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INHERITANCE OF LENGTH OF POD IN CERTAIN CROSSES

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INTRODUCTION

The inheritance of a difference between two plants has sometimes, though not often, been studied both qualitatively and quantitatively. Correns (5)² has shown that this can be done even with differences in flower color. The inheritance of a large-size difference can occasionally be followed by mere inspection, as in crosses of some tall and dwarf races of peas (*Pisum sativum*) (13); sweet-peas (*Lathyrus odoratus*) (1, p. 280-281); beans (*Phaseolus vulgaris*) (8); and maize (*Zea mays*) (10).

Even with accurate measurements, however, it will probably not be possible to keep track of a single small-size difference, for its segregation may be masked by the modifications. But if several small genetic differences affect the size of the same plant organ, it would usually be still less possible to disentangle the segregation in the second generation of a cross, as Johannsen (12) has proved. The masking effect of the modifications may, however, be lessened by choosing those plant organs which are least liable to modification and which are also repeated many times on each plant, such as flowers (6) or pods with the modal number of consecutive ripe seeds (2). In one such case some of the members of a fraternity were grown on poles 8 feet apart, and others were sown at intervals of 4 feet in a thick row of sorghum. Though the crops of the stunted plants averaged only one-twentieth of those of the others, yet the average length of their 5-seeded pods reached 94 per cent of that of the pods of the well-nourished plants.

In the reciprocal crosses described in this paper, the length of pod was first studied qualitatively and then quantitatively. All the families

¹ I express my thanks to Messrs. C. D. Gunn and C. W. Long, of the Florida Experiment Station, for their careful work in measuring pods.

² Reference is made by number to "Literature cited," pp. 419-420.

grown were selected with the aim of obtaining useful agricultural plants. A fairly complete third generation was raised, but the fourth generation was the result of selection and was the opposite of a random sample.

QUALITATIVE INVESTIGATION

The Florida velvet bean (*Stizolobium deeringianum*) was crossed both ways with the Philippine Lyon bean (*S. niveum*). A pertinent description of these plants has been given in my account of the inheritance of semisterility (4). The Florida velvet bean has a short pod (Pl. XL, fig. B), while the pod of the Lyon bean (Pl. XL, fig. C) is about half as long again and is broader. The pods of the first-generation hybrid plants were as long as, or slightly longer than, those of the Lyon. The progeny of the hybrids in the second generation could be divided by inspection into short-podded plants and long-podded plants. The short pods could be identified, even when young, by their greater proportional width. Although both short pods and long pods varied greatly in size on different second-generation plants, yet no case was met with where the classification could not be carried out when all the pods on a plant were taken into account. Plate XL, figures A and D, shows typical pods of second-generation plants with pods shorter than the Florida velvet bean and longer than the Lyon bean pods. The difference between short and long pods was sharply marked in all the segregating third-generation families.

Tables I, II, and III give the results of field inspection, checked by examination of the pods after harvesting.

TABLE I.—Length of pods in first-generation bean crosses

Parentage. ^a	Number of plants with—	
	Long pods.	Short pods.
Florida velvet bean × Lyon bean.....	7
Lyon bean × Florida velvet bean.....	6
Total.....	13

^a The pollen parent is given last throughout this article.

TABLE II.—Length of pods in second-generation bean crosses

Parentage.	Progeny ratio.		Calculated ratio.		Deviation.	Probable deviation.
	Long.	Short.	Long.	Short.		
Florida velvet bean × Lyon bean.....	140	49	141.75	47.25	-1.75	4.0
Lyon bean × Florida velvet bean.....	375	120	371.25	123.75	+3.75	6.5
Total.....	515	169	513	171	+2.0	7.6

The most probable single ratios have been calculated on the hypothesis that there are three chances for the long pod to one chance for the short pod. However, by the theory of probability, a deviation from the whole numbers nearest to these calculated ratios is far more likely to occur than not. The most probable deviation has been calculated by the conventional formula,¹ and is given in the last column of Table II. Since the actual are not greater than the calculated deviations, it is probable that there is no interference with the random segregation of the long and the short pod, with three chances for the long to one chance for the short pod.

The third-generation families of the Florida velvet bean × Lyon bean were grown in an elimination field among crowding sorghum, where there was some selective elimination of short-podded plants (3). Hence the ratios are useless here. Two long-podded parents, however, of those whose families were grown on poles gave a total of 49 long-podded to 13 short-podded (calculated, 46.5 ± 2.3 : 15.5 ± 2.3). In the third generation of the Lyon bean × Florida velvet bean, 17 families of more than 8 members each from long-podded parents were grown on poles. The totals of the 11 segregating families among these amounted to 231 long-podded and 76 short-podded plants, the calculated nearest whole numbers being 230 and 77. The long-podded homozygotes could not be distinguished by inspection from the heterozygotes. These results are given in Table III. The abbreviations used in this and the subsequent tables in this paper are "V" for Florida velvet bean and "L" for the Lyon bean.

TABLE III.—Length of pods in third-generation bean crosses from long-podded parents

Parentage.	Progeny ratio.		Calculated ratio.		Deviation.	Probable deviation.
	Long.	Short.	Long.	Short.		
LV-92.....	23	: 0				
LV-548.....	30	: 0				
LV-569.....	38	: 0				
LV-558.....	20	: 0				
LV-27.....	28	: 0				
LV-311.....	9	: 0				
LV-80.....	25	: 12	27.75	: 9.25	-2.75	±1.8
LV-113.....	22	: 6	21	: 7	+1.0	±1.5
LV-279.....	24	: 6	22.5	: 7.5	+1.5	±1.6
LV-486.....	31	: 7	28.5	: 9.5	+2.5	±1.8
LV-91.....	21	: 4	18.75	: 6.25	+2.25	±1.5
LV-114.....	13	: 4	12.75	: 4.25	+0.25	±1.2
LV-310.....	26	: 8	25.5	: 8.5	+0.5	±1.7
LV-468.....	15	: 10	18.75	: 6.25	-3.75	±1.5
LV-527.....	15	: 8	17.25	: 5.75	-2.25	±1.4
LV-461.....	28	: 8	27	: 9	+1.0	±1.8
LV-392.....	11	: 3	10.5	: 3.5	+0.5	±1.1
Total.....	231	: 76	230.25	: 76.75	+0.75	±5.1

¹ I have used the ordinary formula for probable deviation, which, however, does not seem to be appropriate (except with large numbers) to any but a 1 to 1 segregation. East and Hayes's practical test of this formula with large numbers (?) shows that it will in that case fit a 3 to 1 segregation with sufficient accuracy. Hence, the calculated probable deviations in Table III, where the numbers are small, are not reliable.

Out of these 11 segregating families, 5 show proportions with a greater deviation than the probable and 6 have a less deviation. The chances for deviations above and below the probable are theoretically equal. The greatest deviation is less than three times the probable. In 3 of the families the calculated numbers occur, since fractions of plants are impossible. Of the other families 5 show an excess of long-podded and 3 an excess of short-podded plants. Hence, the ratios for the third generation conform closely to the theory of probability. However, a further test can be made. It seems that a perfectly random distribution, with three chances for long pods to one chance for short pods, should give for any number of equal groups of n plants each a frequency distribution of numbers of long-podded plants in the groups in classes from n to 0 which corresponds to the terms of the binomial $(3 + 1)^n$. If all the segregating families of the third generation are divided into 76 consecutive groups of 4 plants each in the same order as grown in the field, omitting the last 3 plants out of the total of 307, we have the groups as given in Table IV.

TABLE IV.—*Third-generation segregating families in groups of four plants*

Pods.		Groups.		Deviations.
		Found.	Calculated.	
<i>Long.</i>	<i>Short.</i>			
4	: 0	27	24	+3
3	: 1	27	32	-5
2	: 2	18	16	+2
1	: 3	4	4	0
0	: 4	0	0	0

There is, thus, a fair agreement of the actual figures with those calculated for a random distribution with three chances for long to one chance for short pods.

Of the random sample of 17 families from long-podded parents given in Table III, 11 families segregated into long podded and short podded, while 6 families were constantly long podded. The calculated nearest whole numbers are also 11 and 6.

Eleven second-generation short-podded plants gave only short-podded progeny. One of these has been grown to the fifth generation, giving only short-podded progeny. Four second-generation long-podded plants which were constant in the third generation have been grown to the sixth generation on a field scale without throwing any short-podded progeny.

Therefore, the whole of the second-generation plants were probably in the proportion of 1 constant short-podded to 1 constant long-podded to 2 heterozygous long-podded plants.

Now, we must assume, with Mendel, Correns, and Bateson, that this difference of long-podded and short-podded plants corresponds to a difference between the pollen grains and egg cells of the Florida velvet

bean, on the one hand, and those of the Lyon bean, on the other. But, according to the special investigations of Strasburger and his coworkers, only a sperm nucleus without cytoplasm passes from the pollen tube to the egg cell in most angiosperms. If this is the case here, the progeny of the Florida velvet bean \times Lyon bean receives cytoplasm only from the Florida parent; and the progeny of the reciprocal cross has cytoplasm only from the Lyon bean. Hence, the genetic difference which determines the visible difference between long and short pods is a difference of the nuclei, not a difference of the cytoplasm. If we call this particular nuclear difference of the gametes, $E - e$, the nuclear difference of the zygotes (the Florida velvet bean and the Lyon bean plants) will be $E_2 - e_2$. ($E_2 = E + E$.) Since we have no definite base of measurement, it is useful in many cases to take the recessive as our base and to regard e as zero. This is merely a convention.

To sum up, the Florida velvet bean and the Lyon bean have one main genetic difference affecting pod length. This genetic difference segregates in typical Mendelian fashion.

QUANTITATIVE INVESTIGATION

Investigators of the inheritance of differences in size have found that in many cases these differences are inherited as if several genetic differences (factors) were concerned and dominance was lacking. For instance, in East's masterly investigation of the inheritance of flower size in crosses of two species of *Nicotiana* (6), the first-generation mean flower length was near the geometrical mean of the parent flower lengths, while the second-generation mean was only slightly greater. The frequency array of the flower lengths of the second-generation plants formed a continuous series between the two grandparental means, with the mode below the center. If dominance had been present, the second-generation mean would have been less than the first-generation mean and the first-generation mean should have approached that of the long-flowered parent (supposing all factors were positive). Emerson (9) obtained similar results from a cross of short and long squashes (*Cucurbita pepo*). Groth (11) in many crosses of tomato (*Lycopersicon esculentum*) found the first-generation fruit length near the geometrical mean of the parent lengths. However, the strict proof of this absence of dominance demands, I think, the isolation of a family in which only one such genetic difference is segregating.

The hypothesis that size factors act as multipliers was, I believe, first applied by East (6). Groth's results are readily explicable on this hypothesis. A similar assumption has been made by Punnett and Bailey (14).

To sum up, previous work favors the hypothesis that some size factors show no dominance and act as multipliers.

PARENT PLANTS

In 1910 the mean of the averages of all the ripe 5-seeded pods on 11 plants of the Florida velvet bean (pedigreed line) was 62.9 mm. The mean of the average lengths of the 5-seeded pods of 9 plants of the Lyon bean (pedigreed line) was 92.7 mm. Some of these Lyon bean plants grew in a sandy spot and were stunted; hence the calculated mean is probably too low.

In 1912 the mean of the averages of all the 5-seeded pods of 2 pedigreed Florida velvet bean plants was 62.8 mm. and that of 2 pedigreed Lyon bean plants was 94.5 mm. These plants were grown on poles and were kept free from caterpillars. From 4 more Florida velvet bean and 42 more Lyon bean plants, of the same families, large samples were picked, and all the 5-seeded pods in these samples were measured, but in picking such samples the conspicuous best racemes are probably picked first, and the averages (63.2 and 95.6), which include these samples, are probably too high.

To sum up, the most reliable measurement of the average length of the dry 5-seeded pods of the pedigreed line of the Florida velvet bean was probably 62.8 mm. and that of the Lyon bean 94.5 mm.

FIRST GENERATION

The 5-seeded pods of the 7 first-generation plants were not separately measured in 1909, although many pods were measured. The measurements of 883 seeds from all parts of the pod gave an average of 15.5 mm. The measurements of 613 seeds of the Lyon bean from all parts of the pod gave an average of 15.1 mm. The excess of the first-generation seed length over that of the Lyon bean is in part, or wholly, due to the many gaps in the seed rows of the semisterile first-generation plants. These gaps permit the rounding off of the ends of the seeds, whereas the Lyon bean seeds are usually flattened at the ends by mutual pressure. For five seeds, the maximum excess of the hybrids over the Lyon bean thus is 2 mm.

In 1911 the six first-generation plants were more or less frosted. Only three 5-seeded pods were measured, averaging 98 mm.

To sum up, the average length of the 5-seeded pods of the first-generation plants is probably less than 2 mm. above that of the Lyon bean.

SECOND GENERATION

In Table V are given the frequency arrays of the average lengths of the ripe 5-seeded pods of the plants with white shoots of the second generations of the reciprocal crosses. The plants with black shoots (three-sixteenths of the whole) are not included, because they usually either bore no pods or bore few pods on large plants and so had their pod length physiologically increased. A trial showed that when all

young pods except eight were removed from a plant of the Florida velvet bean the length of 5-seeded pods increased from 63 to 73 mm. The plants in 1912 were grown in an especially favorable season, and more of the late plants had time to ripen their pods than in 1910.

TABLE V.—*Frequency arrays of the average lengths of ripe 5-seeded pods of bean plants with white shoots of second generations of the reciprocal crosses (classes of 3 mm.)*

FLORIDA VELVET BEAN × LYON BEAN, 1910																	Average lengths.	Total number of plants.									
Length of pod, mm.	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97			100	103	106	109	112	115			
Florida velvet bean				6	4	1																			Mm.		
Lyon bean												1	5	2	1											62.9	11
F ₁ hybrids																X										92.7	9
F ₂ hybrids	1	4	8	10	9	8	4	1	1			8	17	9	23	25	11	13	10	7	4	2				98?	
F ₂ parents			(1)	(1)							(1)	(2)	(1)	(2)	(3)	(2)	(2)	(6)	(2)	(1)	(1)	a(1)				62.7 and 94.2	46 and 129

LYON BEAN × FLORIDA VELVET BEAN, 1912																	Average lengths.	Total number of plants.									
Length of pod, mm.	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97			100	103	106	109	112	115			
Lyon bean														1	22	16	5									95.6 (94.5)	44
Florida velvet bean				1	5																					63.2 (62.8)	6
F ₁ hybrids																X										98?	
F ₂ hybrids	1	12	16	20	24	12	9	5	1	2	11	21	38	49	60	51	24	33	13	10	3					62.7 and 94.7	100 and 315
F ₂ parents										(1)		(1)	(2)	(4)	(2)	a(1)	(4)										

^a Black plant.

The actual averages ¹ were:

	Short pods.	Long pods.
1910	62.7	94.2
1912	62.7	94.7

These are sensibly the same as the most trustworthy averages (62.8 and 94.5 mm.) for the Florida velvet bean and the Lyon bean in 1912.

The average of the first-generation plants is probably near 95 mm. The average of the long-podded plants of the second generation is 94.7 mm. Therefore, the factor *E* is probably completely dominant.

Thus, in the second generation the short pods and the long pods give the grandparental averages. The minor factors affecting pod length have not perceptibly altered the averages by their segregation, which agrees with the conclusion that *E* was completely dominant and the minor factors showed zero dominance and acted symmetrically with regard to both long and short pod, decreasing and increasing to the same extent each parental pod length. Calculation shows in this case that the increase of the second-generation averages over the parental lengths, which is a consequence of the hypothesis that the factors act as multipliers, is so small as to be negligible.

¹ The averages have been calculated from the actual figures, not from the frequency classes.

Dividing the second-generation variates into groups on each side of the means, we have:

Year.	Number of short pods.		Number of long pods.		Differences.
	Below mean.	Above mean.	Below mean.	Above mean.	
1910.....	24	22	71	58	2 and 13
1912.....	51	49	165	150	2 and 15

In each case there are fewer variates above than below the mean. This agrees with the hypothesis that the factors act as multipliers.

The second-generation means, including both short and long, were 85.9 and 86.9 mm. These two determinations average 86.4 mm. If E is completely dominant and the minor factors act symmetrically, the second-generation mean will be $\frac{1}{4}(62.8 + 3 \times 94.5) = 86.6$. This is sensibly the same as the actual average, 86.4.

If factor E is a multiplier and completely dominant, we may find its multiplying value in several ways:

Parents—

1910..Lyon bean+Florida velvet bean= $92.7+62.9=1.47$. (Lyon bean value is too low.)

1912..Lyon bean+Florida velvet bean= $94.5+62.8=1.50$. (Two plants each.)

1912..Lyon bean+Florida velvet bean= $95.6+63.2=1.51$. (Including samples.)

Second generation—

1910..Long+short= $94.2+62.7=1.50$.

1912..Long+short= $94.7+62.7=1.51$.

This gives 1.50 to 1.51 for the multiplying value of Ee or E_2 compared with e_2 .

The extremes of the two crosses were:

	Short pods.	Long pods.
1910.....	52 and 76	81 and 113
1912.....	53 and 75	79 and 113

The results in the third and fourth generations show that these extreme values are inherited. The values of 1912 are probably the more reliable. If E is completely dominant and the factors are multipliers, the multiplying value of E is given by:

$$\text{Shortest long pod} + \text{shortest short pod} = 79 + 53 = 1.49$$

$$\text{Longest long pod} + \text{longest short pod} = 113 + 75 = 1.51$$

If E had shown incomplete dominance, the second value should have been markedly greater than the first. The average multiplying value of Ee or E_2 is here 1.50.

The square root of the product of the extremes should give the means nearly and the grandparental means more nearly.

$$\begin{aligned} \sqrt{53 \times 75} &= 63.0 & \text{Mean} &= 62.7 & \text{Grandparental mean} &= 62.8 \\ \sqrt{79 \times 113} &= 94.5 & \text{Mean} &= 94.7 & \text{Grandparental mean} &= 94.5 \end{aligned}$$

Lastly the combined multiplying value of all the minor factors (when double) is given thus:

Quotient of extremes of short-podded plants.....	75+53=1.42
Quotient of extremes of long-podded plants.....	113+79=1.43

The standard deviation in the second generation was:

	Short pods.	Long pods.
1910.....	5.1	7.4
1912.....	5.2	6.8

That the standard deviation of the long-podded is greater than that of the short-podded plants is in agreement with the hypothesis that the minor factors act as multipliers. If *E* is completely dominant, there is no difference in the action of *Ee* and *E₂* to increase the standard deviation of the long-podded plants. The ratios of the two standard deviations in each of the two crosses (1.4 and 1.3) are not quite 1.5, as theory would seem to demand if all the variation were genetic. (See, however, below.)

The coefficients of variation were:

	Short pods.	Long pods.
1910.....	8.2	7.8
1912.....	8.3	7.2

If the variation were purely genetic, these coefficients should, I think, be nearly equal. East (6), however, gives the variation coefficient of the corolla-tube lengths of two parent lines of *Nicotiana* spp. as 8.9 for the short-flowered (170) plants and 6.8 for the long-flowered (167) plants. This variation was presumably not genetic. Judging from this, any modifications would tend to increase the coefficient of variation of the short-podded more than that of the long-podded plants. Hence, it is possible that the slight lowering of the standard deviation of the long-podded plants from the theoretical 1.5 to 1.4, or 1.3 times that of the short-podded plants, is an effect of modifications. Hence, this result does not, I think, disagree with the hypothesis that the factors act as multipliers.

That neither short-podded nor long-podded second-generation plants show a significant increase in either range or standard deviation by more than doubling their number seems to indicate that the genetic series can be fully developed with about 50 plants. But the absence of linkage has not been proved, and until this has been done no definite deductions as to the number of minor factors can be made.

The ranges are:

	Short pods. <i>Mm.</i>	Long pods. <i>Mm.</i>	Ratio of long to short pods.
1910.....	24	32	1.33
1912.....	22	34	1.55

On the hypothesis of factors acting as multipliers, the range of the long-podded plants should be about 1.5 times that of the short-podded plants, as it is in the more reliable 1912 results.

To sum up, the results of investigation of the second generations agree with the hypotheses that all the factors act as multipliers; that factor *E* is completely dominant; that the minor factors show zero dominance; that the minor factors act symmetrically with regard to each of the two grandparental lengths, which is not the case in a cross of the Florida velvet bean by the Yokohama bean (*Stizolobium hassjoo*).

THIRD GENERATION

Table VI gives all the third-generation families, grown in the elimination field, which segregated measurable short podded; and also all which did not, but had eight or more measurable survivors. Because of the crowding, these results are not so reliable as those given in Table VII, which include all the families grown on poles in 1913.

TABLE VI.—Frequency arrays of the average lengths of ripe pods of the third generation Florida velvet bean X Lyon bean (classes of 3 mm.)

[The asterisk (*) shows the pod length of the parent plant of the family.]

Parentage.	Progeny.																				Average length of pod. ^a												
	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106		109	112	115	118	121							
VL-292	1	-	1	1	-	1	3	-	3	*	...	-	1	Mm. 84						
VL-133	1	1	-	1	-	1	...	1	...	2	-	3	*	5	-	3	-	2	88						
VL-171	...	1	-	1	-	1	1	1	-	1	-	2	...	*	2	91						
VL-325	1	1	...	1	...	*	1	-	1	92						
VL-88	1	-	1	-	1	1	1	-	1	-	1	93						
VL-509	1	-	1	-	1	1	3	-	1	-	1	2	-	1	...	102						
VL-164	1	-	1	-	1	1	...	2	*	3	-	6	...	6	-	4	-	1	-	1	-	1	...	103	
VL-294	1	1	(107)					
VL-85	1	-	1	1	...	1	-	1	-	1	...	3	*	3	-	2	-	2	...	104			
VL-158	1	-	2	-	3	55					
VL-569	2	*	2	-	3	-	1	-	2	1	-	1	*	2	-	3	-	2	64					
VL-319	1	-	1	*	2	-	3	-	2	83					
VL-147	1	-	1	*	2	-	3	-	2	86					
VL-114	1	-	6	-	2	-	3	-	1	-	3	89					
VL-255	1	-	1	2	-	3	-	1	...	*	1	90					
VL-92	1	-	1	1	...	*	1	-	3	-	1	92					
VL-94	1	1	97					
VL-194	2	...	1	-	1	-	2	-	2	...	*	1	99					
VL-610	1	...	1	*	1	-	1	-	3	-	3	99					
VL-102	2	-	3	-	4	-	4	-	4	...	*	1	-	1	-	2	...	100				
VL-120	1	-	2	...	1	-	1	-	2	101					
VL-177	1	...	2	-	3	-	1	...	*	1	-	1	101					
VL-255 ^b	1	1	...	1	-	1	-	1	101					
VL-515 ^b	1	...	1	-	4	-	3	...	*	10	-	6	-	2	102					
VL-297 ^b	1	-	1	...	1	-	1	-	6	-	2	-	2	-	2	-	102					
VL-480	1	105					
VL-515 ^c	1	...	*	2	-	3	-	5	-	2	...	109		
VL-297 ^c	1	...	1	1	1	1	*	0	2	...	110

^a The averages for the first nine families refer to the long-podded plants alone.
^b Grown in the elimination field in 1911.
^c Grown on poles in 1912.

TABLE VII.—Frequency arrays of the average length of ripe pods of the third-generation Lyon bean × Florida velvet bean (classes of 3 mm.)

[The asterisk (*) indicates the pod length of the parent of the family]

F ₂ parentage.	F ₃ progeny.														Average length of pod.														
	49	52	55	58	61	64	67	70	73	76	79	82	85	88		91	94	97	100	103	106	109	112	115					
LV-113	3	1		1						5	*	5	3	4	*	1										Mm.	80		
LV-279		1		1						5	3	6	2	4	*	1												81	
LV-468		1		1								4		2	1	*	1	3	2	1								90	
LV-461		2										2	7	4	1	*	3	2	1									90	
LV-310														3	3	*	3	2	1		2	1	1					95	
LV-80				3	3	1											3	1	1	1	2	1	1					96	
LV-327					2	1	2							1			3	1	2	1	2	1	1					96	
LV-486			1	1	3	2						2	1			5	6	5	5	1	2	1						96	
LV-114					1	1										1	2	2	2	1	2	1						99	
LV-91					1											1	2	2	1	*6		1	1					101	
LV-92												1		3	1	5	*3	1	1										92
LV-358													1	2	4	*4	4	1	1	1	1	1							95
LV-27												1	1	2	5	5	5	5	*5	1	1	1							98
LV-548												1	2	3	3	3	3	*5	1	1	1								99
LV-569															3	4	3	4	*2	1	3	2							99

In length of pods, VL-319 and LV-113 are the two lowest families from long-podded parents. The family of VL-319 ranges from 76 to 88 mm. and seems homozygous for E; that of LV-113 ranges from 76 to 85 mm., and throws short-podded, ranging from 49 to 58 mm. The parental lengths were 82 and 79 mm., respectively. To all appearances these two families are homozygous recessives for minor factors (regarded as positive).

VL-480 and VL-85 are the two highest families with the highest averages. (VL-297 was a nearly normal black plant throwing velvet.) The family of VL-480 ranges from 97 to 112 mm. and is homozygous for E. VL-85 ranges from 88 or 94 to 112 and throws short-podded of 70 to 73 mm. long. The parental lengths were 113 and 106 mm., respectively. VL-480, as shown in the fourth generation, is apparently homozygous for all minor factors, as well as for E.

Thus, both near the minimum and near the maximum of the second-generation long-podded plants, we find plants homozygous and heterozygous for E. Hence, E is probably completely dominant.

The numbers in each family are not large enough to determine the separate ranges. The fifth and last lines of Table V show the pod lengths of the parents of these families. The correlation between the average pod lengths of the long-podded parents and the averages of the long-podded plants of their progenies is 82 ± 5 per cent for 36 third-generation families.

The range of the short-podded plants in the various families is from 49 or 52 to 73 mm., and that of the long-podded from 73 to 118 mm. in the elimination field (omitting the black plant, VL-297) and from 76 to 115

mm. for the plants grown on poles. These ranges do not seem to differ significantly from the second-generation ranges.

The families are arranged according to the means of their long-podded plants. LV-310, exceptionally, as was marked in the field, throws short-podded plants with pods unusually long in comparison with those of its long-podded progeny. Whether this is a genuine exception can only be determined by growing further generations from it. This is being done.

In Table VIII the averages of the short-podded plants in each family are compared with the averages of the long-podded plants in the same families. If *E* is completely dominant and none of the minor factors show linkage (coupling or repulsion) with *E*, then the average ratio of the pod length of long-podded to short-podded plants should be about 1.5 in each family. With the exception of the family of LV-310, the ratio comes as close to 1.5 as can be expected in small families, averaging 1.52.

TABLE VIII.—Comparison of the length of pods of the short-podded plants in each family with those of the long-podded plants in the same families. Third generation. Parents heterozygous for *E*

Parentage.	Pod length of parent.	Pod length of progeny.		Ratio of lengths.	Difference from parent.
		Average of short-podded plants.	Average of long-podded plants.		
	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>		
LV-113.....	79	51.2	80.3	1.57	+ 1
LV-279.....	88	57.3	81.1	1.42	- 7
VL-292.....	88	53.0	83.8	1.58	- 4
VL-133.....	86	60.2	87.8	1.46	+ 2
LV-461.....	94	56.0	89.6	1.60	- 6
LV-468.....	92	58.4	89.7	1.54	- 2
VL-171.....	101	59.8	90.5	1.51	-10
VL-88.....	103	65.8	93.3	1.42	-10
LV-310.....	95	71.0	95.4	1.34	0
LV-80.....	91	60.3	95.5	1.58	- 5
LV-486.....	100	61.1	96.2	1.58	- 4
LV-527.....	95	62.6	96.4	1.54	+ 1
LV-114.....	98	62.5	99.3	1.59	+ 1
VL-509 <i>a</i>	93	65.8	101.6	1.55	<i>a</i> + 9
VL-164.....	98	65.0	102.7	1.58	+ 5
VL-85.....	106	71.0	103.5	1.46	- 2
Average.....				1.52	- 2

^a Part of this family was grown on poles.

If the minor factors show zero dominance, the average of the long-podded progeny in each family should equal the parental average, the theoretical excess here being negligible. On the whole, the long-podded plants average 2 mm. shorter than their parents. This is in part due to the stunting in the elimination field, and also possibly to the severe drought in 1913. In both cases the third-generation families were

grown under more adverse conditions than were their second-generation parents.

Table IX compares the parental and progeny pod lengths of families not known to throw short-podded. The averages of the progenies are here less than the parental averages by 3.5 mm. (See above.)

TABLE IX.—Comparison of the pod length of the parents and progeny of families not known to throw short-podded. Third generation. Parents probably or certainly homozygous for *E*

Parentage.	Pod length of parent.	Average pod length of progeny.	Difference from parent.	Parentage.	Pod length of parent.	Average pod length of progeny.	Difference from parent.
	<i>Mm.</i>	<i>Mm.</i>			<i>Mm.</i>	<i>Mm.</i>	
VL-57 ^c a.....	82	83	+1	VL-102.....	102	99	- 3
VL-147 a.....	85	86	+1	VL-104.....	103	99	- 4
VL-114.....	93	89	-4	LV-569.....	104	99	- 5
VL-255.....	97	90	-7	VL-120 a.....	101	100	- 1
VL-92 a.....	92	92	0	VL-177 a.....	105	101	- 4
LV-92.....	96	92	-4	VL-251.....	108	101	- 7
LV-558.....	94	95	+1	VL-515.....	104	102 (109)	- 2 (+5)
VL-94 a.....	104	97	-7	VL-297 ^b	115	102 (110)	-13 (-5)
LV-27.....	103	98	-5	VL-480.....	113	105	- 8
VL-610.....	95	99	+4				
LV-548.....	102	99	-3	Average.....			- 3.5

^c F₂ plants not certainly known to be homozygous for *E*.

^b A black plant throwing velvet.

To sum up, investigation of the third generation gives evidence that *E* is completely dominant; that its multiplying value is 1.5 (one family being an exception); that the genetic range of pod length was fully developed in the second generation; that the minor factors show zero dominance.

FOURTH GENERATION

The frequency arrays of fourth-generation families are given in Table X. By this time it was, of course, known which second-generation plants were *Ee*, and only two *Ee* families were grown. It was not possible to select directly for long-podded plants homozygous for *E*, as selection could only be made after growing the progeny. If the minor factors show zero dominance, selection for specially long pods should be speedily efficacious. Among other desirable characters, extra length of pod was sought for. Hence, the chances were that most selected third-generation plants would be the homozygotes in their families with regard to minor factors.

TABLE X.—Frequency arrays of the average length of ripe pods of fourth-generation crosses of beans (classes of 3 mm.)

[The asterisk (*) shows the parental pod length]

F ₃ parentage.	F ₄ progeny.																Average length of pod.										
	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97		100	103	106	109	112	115	118	121		
VL-10-1.....	1		4	2	*	1																				Mm.	58
LV-486-36.....	1		3		*	3																				59	
LV-486-35.....	3		1								2		5	*	1		2		1							56 and 89	
LV-92-2.....												*		3	1	3										91	
LV-92-6.....											1		*	11	8	1										89	
LV-92-35.....											4		4	1		*										87	
LV-92-40.....											2		6	3			*									88	
VL-216-1.....											3		3	9	9	*	1		1							91	
LV-558-17.....												*	2	7	6	3										93	
LV-558-24.....												2	3	*	3	3										93	
LV-558-13.....												1	1		*	3										92	
LV-558-9.....												3	*	2		1										93	
LV-558-11.....												2	3		*	1										94	
LV-569-22.....												5	*	3												92	
LV-569-40.....												1		3		*										95	
LV-569-6.....												4		2												92	
LV-569-23.....												1	3	2	8	*	5									96	
LV-91-16.....														2	3	4	*	0		0	1					99	
LV-91-4.....														4	0		*	3		4						102	
VL-85-15.....						1								2	0	3	*	3		2						.67 and 104	
VL-480-6.....																	4	*	15		3	3	2			107	
VL-515-21.....																*	4		5	6	4	2				105	
VL-515-22.....														1	*	1	12	15	6	1						105	
VL-515-23.....																3	*	6	10	8	2					106	
VL-515-35.....																3	*	2	6	13	5	0	1			108	
VL-515-1.....																3	1	*	0	1	3	2				108	
VL-515-27.....																2	*	5	2	8	0	1				109	
VL-515-31.....																2	4	9	*	10	1	1				107	
VL-297-23.....																*		2	1	5	1					109	
VL-297-19.....																*	2	4	8	10	4	2	3			109	
VL-297-5.....																	2	*	6	11	5	1				109	
VL-297-11.....																1	0	6	7	2	1			*		109	

One family (from *Ee* parent), LV-486-35, shows a ratio of long-podded mean to short-podded mean of 1.5.

In the families of LV-92, the parents ranged from 82 to 97. The progenies did not sensibly differ. Judging by these, LV-92 was homozygous for minor factors. The same applies to the families of VL-297.

On the other hand, the families of VL-515 showed evidence of the segregation of a minor factor; a segregation also marked in the field.

No indubitable evidence of segregation can be seen in the other fourth-generation families.

In Table XI the pod lengths of the third-generation parents are compared with those of their long-podded progenies. The average of the whole shows an insignificant excess of pod length in the progenies.

TABLE XI.—Comparison of the pod lengths of third-generation parents with those of their long-podded progeny

Parentage.	Pod length of parent.	Average pod length of progeny (long-podded).	Difference from parent.	Parentage.	Pod length of parent.	Average pod length of progeny (long-podded).	Difference from parent.
	<i>Mm.</i>	<i>Mm.</i>			<i>Mm.</i>	<i>Mm.</i>	
LV-486-35...	92	89	- 3	LV-91-16...	104	99	- 5
LV-92-2...	81	91	+10	VL-85-15...	105	104	- 1
LV-92-6...	87	89	+ 2	VL-480-6...	105	107	+ 2
LV-92-35...	93	87	- 6	VL-515-21...	98	105	+ 7
LV-92-40...	96	88	- 8	VL-515-22...	99	105	+ 6
VL-216-1...	96	91	- 5	VL-515-23...	101	106	+ 5
LV-558-17...	87	93	+ 6	VL-515-35...	103	108	+ 5
LV-558-24...	94	93	- 1	VL-515-1...	105	108	+ 3
LV-558-9...	94	93	- 1	VL-515-27...	105	109	+ 4
LV-558-13...	95	92	- 3	VL-515-31...	108	107	- 1
LV-558-11...	98	94	- 4	VL-297-23...	98	109	+11
LV-569-22...	93	92	- 1	VL-297-19...	99	109	+10
LV-569-40...	93	95	+ 2	VL-297-5...	107	109	+ 2
LV-569-6...	96	92	- 4	VL-297-11...	121	109	-12
LV-569-23...	100	96	- 4				
LV-91-4...	102	102	0	Average	+0.5

To sum up, the fourth-generation families show either that selection for long pod had been effective in isolating plants homozygous for minor factors or that segregation of the residual minor factors was in most cases masked by the modifications.

SUMMARY

(1) A single genetic difference, E , is responsible for the main difference between short and long pods. This genetic difference segregates in normal Mendelian fashion.

(2) Factor E is completely quantitatively dominant, so that $E_2 = Ee$.

(3) This factor acts as a multiplier, with a multiplying value of about 1.51.

(4) Minor factors for pod length also act as multipliers, with a combined multiplying value (when double) of about 1.42.

(5) These minor factors apparently show zero dominance, in the sense that if $A_2 B_2 C_2 \dots$ are positive double factors with a combined multiplying value of x , the value of $AaBbCc \dots$ is \sqrt{x} .

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PLATE XL

Typical 5-seeded bean pods, showing the length of parents and crosses; *A*, One of the shortest second-generation pods; *B*, the Florida velvet-bean pod; *C*, the Lyon-bean pod; *D*, one of the longest second-generation pods.

