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The Inheritance of Sizes and Shapes in Plants

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THE INHERITANCE OF SIZES AND SHAPES IN PLANTS

A Preliminary Note[1]

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Some years ago Lock reported a cross of a tall race of maize with a shorter race which produced an intermediate height in F_1 and exhibited no segregation in F_2 when crossed back with one of the parents.[2] Castle's results with rabbits are very similar to those of Lock with maize. Castle summarizes his results in part as follows:[3]

> A cross between rabbits differing in ear-length produces offspring with ears of intermediate length, varying about the mean of the parental ear-lengths. . . . A study of the offspring of the primary cross-breds shows the blend of the parental characters to be permanent. No reappearance of the grand parental ear-lengths occurs in generation F_2, nor are the individuals of that second generation as a rule more variable than those of the first generation of cross-breds. . . . It seems probable that skeletal dimensions, and so proportions of skeletal parts, behave in general as blending characters. The linear dimensions of the skeletal parts of an individual approximate closely the mid-parental dimensions.

From his own work with rabbits and Lock's work with maize, Castle offers this somewhat guarded generalization:[4]

> It is probable that in plants, as well as in animals, linear dimensions are in general blending in their inheritance. . . . The obviously blending inheritance of height in this case [maize] does not contradict the known Mendelian behavior of the growth habit in such plants as the

[1] This paper was presented, in substance, in a lecture before the section of plant physiology of the Graduate School of Agriculture, Ames, Iowa, July 8, 1910. The complete records are to be published later by the Nebraska Agricultural Experiment Station.

[2] Lock, R. H., *Ann. Roy. Bot. Gard. Paradeniya,* 3 (1906), p. 130.

[3] Castle, W. E., et al., Carnegie Inst., Pub. No. 114 (1909), pp. 35, 43.

[4] *Loc. cit.,* pp. 43, 44.

sweet pea. . . . Dwarfness is plainly such a discontinuous variation in plants as is hypophylangia in man, and its inheritance is quite different from that of ordinary variations in height. The former is a discontinuous variation, Mendelian in its inheritance; the latter belongs to a series of continuous variations, and is blending in its inheritance.

While, in case of most of the crosses that I have studied where the parents differ in size, the F_1 individuals show an intermediate size, in no case have I observed anything corresponding to Castle's results with rabbits or Lock's results with corn. In every case with which I am acquainted, there has been segregation of size characters in F_2 following a "blend" in F_1. The cases in which this behavior has been studied most carefully are: size and shape of fruits of summer squashes and gourds, varieties of *Cucurbita pepo;* size and shape of bean seeds, *Phaseolus vulgaris;* size of grains and height of stalks of *Zea mays.*

Size of Maize Grains.—Queen's Golden pop corn, having small grains, was crossed with Black Mexican sweet corn, having grains of medium size. The grains of F_1 plants are intermediate between the parents in size and show no more variation in size than do the grains of the parent plants.[5] F_2 grains, as regards size, while uniform for any one plant, show marked variation between different plants. The actual measurements can not be reported at this time, but an examination of the material on hand shows that there are some ears with grains fully as large as those of Black Mexican, others with grains quite as small as those of Queen's Golden, still others whose grains are about the size of the F_1

[5] On ears of F_1 plants of this cross there are of course about three smooth starchy grains to one wrinkled, sugary grain. While, on account of "double fecundation," the endosperm, like the embryo, of F_1 plants is to be regarded as F_2, exhibiting the ordinary F_2 segregation, the size of grains is a plant character and to be regarded as F_1. The wrinkled grains are apparently of practically the same size as the smooth ones, though there is probably considerable difference in weight between the two lots. In a study of weights, where one parent is sugary and the other starchy, it would be advisable to use only the starchy grains of F_1 plants, and for the sugary parent only starchy, "xenia," grains produced through cross-pollination by the starchy parent. It would doubtless be better, however, to avoid this difficulty by the use of only starchy or only sugary parents.

grains, and finally grains intermediate in size between F_1 and each of the parents. What will happen in F_3 can not be told until this season's crop has been studied.

Height of Maize Stalks.—Tom Thumb pop corn is the smallest variety of maize that has come to my notice and is fully as early as any I have seen. Plants, as grown at Lincoln in 1909 and 1910, averaged about 90 cm. in height, and had on the average about eight nodes. In 1909 they ripened in seventy days from planting. This dwarf early race was crossed with a late dent corn obtained from Missouri. The stalks of the latter are above medium height for dent varieties grown in this section, though in the dry seasons of 1909 and 1910 they have reached an average height of only about 225 cm. The average number of nodes is about nineteen. The plants failed to ripen fully in 1909, owing to late planting, but were within perhaps a week of full maturity at the time of the first frost, 120 days after planting. The F_1 plants, as grown in both 1909 and 1910, are as uniform in height as either parent, with an average height of about 182 cm. (about 25 cm. above mid-parental height) and an average number of nodes of about 12 ($1\frac{1}{2}$ nodes below the mid-parent). In 1909 the F_1 plants ripened in about 100 days from planting (practically the mid-parental season). The F_2 plants (about 250 are now growing) range in size from that of the Tom Thumb parent to above that of the F_1 plants. No plant, however, is so tall as the large dent parent. While records have not as yet been made of heights, number of nodes and earliness in case of all plants, there is apparently little correlation between height and earliness. Some of the earliest plants are above medium height and some of the latest are very short. As to correlation between number of nodes and height and between number of nodes and earliness, nothing can now be said.

Size and Shape of Summer Squashes.—A cross of Yellow Crookneck and White Scallop has been grown, and F_1 and F_2 studied in small numbers. The fruit of

Crookneck has a long neck with a bowl of only medium diameter. Scallop has very flat fruits. F_1 is intermediate in both dimensions and therefore also in shape, *i. e.*, in ratio of length to breadth. F_2 shows a complete series of dimensions and of shapes from one parent to the other. The mean dimensions and shapes and the coefficients of variation in sizes and shapes for parents, F_1 and F_2 are given in the following table.

Race or Hybrid.	Means.			Coefficients of Variation.		
	Length, cm.	Diameter, cm.	Shape, L : D.	Length, Per Cent.	Diameter, Per Cent.	Shape, Per Cent.
Crookneck	39.6	11.4	3.47	17.0	12.0	13.8
Scallop	7.4	17.8	.41	15.8	12.6	26.8
Mid-parent	23.5	14.6	{ 1.94[6] 1.60[7]	16.4	12.3	20.3
F_1 Hybrid	17.5	17.5	1.00	19.0	12.6	26.0
F_2 Hybrid	19.6	13.2	1.48	42.7	42.5	58.8

Size and Shape of Gourds.—A cross of Striped Spoon gourd with Filipino Horned gourd has been studied.[8] The Spoon gourd has a small, relatively long fruit. The relation of length of the whole fruit to the diameter of the bowl is similar to Crookneck squash. The Horned gourd has a short, relatively thick fruit. The ratio of length to breadth is greater than in case of Scallop squash. The following table gives the mean sizes and shapes and coefficients of variation in size and shape of the parents, F_1 and F_2.

Race or Hybrid.	Means.			Coefficients of Variation.		
	Length, cm.	Diameter, cm.	Shape, L : D.	Length, Per Cent.	Diameter, Per Cent.	Shape, Per Cent.
Horned	10.3	9.0	1.14	9.4	9.9	10.9
Spoon	14.0	4.2	3.36	15.6	16.0	11.8
Mid-parent	12.2	6.6	{ 2.25[9] 1.85[10]	12.5	12.9	11.4
F_1 Hybrid	12.9	5.6	2.27	15.8	15.7	13.4
F_2 Hybrid	15.7	5.5	2.87	37.5	21.2	40.7

[6] Mean of parent shapes.

[7] Shape of mid-parent.

[8] Most of the work with this cross is being done by F. W. HofMann, a graduate student in plant breeding at the University of Nebraska.

[9] Mean of parent shapes.

[10] Shape of mid-parent.

Size, Shape and Weight of Bean Seeds.—Numerous crosses of beans differing in size and shape of seeds have been under observation. In only a few cases, however, have exact measurements been made. It will be sufficient to report here combinations of three races: Fillbasket Wax with large flat seeds; Longfellow with long, slender seeds; and Snowflake Navy with small round seeds. The mean dimensions, shapes and weights and the coefficients of variation for parents, F_1 and F_2, are given in the tables below. The parent races and the F_1 plants from which these records were taken were grown in the garden at Lincoln in 1909. The F_2 plants were grown in a greenhouse during the following winter. The different generations are not, therefore, perfectly comparable. In general the various races of beans and F_1 plants that have been grown from time to time both indoors and out have not been observed to exhibit greater variations when grown in the greenhouse than when grown in the garden, though the dimensions and weights of seeds are often noticeably larger in case of greenhouse-grown plants.

In case of the beans, summer squashes and gourds, the mean dimensions and shapes of both F_1 and F_2 are, with some exceptions, more or less like those of the mid-

MEANS

Race or Hybrid.	Weight, c. g.	Length, mm.	Breadth, mm.	Thickness, mm.	L : B	L : T	B : T
Longfellow	28.3	12.9	5 6	4.6	2.3	2.8	1.2
Snowflake	16.4	8.3	5.7	4.7	1.5	1.8	1.2
Mid-parent	22.4	10.6	5.7	4.7	1.9	2.3	1.2
F_1 Hybrid	18.4	10.1	5.7	4.3	1.8	2.4	1.3
Fillbasket	32.2	13.8	7.6	4.4	1.8	3.2	1.7
Longfellow	28.3	12.9	5.6	4.6	2.3	2.8	1.2
Mid-parent	30.3	13.4	6.6	4.5	2.1	3.0	1.5
F_1 Hybrid	28.4	13.0	6.5	4.7	2.0	2.8	1.4
F_2 Hybrid	36.8	14.1	7.0	5.0	2.0	2.9	1.4
Fillbasket	32.2	13.8	7.6	4.4	1.8	3.2	1.7
Snowflake	16.4	8.3	5.7	4.7	1.5	1.8	1.2
Mid-parent	24.3	11.1	6.7	4.6	1.7	2.5	1.5
F_1 Hybrid	25.4	11.4	6.4	4.5	1.8	2.5	1.4
F_2 Hybrid	28.6	11.3	6.9	4.8	1.6	2.3	1.4

COEFFICIENTS OF VARIATION

Race or Hybrid.	Weight, Per Cent.	Length, Per Cent.	Breadth, Per Cent.	Thickness, Per Cent.	L : B Per Cent.	L : T Per Cent.	B : T Per Cent.
Longfellow	6.09	3.27	3.57	4.54	0.61	1.76	2.46
Snowflake	9.40	2.89	3.68	5.38	2.97	5.74	4.29
Mid-parent	7.75	3.08	3.63	4.96	1.79	3.75	3.28
F_1 Hybrid	9.19	1.11	2.84	1.69	3.18	4.35	3.73
Fillbasket	7.93	3.22	2.20	3.78	3.39	6.00	3.85
Longfellow	6.09	3.27	3.57	4.54	.61	1.76	2.46
Mid-parent	7.01	3.25	2.89	4.16	2.00	3.88	3.16
F_1 Hybrid	7.63	3.53	1.43	3.37	3.35	2.55	2.95
F_2 Hybrid	17.43	8.83	10.33	9.45	7.61	12.88	13.10
Fillbasket	7.93	3.22	2.20	3.78	3.39	6.00	3.85
Snowflake	9.40	2.89	3.68	5.38	2.97	5.74	4.29
Mid-parent	8.67	3.06	2.94	4.58	3.18	5.87	4.07
F_1 Hybrid	9.90	3.47	2.70	3.83	1.29	5.04	7.06
F_2 Hybrid	24.48	8.32	5.96	8.95	7.26	39.74	9.01

parents. The most noticeable feature of the records, however, is the coefficient of variation in F_2 as compared with the parents and with F_1. The coefficient of variation is not, on the whole, materially greater for F_1 than for the parents. In F_2, on the contrary, it is noticeably greater than in F_1. It is usually twice and in some cases six or seven times as great as in F_1. This is merely a mathematical way of expressing the fact that the F_2 individuals exhibit marked segregation of size and shape characters. If the intermediates seen in F_1 were tending to breed true as blends, the coefficients of variation for F_2 would not be appreciably greater than for the parents and for F_1. This segregation in F_2 is so pronounced as not to need statistical treatment for its proper appreciation. Even a casual examination of the material can not fail to impress one with the fact that about all grades from one parent to the other are represented in F_2. As a matter of fact, some individuals among the F_2 gourds are decidedly larger than either parent.

If such results as those reported here are to be "explained" by assuming that variation is increased (in some mysterious way?) by hybridization, we can doubtless also explain, in the same way, why this increase in

variation is deferred until F_2. While predictions can not be made with much assurance before F_3 has been studied, it seems probable, nevertheless, as suggested by East,[11] that we shall eventually find that sizes and shapes are not simple characters, but that a particular mean size in reality depends upon two or more, perhaps upon several, distinct factors, a part, or all, of which exhibit incomplete dominance. If this were true, we should expect intermediates (blends) in F_1 and a range of variation from one parent to the other, or sometimes even beyond the parents, in F_2 just as we do find in case of many plant characters. It should also follow that certain F_2 sizes breed true in F_3 while others continue to break up, the variation in some cases extending over the same range as in F_2 and in other cases over variously restricted ranges. There is some evidence that this suggested behavior in F_3 occurs not only in regard to size characters, but also in case of certain colors where blends are seen in F_1, but observations are as yet too meager to be presented.

I am of course not unmindful of the many chances for mistakes in interpretation of the facts secured in a study of size and shape characters. In the apparently simple cases of height of maize stalks or of bean plants, it must be remembered that parents differing in height may also differ in number of nodes, so that segregation in the latter character might bring about differences in height. Number of nodes and average internode length must both be studied instead of merely the product of these, actual height. Or perhaps, parents can be found that differ in height but have the same number of nodes. Confusion resulting from increased fluctuations due to differences in soil and season can be lessened by growing some plants of all generations to be studied in the same season (from seed kept for the purpose or by repeated crosses), and on as uniform soil as can be had. Even in the same summer plants with different periods of de-

[11] East, E. M., Amer. Nat., 44: 72, 73 (1910).

velopment may be subjected to very different weather conditions. This is of so much importance in maize, for instance, that I am now beginning a study of size inheritance of crosses between parents differing greatly in size but only slightly in earliness.

There may possibly be definite correlations between different dimensions, as length and breadth of the same plant part. That is to say, shapes may be definitely inherited. Observations on F_2 bean seeds where the parents differ in size but not in shape indicate that length and breadth are probably not inherited independently of each other. Large round beans crossed with small round ones do not give any long slender beans in F_2 but only large, medium and small, round ones. On the other hand, when the parents differ in shape as well as in size, intermediate and parental shapes as well as intermediate and parental dimensions occur in F_2.

In short, the inheritance of sizes and shapes is not the simple matter that the inheritance of, say, color is—and recent developments indicate that color inheritance is not always a simple three-to-one affair. It is certainly well that most effort has first been directed to a solution of some of the more simple problems of genetics. Without a knowledge of the later studies in color inheritance, one could scarcely hope to get far in the investigation of the inheritance of dimensions, weights and shapes, to say nothing of such questions as whether "yield Mendelizes," which some are impatient to have answered at once.

It has been the purpose of this paper to present a few facts and to suggest many problems with the hope that the attention of other students of genetics will be directed to an interesting and important field not much worked as yet.