant departure from this type of result may indicate an interaction. Fourfold tables were con-

structed for each possible group of two gene combinations in the F_2 . Only two groups, $R-g$, and E_1E_2-g , gave consistent evidence of interactions in F_2 's 334 and 344, and these were of the type predicted by RASMUSSEN. However, neither of these groups showed evidence of an interaction in a more recently calculated F_2 , 354. In conclusion, there were no consistent results showing definitely an interaction between the size genes associated with any two color characters.

SUMMARY

In populations derived from the cross *Nicotiana Langsdorffii* $\times$ *N. Sanderae*, each of the color genes studied was found to be linked with genes affecting corolla size. There were apparently a large number of size genes involved, and these had effects of comparable magnitude. None with major effects was detected. Some, if not all, are non-dominant in the sense that Aa has less effect than AA. The size genes were proved to act in a cumulative manner. There was no consistent indication of any interaction between the size genes linked with any two color genes. Linkage was found between the self-sterility locus and size genes.

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