

HYBRID VIGOR AND GROWTH RATES IN A MAIZE CROSS AND ITS RECIPROCAL¹

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INTRODUCTION

With the development and rapid commercial utilization of hybrid corn, the phenomenon of hybrid vigor is becoming of increasing practical importance. The theoretical aspects of hybrid vigor have received considerable attention, but certain phases of the phenomenon have not yet been adequately explained. The two current theories as to the cause of hybrid vigor are (1) physiologic stimulation due to the interaction of unlike germ plasms and (2) dominant favorable growth factors. Observational genetic evidence and results from convergent improvement studies (*1*)² are in agreement with the second hypothesis.

Ashby (*1, 2*) has reported on a series of experiments which he interprets as requiring some modification of the dominant-favorable-growth-factor hypothesis and which seem not to be in accord with extensive observations on hybrid vigor in maize.

He (*1, p. 458*) suggests that hybrid vigor may be manifested in four ways:

1. More meristematic centres may be present in the hybrid, giving more leaves and tillers.
2. The leaves of the hybrid may be more efficient in photosynthesis.
3. The embryo may be bigger, so that the capital with which the hybrid germinates is bigger.
4. Finally, the falling off in the sigmoid curve of growth might occur much later for the hybrid than for its parent * * * [and concludes that] Hybrid vigour in these strains is nothing more than the maintenance of an initial advantage in embryo size.

This conclusion assumes that reciprocal hybrids differing in embryo weights must also differ in the weight of the mature plant.

Extensive observations of reciprocal maize hybrids have indicated that such hybrids are essentially similar in their general plant development unless distinct differences in seed condition are involved. Since the phenomenon of hybrid vigor in maize is of such great practical as well as theoretical importance, and since Ashby's conclusions are so contrary to the beliefs commonly held by corn breeders, it was decided to repeat Ashby's experiments in considerable detail.

MATERIAL AND METHODS

Later generations of the inbred strains of corn (*Zea mays* L.) used by Ashby (*2*), 228-4-8, 228-6-5, and their reciprocal hybrids, were employed in this study. In 1933 the material was grown at the Arlington Experiment Farm, Arlington, Va., near Washington, D. C.,

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² Reference is made by number (*italic*) to Literature Cited, p. 829.

and in 1935 at Columbia, Mo. The two seasons were very dissimilar, 1933 being quite favorable for corn and 1935 very unfavorable.

The method of planting was the same in each year, the plants being checked in hills 3.3 feet apart in each direction. The two inbred lines were compared directly, one plant of each line being grown in each hill. The same system was used for the two reciprocal hybrids. Plantings made in this manner had two advantages when inbred was compared with inbred or hybrid with hybrid: (1) Sampling errors were reduced because of the elimination of correlated variation, and (2) competition should accentuate any differences in growth rate which might exist. These advantages do not apply to the important comparison of inbred with hybrid. It is possible that this planting arrangement may actually have reduced the reliability of such comparisons.

Ten plants of each inbred and hybrid were harvested at 5-day intervals throughout the growing season. All harvests were made from perfect-stand hills, hills adjacent to a missing hill being discarded. In harvests made after silking, plant and ear weights were recorded separately. The data presented deal almost exclusively with plant weights.

A comparison of growth rates for the 1933 crop was made by two methods. The first consisted in fitting a straight line to the dry weights obtained from the first nine harvests. A measure of the significance of slope is provided by Fisher (5). The second method consisted in fitting a curved regression line of the form $Y = a + bx + cx^2 + dx^3$. . . to the entire period of growth. The y values were the differences between the logarithms of the dry weights at each harvest period. According to Fisher's terminology, a' is the mean difference and b' and c' are proportional to the difference in slope and change in slope, respectively. The contributions of these various items (a' , b' , c' , etc.) to the total variance can be readily measured.

EXPERIMENTAL RESULTS

1933 CROP

The dry weights of seeds, embryos, and successive plant harvests for the inbred parents and their reciprocal hybrids are available. The weights of shelled grain at successive harvests were obtained in only one season and then only for the hybrids; as these data are somewhat unrelated to the rest of the material to be presented, they will be considered first. The detailed results are presented in table 1. The yields are below normal and somewhat erratic. This may be a result of flooding; water stood 6 feet deep over these plots between August 22 and 24, at which time the ears were in the milk stage. Regardless of the variability, the grain yields of the reciprocals are not significantly different in trend or at the final harvest period.

TABLE 1.—Dry weight of shelled grain of the hybrid 4-8×6-5 and its reciprocal at successive harvests in 1933

Date of sampling	Weight ¹ of shelled grain per plant		Date of sampling	Weight ¹ of shelled grain per plant	
	4-8×6-5	6-5×4-8		4-8×6-5	6-5×4-8
	<i>Grams</i>	<i>Grams</i>		<i>Grams</i>	<i>Grams</i>
Aug. 7	26.1±1.27	27.5±2.97	Sept. 2	165.8±5.57	158.4± 7.12
Aug. 12	49.4±3.67	41.6±3.51	Sept. 6	149.6±7.28	146.4±11.63
Aug. 18	110.0±4.71	91.2±7.08	Sept. 11	149.4±8.81	144.4± 7.35
Aug. 29	149.1±5.60	133.8±5.39	Sept. 16	173.0±4.62	162.6± 6.12

¹ The standard error, and not the probable error, is shown.

The dry weights for seeds, embryos, and plants of the successive harvests are presented in table 2. Here, as in Ashby's results, the inbred 228-6-5 has the smaller kernel and embryo. The difference in embryo weights for the two inbreds is not significant, whereas the difference between the reciprocal hybrids is significant. The logarithms of the weights of the plants at the successive harvests are shown graphically in figures 1 and 2.

TABLE 2.—Dry weights of seeds, embryos, and plants at successive harvests of two inbred lines of *corr.* and their reciprocal hybrids in 1933

Part of plant or date of harvest	Individuals in sample	Mean dry weight ¹ for indicated parent or hybrid			
		4-8 selfed	6-5 selfed	4-8×6-5	6-5×4-8
	<i>Number</i>	<i>Grams</i>	<i>Grams</i>	<i>Grams</i>	<i>Grams</i>
Seeds.....	50	0.2228±0.0018	0.1891±0.0021	0.2575±0.0012	0.2314±0.0023
Embryos.....	50	.0029±.0005	.0026±.0004	.0035±.0006	.0020±.0007
Plants harvested:					
May 29.....	10	.060 ± .012	.041 ± .004	.105 ± .002	.078 ± .005
June 3.....	10	.129 ± .023	.088 ± .010	.270 ± .022	.197 ± .006
June 8.....	10	.388 ± .042	.289 ± .010	.812 ± .059	.626 ± .031
June 13.....	10	1.643 ± .226	.785 ± .096	3.926 ± .206	2.511 ± .341
June 18.....	10	2.862 ± .430	1.369 ± .084	8.309 ± .267	6.535 ± .448
June 23.....	10	6.909 ± .956	2.853 ± .221	18.476 ±1.40	13.286 ±1.25
June 28.....	10	15.31 ± .856	10.74 ± .646	31.399 ±2.90	25.008 ± .993
July 3.....	10	27.51 ±2.50	18.05 ± 2.06	62.8 ±5.13	60.6 ±5.50
July 8.....	10	34.29 ±2.83	31.35 ± 1.36	93.0 ±5.18	86.6 ±6.28
July 13.....	10	44.77 ±4.61	35.32 ± 2.94	136.1 ±3.96	124.7 ±4.86
July 18.....	10	63.80 ±5.47	53.0 ± 3.57	167.8 ±7.70	175.2 ±4.33
July 23.....	10	93.25 ±5.92	63.25 ± 5.81	204.1 ±7.81	190.4 ±4.53
July 28.....	10	97.00 ±6.52	94.38 ±12.27	233.6 ±6.48	234.3 ±3.70
Aug. 2.....	10	147.25 ±5.83	115.25 ± 5.56	246.0 ±8.10	240.6 ±8.25
Aug. 7.....	10	175.50 ±6.78	122.75 ± 5.47	275.6 ±6.45	279.7 ±6.56

¹ The standard error, and not the probable error, is shown.

The straight-line regressions, fitted to the logarithms of the dry-weight determinations for the first 45 days for the two parental lines and their reciprocal hybrids, were as follows:

Parent or hybrid:	<i>Value of y</i>
228-4-8.....	0.07277 + $\bar{2}$.53064 <i>x</i>
228-6-5.....	.07390 + $\bar{2}$.29566 <i>x</i>
228-4-8 × 6-5.....	.07579 + $\bar{1}$.81698 <i>x</i>
228-6-5 × 4-8.....	.07858 + $\bar{1}$.64024 <i>x</i>

The differences in the slope of the four regression lines as indicated by the regression coefficients are not statistically significant. This suggests that during the 45-day period the inbreds and their reciprocal hybrids all grew at approximately the same rate.

An analysis of the data for the entire growth period by means of the curved regression line leads to essentially the same conclusion. The *F* values (15) for the various constants are presented in table 3. In no case is there a significant difference in slope (*b'*). This indicates no significant dissimilarity of growth rates during the period studied.

The difference between the mean dry weights (*a'*) is significant in every comparison. For the reciprocal hybrids, however, the difference in mean dry weight is of limited biological significance, as the two hybrids do not differ statistically in weight after the 40-day period. In the comparisons of the change in the slope of the regression lines (*c'*), the inbred lines in each case differ significantly from the hybrids because of the earlier cessation of growth in the hybrid (fig. 1). With the exception of the failure to find a continuing difference between reciprocal hybrids, the results are in apparent harmony with those presented by Ashby.

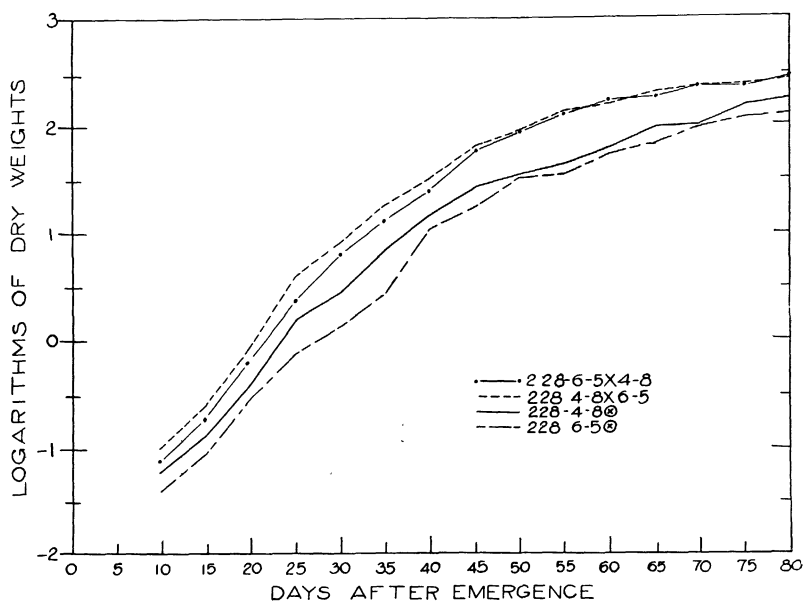


FIGURE 1.—Growth rates of two inbred strains of corn and their reciprocal hybrids in 1933.

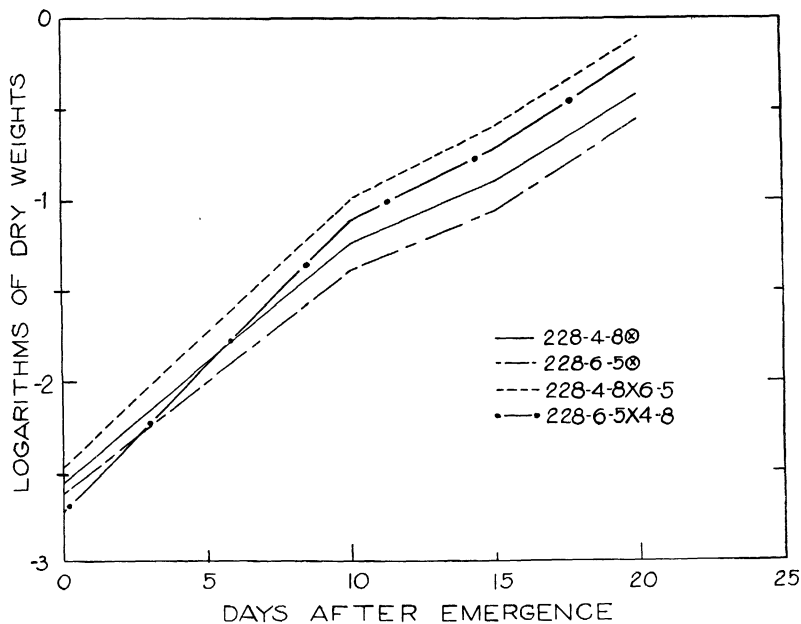


FIGURE 2.—Growth rates of two inbred strains of corn and their reciprocal hybrids during the early seedling stage in 1933.

TABLE 3.—Comparisons of the regression constants of two inbred lines of corn and their reciprocal hybrids grown in 1933

Comparison	Value ¹ of <i>F</i> for indicated constant		
	<i>a'</i>	<i>b'</i>	<i>c'</i>
4-8 selfed and 6-5 selfed	50.68	0.40	0.43
4-8 selfed and (4-8 × 6-5)	562.16	.64	19.94
6-5 selfed and (6-5 × 4-8)	274.35	.00	11.35
(4-8 × 6-5) and (6-5 × 4-8)	18.18	1.00	.22

¹ 4.84 is the lowest value *F* may take for significance when $P=0.05$; 9.65 is the lowest value *F* may take for significance when $P=0.01$.

Before proceeding further with the analysis it is desirable to evaluate the reasonableness of the indicated conclusions. If the dry weight at the end of the 45-day period is expressed as a percentage of the initial weight, the values for the inbreds 4-8 and 6-5 and the hybrids 4-8 × 6-5 and 6-5 × 4-8 are 572, 765, 886, and 1,110, respectively. When each hybrid is compared with its maternal inbred, the ratio of these percentages is approximately 1.5 to 1. This indicates that the hybrid actually has grown at a rate approximately 50 percent greater than its maternal inbred parent. The failure to establish the significance of this difference may be due to several causes. The sampling may have been inadequate to represent the population, or the variability from sample to sample so great that a very large difference in growth rate would be necessary for significance.

On the basis of the variability observed in the nine harvests covering the initial 45-day period, a difference in growth rate of 75 percent would be necessary to give odds of 20 to 1. As indicated previously, a difference of approximately 50 percent was observed. The difference necessary for significance covering the entire growth period has not been calculated but it doubtless would be somewhat greater than for the 45-day period.

The results published by Ashby appear less conclusive when one considers the percentage increase in dry matter as a measure of growth rate. Expressing the final harvest weight as a percentage of the initial harvest weight and comparing the faster growing inbred with its F_1 hybrid, differences of 21 and 46.9 percent are found for the material presented in his first and second study, respectively. In each case he concluded that the inbred and hybrid were equivalent in growth rate. It is clearly evident that the high degree of variability present in Ashby's and in the writer's material precludes any very definite conclusions as to the equivalence of growth rate in inbreds and hybrids.

1935 CROP

The detailed data for the 1935 harvests are presented in table 4 and are shown graphically in figure 3. In contrast to the 1933 data, the inbred 228-6-5 has the higher embryo and grain weight. The hybrid 6-5 × 4-8 has a smaller grain and embryo weight than the maternal inbred itself. The reciprocal hybrid, however, shows an increase in both grain and embryo weight over its maternal inbred parent. These variations in embryo weight are probably the result of variation in soil fertility and relative plant development. Selfed

seed produced on a favored inbred plant may have larger kernels and embryos than hybrid seed produced on a less favored plant of the same inbred strain.

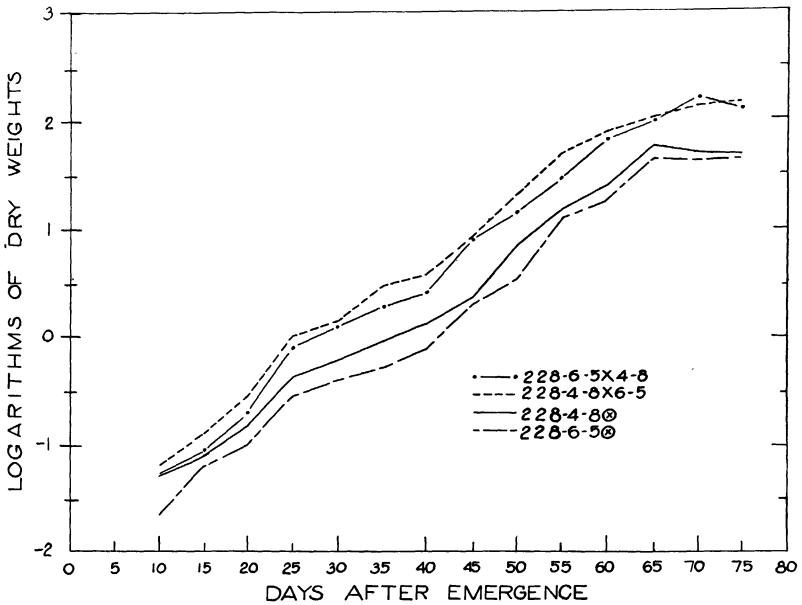


FIGURE 3.—Growth rates of two inbred strains of corn and their reciprocal hybrids in 1935.

TABLE 4.—Dry weights of seeds, embryos, and plants at successive harvests of two inbred lines of corn and their reciprocal hybrids in 1935

Part of plant or date of harvest	Mean dry weight ¹ for indicated parent or hybrid			
	4-8 selfed	6-5 selfed	4-8 × 6-5	6-5 × 4-8
Seeds.....	0.215 ± 0.007	0.265 ± 0.001	0.246 ± 0.002	0.225 ± 0.001
Embryos.....	.0031 ± .0003	.0034 ± .0005	.0035 ± .0003	.0029 ± .0002
Plants harvested:				
June 18.....	.053 ± .003	.024 ± .001	.066 ± .003	.054 ± .002
June 23.....	.096 ± .007	.060 ± .004	.136 ± .005	.086 ± .003
June 28.....	.159 ± .039	.104 ± .011	.284 ± .020	.201 ± .013
July 3.....	.434 ± .015	.302 ± .006	1.027 ± .030	.825 ± .079
July 8.....	.578 ± .025	.427 ± .012	1.401 ± .110	1.317 ± .034
July 13.....	.902 ± .074	.538 ± .009	3.191 ± .248	2.086 ± .191
July 18.....	1.307 ± .116	.719 ± .039	3.786 ± .217	2.612 ± .189
July 23.....	2.433 ± .287	2.179 ± .294	8.444 ± .562	8.111 ± .959
July 28.....	7.110 ± .413	3.571 ± .448	21.700 ± 1.277	14.500 ± .633
Aug. 2.....	15.69 ± .563	12.679 ± .464	47.662 ± 3.543	37.297 ± 2.602
Aug. 7.....	25.116 ± 1.902	18.900 ± 1.489	77.116 ± 1.704	72.137 ± 5.304
Aug. 12.....	58.548 ± 1.277	44.506 ± 2.075	105.971 ± 2.546	99.930 ± 3.405
Aug. 17.....	48.848 ± 1.410	45.415 ± 1.033	132.619 ± 2.049	153.614 ± 8.702
Aug. 22.....	50.482 ± 4.549	45.512 ± 4.593	141.288 ± 6.345	128.460 ± 8.434

¹ The standard error, and not the probable error, is shown.

The difference in weight of embryo for the hybrid 4-8 × 6-5 and its reciprocal was not very great in either year. In order to obtain a greater difference in embryo weight, one set of the hybrid ears 6-5 × 4-8 was harvested April 20 and another set was harvested

May 4. This material was grown in the greenhouse and the sequence of silk and pollen prevented making the cross reciprocally. The difference between the embryo weights of the prematurely and normally harvested corn was slightly greater than that of the two lots of reciprocal hybrids previously compared. This initial difference in embryo weight, however, was ineffective in modifying the expression of vigor. The mean dry weights of plants (table 5) from the two lots of seed are quite similar for practically every harvest. There is no significant difference between the final dry weights.

TABLE 5.—Mean dry weights of seeds, embryos, and plants at successive harvests of the hybrid (6-5 × 4-8) harvested before and at maturity in 1935

Part of plant or date of harvest	Mean dry weight ¹ for the hybrid 6-5 × 4-8 at—		Part of plant or date of harvest	Mean dry weight ¹ for the hybrid 6-5 × 4-8 at—		
	Premature harvest ²	Normal harvest		Premature harvest ²	Normal harvest	
	Grams	Grams		Grams	Grams	
Seeds.....	0.214 ± 0.001	0.278 ± 0.002	Plants harvested—Contd.			
Embryos.....	.0027 ± .002	.0036 ± .0002		July 23.....	13.111 ± 0.926	14.777 ± 1.445
Plants harvested:				July 28.....	33.300 ± 1.352	43.300 ± 2.553
June 18.....	.054 ± .002	.065 ± .003		Aug. 2.....	76.319 ± 3.600	80.734 ± 1.910
June 23.....	.112 ± .006	.124 ± .008		Aug. 7.....	107.064 ± 1.524	113.034 ± 4.068
June 28.....	.288 ± .017	.342 ± .022		Aug. 12.....	130.846 ± 2.170	167.182 ± 6.135
July 3.....	.933 ± .056	.883 ± .035		Aug. 17.....	145.350 ± 3.116	180.586 ± 7.259
July 8.....	1.719 ± .059	1.891 ± .058		Aug. 22.....	169.565 ± 6.384	163.583 ± 6.426
July 13.....	3.757 ± .277	3.848 ± .274				
July 18.....	5.138 ± .468	5.353 ± .807				

¹ The standard error, and not the probable error, is shown.

² The premature harvest was 2 weeks earlier than the normal harvest.

The evaluation of the curved regression constants is presented in table 6. The difference between mean dry weights (a') is significant in every comparison. However, as pointed out for the 1933 results, the difference between the reciprocal hybrids is of little practical importance. The final plant weights were not significantly different. The difference in rate of growth (b') for the two inbreds probably is significant, the value for P lying between 0.01 and 0.05. The difference in growth rate between the 228-4-8 inbred and the hybrid 4-8 × 6-5 is clearly significant. The inbred 228-6-5 and the hybrid 6-5 × 4-8 do not differ significantly in slope, though the F value approaches the 5-percent point. The ratio of the percentage growth for this hybrid and its maternal inbred for the initial 45-day period is 1.8 to 1.0, or an indicated difference in growth rate of 80 percent.

TABLE 6.—Comparisons of the regression constants of two inbred lines of corn and their reciprocal hybrids grown in 1935

Comparison	Value of F_1 for indicated constant		
	a'	b'	c'
4-8 selfed and 6-5 selfed.....	41.272	5.491	0.183
4-8 selfed and (4-8 × 6-5).....	387.172	15.953	21.018
6-5 selfed and (6-5 × 4-8).....	279.818	4.249	6.375
(4-8 × 6-5) and (6-5 × 4-8).....	19.324	3.901	1.505
(6-5 × 4-8) from prematurely and (6-5 × 4-8) normally harvested seed.....	16.211	.02 ²	.144

¹ 4.96 lowest value F may take for significance when $P=0.05$. 10.04 lowest value F may take for significance when $P=0.01$.

DISCUSSION

In a recent study Engledow and Pal (4) concluded that Ashby's explanation of hybrid vigor in maize was inapplicable to wheat. The following discussion is concerned with the agreement and discrepancies of the data presented here and the expectations based on Ashby's conclusions. The discussion will be facilitated by considering each of his postulates separately. His first postulate is that the F_1 hybrid of a cross between two inbreds exhibits the growth rate of the faster growing parent. In a consideration of this postulate it is desirable to make some subdivision of the growth period. The following subdivision is in harmony with the sampling periods and appears useful: (1) From fertilization to maturation of the seed, (2) from germination through the early seedling stage, and (3) from the late seedling stage to mature plant. The first two stages are essentially similar and are subdivided only because they are separated in time by the dormancy of the mature embryo. It should be emphasized that Ashby's studies were concerned almost entirely with the third stage of growth.

Inbred and hybrid embryos can be produced on the same ear and must therefore have their origin in egg cells of the same average weight. As any conceivable difference in weight of sperms from the two types of pollen could not cause more than a trivial difference in weight of the zygote, the inbred and hybrid zygotes are necessarily of similar weight. Since hybrid embryos in general are heavier than selfed embryos,³ it is clear that the logarithmic growth lines must differ in their slope in the first period. A large amount of data relating to the mature weights of selfed and hybrid seeds has been presented by Kiesselbach (8).

Information regarding the second phase of growth is very meager. However, on the basis of the data illustrated in figure 2, it appears that during germination and for at least the first 15 days of seedling growth the rates for inbred and hybrid are decidedly different.

The extensive data dealing with the third stage of growth cannot be used as a critical test of this postulate. Under conditions in which sampling errors obscure differences in growth rates of the magnitude of 50 percent any conclusions as to the equivalence of growth rate in inbred and hybrid are unwarranted.

Lindstrom (10) has presented data which he interprets as a disproof of Ashby's hypothesis. He removed a portion of the leaf area of the hybrids at different stages and compared their final growth with that of the inbred parents. The F_1 hybrids exceeded the inbred parents in final plant weight, and he concludes that "This can only mean that the cut-back F_1 hybrids grew at a faster rate than their untouched parents." The writer is in agreement with the idea that F_1 hybrids grow at a faster rate than their parental inbreds. There is some doubt, however, that this has been conclusively proved by the above experiments. The clipping of leaves does not remove "capital" in the sense in which Ashby and physiologists in general have used the word. The tissues removed are no longer meristematic but are fully differentiated and have attained approximately their ultimate size. If one considers the clipping to have affected only the "net rate of interest" or the "efficiency index" then the results are not necessarily at variance with Ashby's conclusions. The reduction in leaf area and conse-

³ This statement applies only to inbred or closely line-bred material.

quently the reduction in efficiency index would be expected to be temporary. Even under conditions in which the hybrid and inbred grow at exactly the same rate, the hybrid starting with the larger capital could suffer a temporary reduction in efficiency index and still produce a greater final weight than the inbred parents. But, assuming that the tissues removed by clipping of leaves do represent capital, data showing that the dry matter of the decapitated hybrid was reduced to equivalence with the parental inbred would be essential before one could consider a difference in growth rate as having been proved.

Although the present data are in many respects inadequate, they do indicate that for the first two phases of growth the rate for the hybrid is in excess of that for either parent. It has not been possible to demonstrate a statistically significant difference in growth rate of hybrid and inbred during the third period, but it has been demonstrated that only very large differences would appear significant because of the large sampling errors involved. The data suggest that the difference in growth rates between inbred and hybrid may not be as great during this stage as in the two earlier stages. A possible explanation for this may be in the type of growth involved. Within 25 to 35 days after planting, the morphological foundation of the corn plant is largely completed; the growing point becomes differentiated into a tassel, and growth by cell division becomes of minor importance. Growth by cell differentiation and enlargement has been increasing in importance during the period and from this point on becomes the dominating element.

The presence of two distinct phases of growth in the life of an organism appears to be a common phenomenon in biology. Huxley (7, p. 118) in this connection states:

In the first, the general form of the part is being laid down, and this process is accompanied by very rapid alterations of form, and by marked histological changes; in the second, histological changes are absent or of an entirely secondary nature, and the form changes are confined to quantitative alterations in the proportion of the definitive structural plan. * * * Thus not only definitive form-plans, but also marked differences in size, are established in the short first phase, and effects of growth during the second phase are confined to a quantitative modification of the already diversified organization given at the close of the first phase.

Similar growth rates during a particular stage of development have been reported for markedly differing size structures in a wide variety of organisms. The works of Houghtaling (6) on tomatoes, of Sinnott and Kaiser (14) on *Cucurbita*, and of Dobzhansky and Duncan (3) on *Drosophila* larvae are only a few of the many cases that might be cited.

Ashby's second postulate, namely, that rate of growth is inherited as a simple dominant or dominant complex contributed by one of the parents, does not appear to be true for either the first or second growth period. Because of the large sampling errors, the data presented here on the third growth period cannot be considered as critical. However, every person who has had experience with corn breeding can cite numerous instances of the expression in the hybrid of characters from the two parents that certainly are related to growth rate, as, for example, leafiness and the possession of a good root system.

Ashby's third postulate, namely, that reciprocal hybrids differing in embryo weight should differ in degree of vigor, is only partially

substantiated. The initial difference between such hybrids persists for a time but disappears before the completion of growth. The results for both seasons are in agreement on this point. It seemed desirable to compare the growth rate of hybrids in which greater differences in embryo weights were involved. These differences were obtained by comparing normal and prematurely harvested seed. The data from this source are presented in tables 5 and 6. Here again initial differences in embryo size failed to persist. It has not been possible to show a difference in growth rate in such cases, but it seems probable that the explanation for the failure of such differences to persist lies in the slightly longer growth period of the hybrid having the smaller embryo. In every case such a hybrid comes into sexual maturity slightly later than its reciprocal having the larger embryo. These results are in essential agreement with those presented by Passmore (11) on reciprocal *Cucurbita* hybrids.

In the present experiments, variations in embryo size within a genotype have not been of importance. This is in agreement with the work of Kotowski (9), on peas, beans, and cabbage; Passmore (11), on *Cucurbita*; and Robinson (13) and others, on corn.

Ashby's fourth postulate, namely, that hybrid vigor is nothing more than the maintenance of an initial difference in embryo size, is not supported by these results. In both 1933 and 1935 the hybrid 6-5 \times 4-8 actually had a smaller embryo than the inbred 228-6-5. As this hybrid and its maternal inbred have been shown to have the same efficiency index within the limits of sampling error, this postulate would require that the hybrid be inferior to or at least no better than the inbred. Actually the hybrid weighed more than twice as much as the inbred parent at maturity. The increased size of the hybrid is in part accounted for by a more rapid growth rate during the second growth phase.

Ashby was of the opinion that his results required some modification of the dominant-favorable-growth-factor hypothesis. This does not appear to be essential. His results could be interpreted quite simply on the assumption that the vigor of the hybrid is due to the inheritance of a large embryo size from one parent and a rapid growth rate from the other. Each of these components is the resultant of the action of a large number of factors. The dominant-favorable-growth-factor hypothesis does not require that the hybrid exceed the parents in every respect, but rather that the combined effect of all factors shall produce a greater end product. The most favorable factors contributed by each parent find expression in the hybrid. This interpretation is in accord with the fact that favorable genic modifications tend to be dominant.

The results of these experiments are of some interest in connection with the two theories on the nature of hybrid vigor. The differing growth rates during the various growth stages find a ready explanation on the basis of the dominant-favorable-gene hypothesis, in the assumption that genes have a specific time of action. The more rapid growth rate of the hybrids during the first two stages of growth would thus be attributed to the complementary action of genes which produce their characteristic effect early in the development of the organism.

The results are more difficult to explain on the theory that hybrid vigor is due to a physiologic stimulation resulting from unlike germ

plasm. If the data presented can be considered as typical, then one must assume that stimulation increases from the first to the second growth period and decreases with the third.

The mechanism by which hybrid vigor is expressed is still unknown, but, as the difference in growth rate between hybrid and inbred is greatest during the period when size increase is primarily by cell division, it is suggested that rate of cell division must be one important factor. Further studies on this problem are under way.

SUMMARY

Data are presented on the growth rates of two inbred strains of corn and their reciprocal hybrids.

The growth period from fertilization to maturity of the corn plant is divided into three phases: (1) From fertilization to maturity of seed, (2) from germination through the early seedling stage, and (3) from the late seedling stage to maturity.

By means of this classification it is shown that the hybrids grew faster than either parent during the first two phases of growth, but differences in the rate of growth during the third period have not been established statistically because of large sampling errors. The differences in the amount of growth are quite significant.

In the first two phases, the inheritance of growth rate cannot be ascribed to a complex from one parent only. The rate must represent the action, complementary or additive, of factors from both parents. The data presented are not critical for the third period.

The reciprocal hybrids were alike in growth rates and in total amounts of growth. Within a genotype, embryo weights were found to be of little importance in determining final weight, as initial differences in embryo weight failed to persist.

Hybrid vigor cannot be attributed to the maintenance of an initial difference in embryo size.

The differing growth rates for the three phases of growth are readily explained on the basis of the complementary action of dominant genes.

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